

Chitons (Mollusca, Polyplacophora) from Alacranes Reef, Yucatan, Mexico

Adriana Reyes-Gómez¹, Deneb Ortigosa^{2,3}, Nuno Simões³

1 Departamento de Ecología, Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Carretera a Nogales km. 15.5, Las Agujas Nextipac C.P. 45110, Zapopan, Jalisco, México **2** UMDI-Sisal, Facultad de Ciencias, Universidad Nacional Autónoma de México. Apartado postal 70-153, C.P. 04510, Ciudad de México, México **3** Departamento de Biología, Facultad de Ciencias del Mar y Ambientales, Universidad de Cádiz, Polígono del Río San Pedro s/n, Apartado 40, C.P. 11510, Puerto Real, Cádiz, Spain

Corresponding author: Adriana Reyes-Gómez (quintonreyes@yahoo.com)

Academic editor: E. Neubert | Received 12 September 2016 | Accepted 7 March 2017 | Published 3 April 2017

<http://zoobank.org/9117BAF1-7E9B-4E25-99EC-7C8C6A8F456E>

Citation: Reyes-Gómez A, Ortigosa D, Simões N (2017) Chitons (Mollusca, Polyplacophora) from Alacranes Reef, Yucatan, Mexico. ZooKeys 665: 1–36. <https://doi.org/10.3897/zookeys.665.10476>

Abstract

This study represents the first comprehensive chiton study from Alacranes Reef, the largest reef system in the Gulf of Mexico. Nine chiton species were found in seven localities within the area, in the intertidal and subtidal to 12 m depth. SEM examination of *C. janeirensis*, *A. hemphilli*, *T. schrammi* and *C. floridanus*, showed variations in the sculpture and radular teeth morphology when compared to specimens of the same species from Florida Keys, Bahamas and Puerto Rico. The distribution ranges of *T. schrammi*, *L. liozonis* and *S. floridana* are extended into the south-western area of the Gulf of Mexico. Altogether, combining previous literature and the present survey, reports eleven chiton species which have now been recorded within the Alacranes reef area.

Keywords

Biodiversity, marine reserves, coral reef, mollusks, Campeche Bank, Gulf of Mexico

Introduction

The Gulf of Mexico has diverse coastal geomorphology, climate and hydrology processes (Wiley et al. 1982). The Alacranes (or Scorpion) Reef National Park (the acronym, PNAA, refers to the Spanish name: Parque Nacional Arrecife Alacranes) is the largest coral reef in the Gulf of Mexico, with a unique atoll shape and is recognized as a Marine Protected Area. It is located 135 km north of Puerto Progreso, Yucatan, and it is considered the best-known Mexican reef, for its accumulated geological and paleontological data sets (e.g. Fosberg 1961, Chavez et al. 1985). Malacological studies at the PNAA have been mainly focused on bivalve and gastropod species (Rice and Kornicker 1962, 1965, Ekdale 1974, Boudreaux 1987, González et al. 1991, Hicks et al. 2001, Sanvicente-Añorve et al. 2012a, 2012b, Ortigosa et al. 2015). Chitons have been included only in species listings, based on their observed occurrences in areas near to the PNAA, especially in Mexican states of Yucatan and Quintana Roo (Ekdale 1974, Vokes and Vokes 1983, Watters 1981, 1990, Bullock 1985, 1988, Lyons 1985, 1988, Hicks et al. 2001, Reyes-Gómez and Salcedo-Vargas 2002, Lyons and Moretzsohn 2009). For the Mexican Caribbean, 19 species are known whereas only six have been recorded from particular localities within the PNAA. Here, as in much of the world, chiton species tallies have been based so far on only morphological comparisons, mostly from details of the shell plates (valves) as supplemented by girdle and radular tooth features (Irisarri et al. 2014). In this study, we described and figured these morphological characters and update the chiton checklist for the Alacranes Reef.

Materials and methods

Samples were obtained at PNAA reef (Figure 1) as part of a multidisciplinary biodiversity project during two surveys in May-June 2008 and July-August 2009 (Table 1). The chiton species were collected in the intertidal zone of Perez Island and in several different reef environments, by snorkeling and SCUBA, from the intertidal up to 12 m depth. Collecting protocol followed direct searching on reef structures and boundaries, as well as other hard substrates including wood, dead coral, and algae. All specimens collected were anesthetized in 8% clove oil or magnesium chloride, followed by preservation in 70–100% ethanol. The plates, girdle elements and radula were examined using a scanning electron microscope (SEM) following García-Ríos (2015) methodology for cleaning and coating the structures. The images were taken with a Hitachi SU1510.10.0kV SEM at the Instituto de Biología (IB), or with a JEOL JSM6360LV SEM at the Instituto de Ciencias del Mar y Limnología (ICMyL), both part of the Universidad Nacional Autónoma de México (UNAM). The specimens were held and vouchered in the Colección Nacional de Moluscos (CNMO) at the Instituto de Biología, UNAM. Systematic arrangement follows Sirenko (2006), and Irisarri et al. (2014) for *Acanthochitonina* Bergenhayn, 1930.

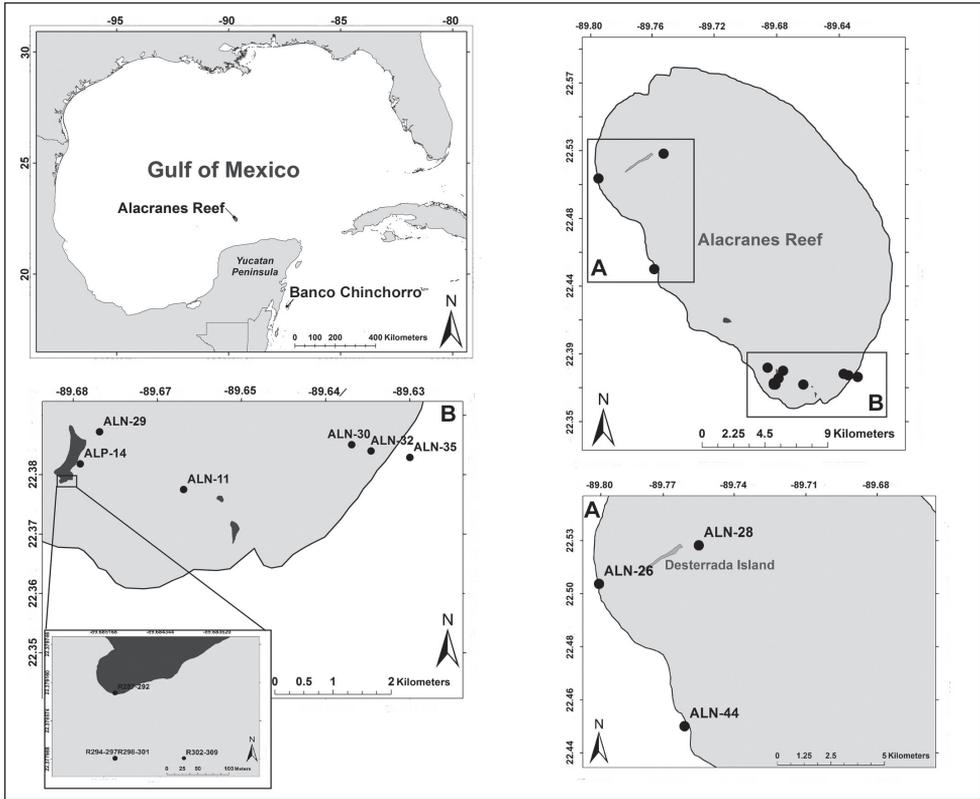


Figure 1. Location of the Arrecife Alacranes National Marine Park in the Gulf of Mexico. **A** General view of the sampling sites at the Alacranes reef **B** Southern area of the reef and Perez Island collecting sites.

Table 1. List of stations within the National Marine Park Arrecife Alacranes showing the georeferences and the depth in which the specimens were collected.

Site	Latitude	Longitude	Date	Type of sampling	Depth
R287-292	22.379	-89.685	02-Jun-2008	Intertidal (by hand)	0–1 m
R294-297	22.378	-89.685	03-Jun-2008	Intertidal (by hand)	0–1 m
R298-301	22.378	-89.685	04-Jun-2008	Intertidal (by hand)	0–1 m
R302-309	22.378	-89.684	05-Jun-2008	Intertidal (by hand)	0–1 m
ALN-11	22.378	-89.666	04-Aug-2009	Snorkel	1–2 m
ALN-14	22.389	-89.689	05-Aug-2009	Snorkel	1–2 m
ALN-26	22.512	-89.798	08-Aug-2009	Scuba	12 m
ALN-28	22.528	-89.756	08-Aug-2009	Scuba	12 m
ALN-29	22.387	-89.679	08-Aug-2009	Scuba	12 m
ALN-30	22.385	-89.640	09-Aug-2009	Scuba	12 m
ALN-31	22.384	-89.632	09-Aug-2009	Snorkel	1–2 m
ALN-32	22.384	-89.637	09-Aug-2009	Scuba	12 m
ALN-35	22.383	-89.631	10-Aug-2009	Scuba	12 m
ALN-44	22.453	-89.762	13-Aug-2009	Scuba	12 m
ALP-14	22.382	-89.682	08-Aug-2009	Intertidal (by hand)	0–1 m

Results

A total of 58 specimens belonging to five families, seven genera, and nine species were found. The most diverse family was the Acanthochitonidae Pilsbry, 1893 with four species, followed by Ischnochitonidae Dall, 1889 with two, and Chitonidae Rafinesque, 1815, Callistoplacidae Pilsbry, 1893, and Lepidochitonidae Iredale, 1914 with one species each. *Tonicia schrammi* (Shuttleworth, 1856) and *Lepidochitona liozonis* (Dall & Simpson, 1901) are new records for the Gulf of Mexico or Caribbean coasts of Mexico (see Appendix).

Ischnochiton erythronotus (C. B. Adams, 1845), *Stenoplax bahamensis* Kaas & Van Belle, 1987, *Calloplax janeirensis* (Gray, 1828) and *Cryptoconchus floridanus* (Dall, 1889) were sampled in both surveys. In addition, the results of a literature review and present findings herein reported, increases to 21 species for the overall known diversity of chitons from the eastern coasts of Mexico (see Appendix).

Systematics

Class Polyplacophora Gray, 1821

Order Chitonida Thiele, 1910

Suborder Chitonina Thiele, 1910

Family Ischnochitonidae Dall, 1889

Genus *Ischnochiton* Gray, 1847

***Ischnochiton erythronotus* (C. B. Adams, 1845)**

Figures 2A–H, 3A–G

Material examined. 20 specimens; 0.5–16 mm long, 0.3–8.5 mm wide. Laguna Arrecifal Desterrada (CNMO4980), Isla Perez (CNMO4981, CNMO4982, CNMO5002), Cabaña y Playa CONANP (CNMO4983, CNMO4984, CNMO4989, CNMO4998, CNMO5000, CNMO5003, CNMO5004), Cabezas entre Blanca y Pajaros (CNMO4985), Playa Norte (CNMO4986, CNMO4988, CNMO5001), Playa Arrecifal (CNMO4987).

Description. Small-sized chitons, broad oval shape. Color of tegmentum and girdle very variable, mostly creamy, red, purple or light green and mottled with dark brown dots or patches (Figure 2A–H). Tegmentum sculptured with irregular concentric riblets and longitudinal narrow ribs. Head valve (Figure 3A), semicircular, not notched, sculpturing of irregular concentric ribs, broken into numerous riblets, forming fine radial indicated grooves. Tail valve (Figure 3B), wider than long, mucro postmedian, somewhat elevated; antemucronal area with 9–11 narrow, sometimes branched longitudinal narrow ribs; postmucronal area with concentric riblets and nodules, forming 19–23 radial grooves. Intermediate valves (Figure 3C), semi-rectangular outlined, side margins rounded and posterior margin from slightly concave to straight;

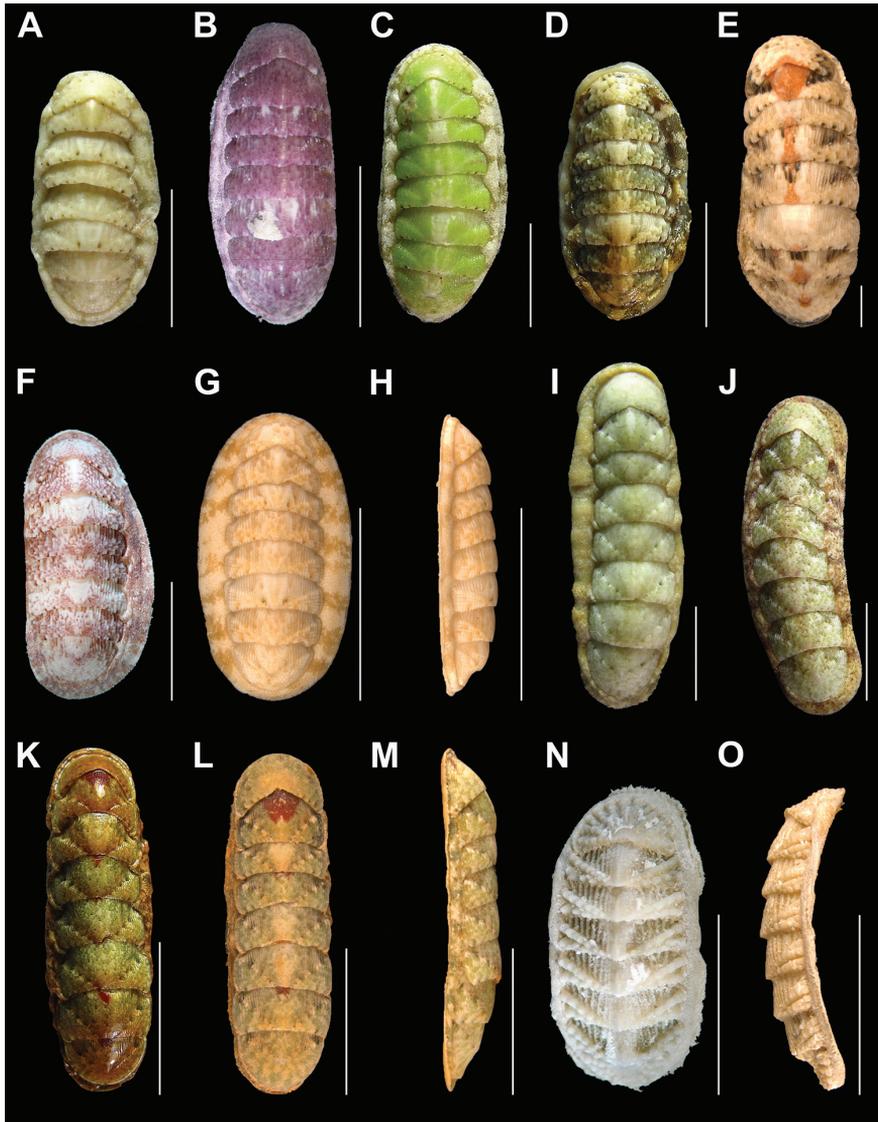


Figure 2. *Ischnochiton erythronotus* (C. B. Adams, 1845), **A–H**: in dorsal view, showing the tegmentum color variability **A** specimen from Laguna Arrecifal Desterrada (CNMO4980, 15.2 mm length) **B** specimen from Isla Perez (CNMO4981, 93.7 mm length) **C** specimen from Cabaña y Playa CONANP (CNMO4983, 11.7 mm length) and **D** (CNMO5003, 12.9 mm length) **E** specimen from Cabezas entre Blanca y Pajaros (CNMO4985, 13.6 mm length) **F** specimen from Playa Norte (CNMO4988, 14.2 mm length) **G** specimen from Playa Arrecifal (CNMO4987, 15.2 mm length length) and **H**, in lateral view. *Stenoplax bahamensis* Kaas & Van Belle, 1987 **I–M**: in dorsal view, showing the tegmentum color variability **I** specimen from Playa Norte (CNMO4942, CNMO4943, 22.1 mm length) **J** specimen from Pared Arrecifal (CNMO4957, 24.5 mm) **K** Laguna Desterrada (CNMO4974, 23.4 mm length), and **L** and **M**, in dorsal and lateral view (CNMO4974, 22.8 mm length). *Calloplax janeirensis* (Gray, 1828) **N** specimen from Isla Perez (CNMO4994, 12.5 mm length), in dorsal view and **O** (CNMO4990, 13.4 mm length), in lateral view, SB = 1 cm.

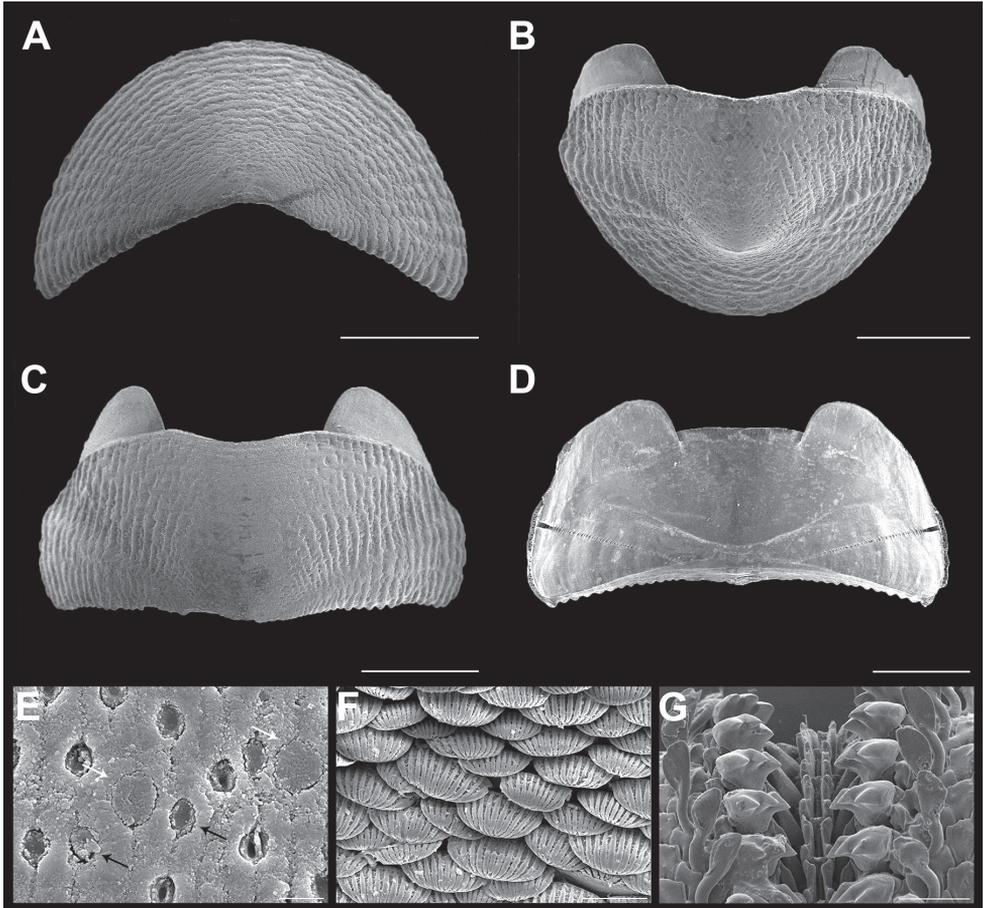


Figure 3. *Ischnochiton erythronotus* (C. B. Adams, 1845). Scanning electron images of a specimen from Laguna Arrecifal Desterrada (CNMO4980, 15.2 mm length); **A** head valve (I) in dorsal view, SB = 1 mm. **B** dorsal view of tail valve (VIII), SB = 1 mm **C** dorsal view of intermediate valve IV, SB = 1 mm **D** ventral view of intermediate valve IV, SB = 1 mm **E** detail of aesthete system, white arrows indicating the megal aesthetes, black arrows indicating the microaesthetes of intermediate valve IV, SB = 10 μ m **F** girdle scales detail, SB = 100 μ m **G** detail of radular teeth, SB = 100 μ m.

lateral areas somewhat elevated, sculptured as the head valve, with two to three radial grooves; pleural areas with 12–14 longitudinal ribs, which fade towards the jugal area. Articulamentum laterally short; apophyses narrow, subtriangular shaped, jugal sinus wide and smooth (Figure 3D), slit formula 8–10/1/7–10. Megal aesthetes surrounded by 7–8 large microaesthetes (Figure 3E). Girdle variable in color as tegmentum, with alternating irregular bands of dark and lighter color, dorsally with wide, short scales (Figure 3F), with 10–12 wide and flat ribs. Radula (Figure 3G), with major lateral teeth tricuspid, the outer cusp is shorter than the others, central tooth very narrow anteriorly wider and spatulated.

Habitat. Found in intertidal to shallow subtidal to 12 m depth. Found on dead coral, wood, rock, and sunken turtlegrass, *Thalassia testudinum* Banks ex König.

Remarks. This species displays a considerable intraspecific variation in color and valve sculpturing; also observed in chitons from Cozumel Island and in Banco Chinchorro reef (in the most southern region of Quintana Roo) (CNMO5558), which was also noted by García-Ríos (2003) for specimens from Puerto Rico and Ferreira (1978a) for Jamaica specimens. This variability was found in both, the juvenile and adult chitons morphology. In general, specimens reaching a length from 8–12.1 mm showed more regular and less broken ribs, whereas animals between 13.5–16 mm length developed branched ribs, particularly in pleural areas, and occasionally showed nodule formations on the head and the postmucronal area of the tail valve. This is the most common and abundant chiton species in the PNAA.

Genus *Stenoplax* Carpenter MS, Dall, 1879

***Stenoplax bahamensis* Kaas & Van Belle, 1987**

Figures 2I–M, 4A–H

Material examined. 15 specimens; 11–25.4 mm long, 3–8.1 mm wide. Playa Norte (CNMO4942, CNMO4956, CNMO4973, CNMO4976), Isla Perez (CNMO4943, CNMO4944, CNMO4977), Pared Arrecifal (CNMO4957), Blanca y Pajaros (CNMO4961), Laguna Desterrada (CNMO4974, CNMO4975), Laguna Arrecifal (CNMO4978).

Description. Medium-sized, elongate-oval chitons, around three times longer than wide. Color of tegmentum variable, mostly cream, dark and lighter green, light brown, with scattered dark brown spots (Figure 2I–M). Tegmentum with nodulose ribs, arranged concentric to the apex. Head valve (Figure 4A), semi-circular, slightly notched; sculpturing with nodulose ribs, break into numerous and regular nodules, particularly to the periphery. Tail valve (Figure 4B), with elevated postmedian mucro; postmucronal area sculptured as head valve, antemucronal area with 37–42 nodulose ribs. Intermediate valves (Figure 4C), with side margins somewhat rounded; lateral areas elevated, with 14–18 concentric nodulose ribs; pleural areas with 16–19 longitudinal ribs; the ribs next to lateral areas developed few small irregular to rounded lobules or pustules. Articulamentum slightly light blue; apophyses narrow and long twice as wide, wing shaped; jugal laminae smooth and wide (Figure 4D); slit formula 9–13/1/9–13. The ribs next to the postmucronal region tend to form more lobule or pustule like formations than intermediate valves (Figure 4E). Megalaesthetes small and surrounded by 4–6 smaller micraesthetes (Figure 4F). Girdle covered with tiny scales (Figure 4G), each with 11–13 wide, somewhat flat ribs on its surface. Radula (Figure 4H), with tricuspid major lateral tooth, cusps pointed and rather irregular in shape and length, the central and minor lateral teeth about the same length and as narrow and short spatulated shaped.

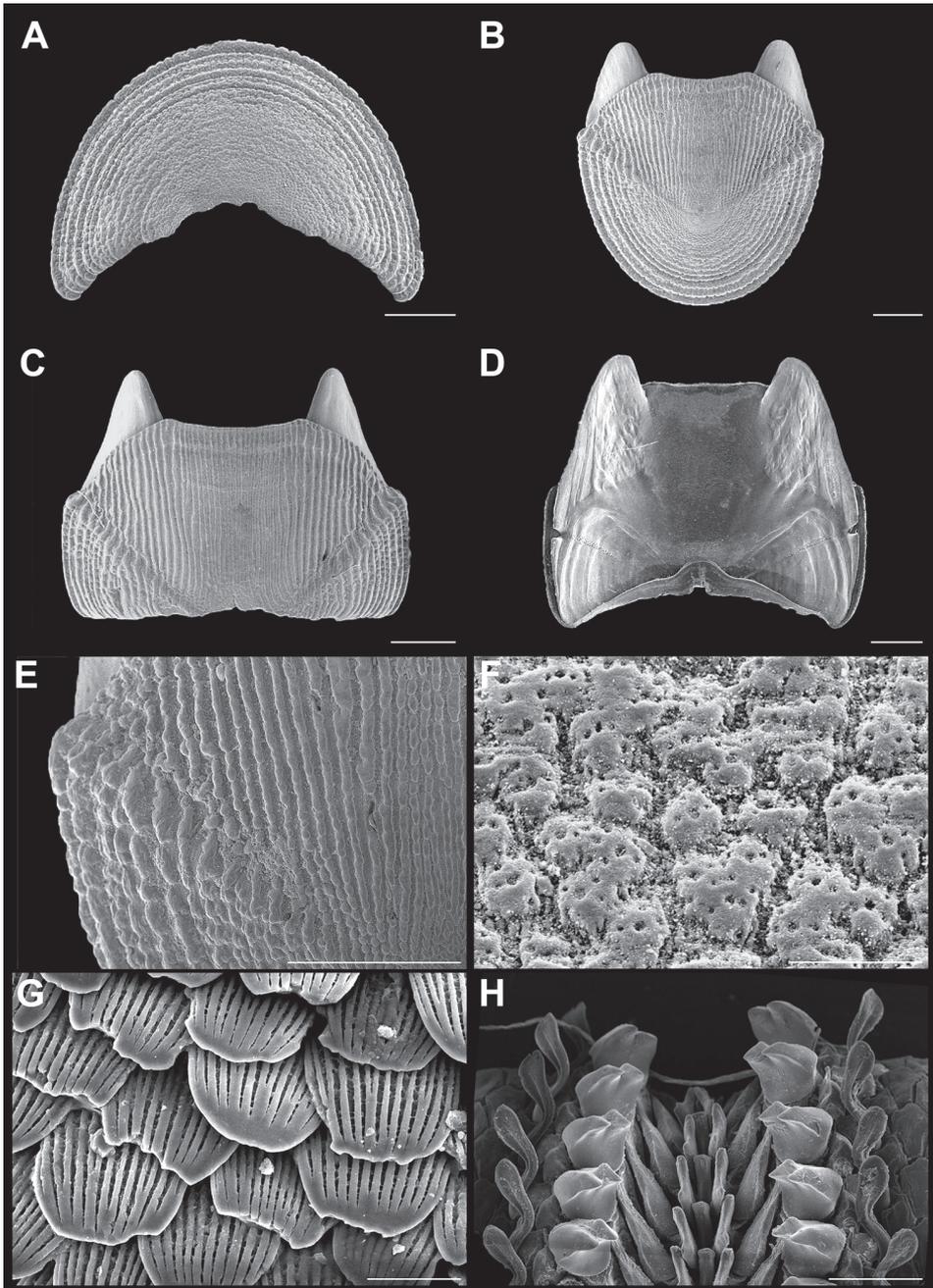


Figure 4. *Stenoplax babamensis* Kaas & Van Belle, 1987. Scanning electron images of specimen from Playa Norte (CNMO4973, 23.6 mm length). **A** head valve (I) in dorsal view, SB = 1 mm **B** dorsal view of the tail valve (VIII), SB = 1 mm **C** dorsal view of intermediate valve IV, SB = 1 mm **D** ventral view of intermediate valve IV, SB = 1 mm **E** detail of intermediate valve IV, showing the adjacent sculpturing of the lateral and central areas, SB = 1 mm **F** aesthetes detail of valve IV, SB = 100 μ m **G** girdle scales detail, SB = 50 μ m **H** detail of radular teeth, SB = 150 μ m.

Habitat. Found in intertidal to shallow subtidal to 12 m depth, on sunken wood, rock and turtlegrass, *T. testudinum*.

Remarks. According to Arce and García-Ríos (2015), the sculpturing of small adults of *S. floridana* (18.6 mm) is very similar to *S. bahamensis* adults (31.8 mm), with somewhat continuous ribs in lateral areas. And the juvenile forms of both species (9.6 and 8.6 mm respectively) are almost identical, making their identification quite difficult.

PNAA *S. bahamensis* juveniles (ranging from 11–14.2 mm length), showed continuous ribs in lateral and central areas, with few granular formations next to the diagonal ridge; and our comparison with *S. floridana* was limited to one adult specimen.

Our observations of adult specimens agree with previous authors (Bullock 1985, Kaas and Van Belle 1987), that distinguish *S. bahamensis* from *S. floridana* by the absence of inconspicuous pustule formation next to the lateral area (Figure 4E). Examination of *S. floridana* (26.7 × 9.2mm) (CNMO5557) from Banco Chinchorro, Quintana Roo (Figure 14E–G), revealed central areas with granulate ribs, and lateral areas raised higher, with strong tuberculated discontinuous ribs, also present in head valve and postmucronal area of tail valve, whereas *S. bahamensis* develops lower lateral areas with more continuous ribs.

Bullock (1985) contributed on the knowledge of Caribbean *Stenoplax* s.s. species. He presented an exhaustive review of species aesthete density, major lateral tooth outline and sculpturing morphology. Based on his observations, he grouped *S. bahamensis* and *S. floridana* in a single lineage, defined on the reduced rib width, fewer aesthetes and elongate denticle cap. In addition to the examination, he also included the basal spot of the major lateral tooth, and an outline of the denticle cap, which according to him was distinctive, and useful as taxonomic character to distinguish among other chiton species. However, the differentiation of *Stenoplax* Caribbean species we have used here relies more on adult sculpturing differences (on how broken the ribs can appear, and if there is pustule development (Figure 14G) in the diagonal ridge of intermediate valves).

Family Callistoplacidae Pilsbry, 1893

Genus *Calloplax* Thiele, 1909

Calloplax janeirensis (Gray, 1828)

Figures 2N–O, 5A–H

Material examined. Four specimens; 9–15.2 mm long, 4.9–7.1 mm wide. Isla Perez (CNMO4981, CNMO4990, CNMO4994).

Description. Medium-sized chitons with elongate body shape. Color yellow, creamy, or light brown (Figure 2N–O). Tegmentum strongly sculptured with large, raised coalesced pustules. Head valve (Figure 5A), semi-circular, with large lobulose pustules, arranged in 8–10 radiating, bifurcated rows, uplifted notch. Tail valve (Figure 5B), wider than long; mucro postmedian, not elevated and pointed; antemucronal area with 17–19 longitudinal, pustulose ribs, the pustules on the jugal area are less coalesced and

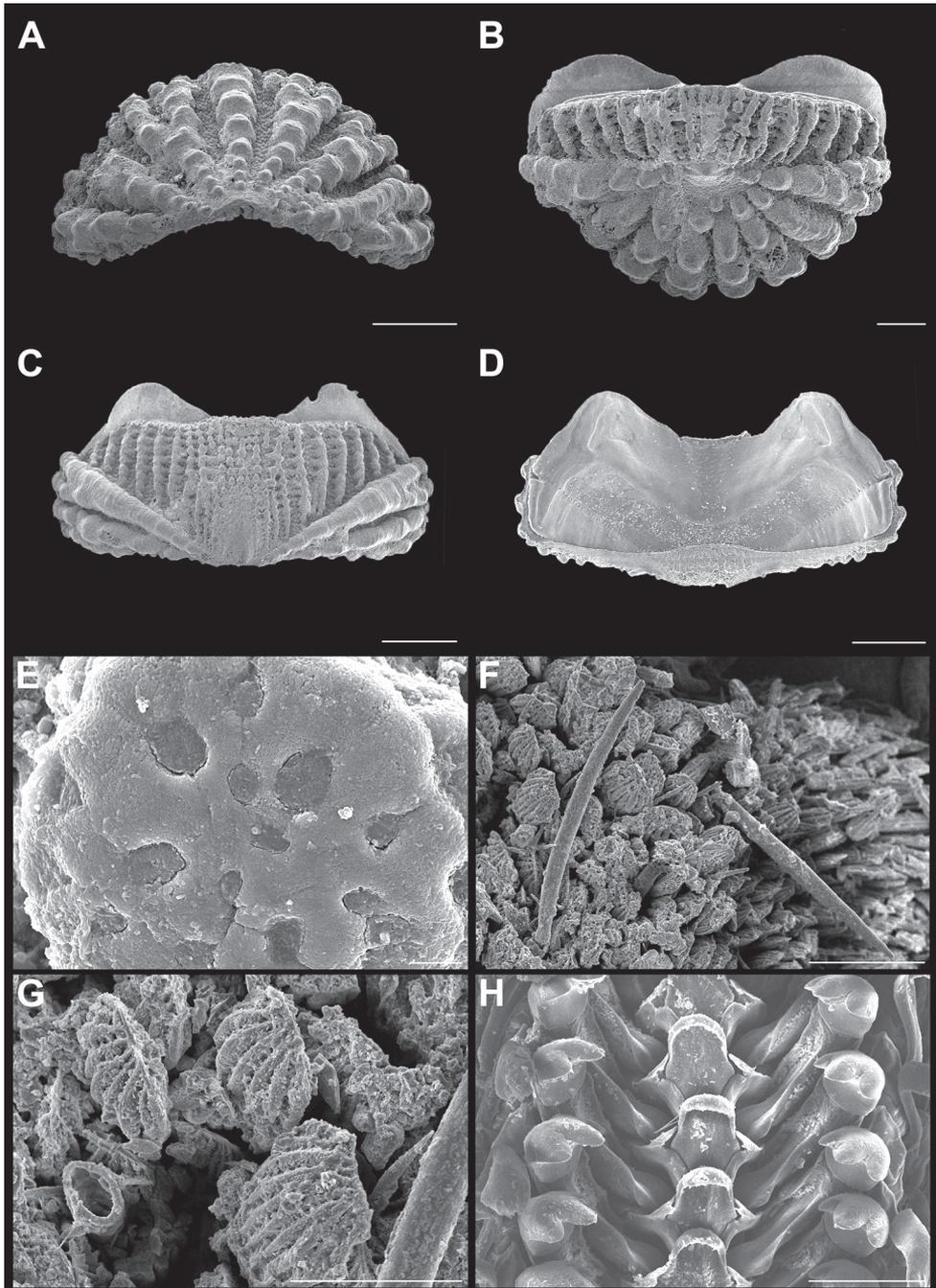


Figure 5. *Calloplax janeirensis* (Gray, 1828). Scanning electron images of a specimen from Isla Perez (CNMO4981, 13.9 mm length). **A** dorsal view of head valve (I), SB = 1 mm **B** dorsal view of tail valve (VIII), SB = 1 mm **C** dorsal view of intermediate valve IV, SB = 1 mm **D** ventral view of intermediate valve IV, SB = 1 mm **E** pustule detail with aesthetes, SB = 10 μ m **F** girdle scales and hyaline needles, SB = 100 μ m **G** detail of girdle spicules, SB = 50 μ m **H** detail of radular teeth, SB = 100 μ m.

arranged longitudinally; postmucronal area with 8–9 coarsely pustulose radial ribs. Intermediate valves (Figure 5C), semi-rectangular shaped, posterior margin almost straight; lateral areas heavily elevated with 2–3 coarsely pustulose bifurcate ribs; the rib adjacent to central area usually raised more than those near the posterior margin; central areas narrower than combined lateral areas, wider near its center; pleural areas with 7–8 longitudinal ribs, which can develop sub-riblets; 5–7 pustulose ribs in jugal areas, which fade toward the apex. White to slightly blue articulation; apophyses and insertion plates short and wide (Figure 5D); slit formula 7–9/1/8–10. Pustules bear large megalæsthetes and between them, the micraesthetes appear somewhat scattered (Figure 5E). Girdle colored in alternating irregular bands of green, cream and yellow; covered with small and medium strong ribbed scales, and hyaline long needles (Figure 5F), the scales are somewhat wider than longer, its apical end develop a flattened pit (Figure 5G), and between the scales occur single curve spicules, scattered with no apparent order. Radula (Figure 5H) with major lateral tooth tridentate, with broad and wide cusps; central tooth spatulate in shape, its distal end bending outwards and longer than minor lateral teeth.

Habitat. Found in intertidal, on rock buried in sand, associated with crustose coralline red algae.

Remarks. When Thiele (1909) described the genus *Calloplax* based on only its type species, *Chiton janeirensis* Gray 1828, he emphasized differences of its tegmental nodulose ribs contrasted with those of the distinct pustules for selected members of *Chaetopleura* Shuttleworth, 1853, where Pilsbry (1892) had previously assigned this species. Smith and Ferreira (1977), Ferreira (1978b) and Ferreira (1982) expanded Thiele's genus to include three other species, with Ferreira (1978b) transferring it from Chaetopleuridae to Callistochitonidae, and then later (1982) transferring it back. Ferreira (1978b) designated and figured a lectotype from among the syntypes of *Chiton janeirensis* from the type locality of Rio de Janeiro, Brazil. Lyons (1985) questioned the reassignment of family status for *Calloplax janeirensis*, emphasizing the morphological similarities between *Calloplax* and *Chaetopleura* genera, also noted by Ferreira (1978b; 1982). Lyons (1985) acknowledged the uncertainty regarding both genera, and based on similar girdle elements and the continuity in the range of tegmental sculpturing in species assigned to *Chaetopleura* or *Calloplax*, he suggested that *Calloplax* should be considered a synonym of *Chaetopleura* s.s. This was later followed by Bullock et al. (1994) and Lyons and Moretzsohn (2009), but Van Belle (1983), Kaas and Van Belle (1994; 1998) and Sirenko (2006) recognized it as a separate genus and have followed Ferreira (1978b) in placing it in a subfamily or family, respectively, associated with *Callistochiton*, not *Chaetopleura*, based on the presence of heavily sculptured ribs, and the insertion plate slits that generally correspond in number and position to the dorsal radial ribs, which, according to these authors is not a state of character of Chaetopleurinae. Recognizing that its status remains controversial, here we have preferred to follow Sirenko (2006) for the assignment of *Calloplax* as a distinct genus within Callistochitonidae.

PNAAs specimens (up to 15.2 mm), bear resemblance on sculpturing and number of ribs (I: 8 ribs; IV 2–3 ribs; VIII 9 ribs) to a 10.5 mm specimen of *C. janeirensis*

described by Lyons (1985: figs 22–24) from Dry Tortugas, Florida Keys, for which he figured valves I (11 ribs), IV (2 ribs) and VIII (8 ribs). PNAA specimens show ribs that tend to merge and bifurcate, and the lateral areas seem to develop three pustulose ribs, which became two, after both ribs next to diagonal ridge merged into one. On the contrary, Florida Keys specimens show more rounded pustules, the ribs remain separate or well-defined, and the lateral areas display two separated ribs. The number of ribs on the pleural areas (8 ribs), antemucronal area (18 ribs) and postmucronal areas of tail valve (8 ribs), are similar in both species. Such differences between Florida Keys and PNAA can be explained by the chiton's size. We assume that Lyons (1985) described a juvenile specimen. Examination of the lectotype (NHMUK 1977041/2) from Rio de Janeiro (16.2 mm) (Figure 14C), showed rounded pustules aligned in ribs, 12 on head valve, 3–4 on lateral areas, and 15 ribs on postmucronal area of tail valve. When comparing with the PNAA specimen (15.2 mm), the lectotype has no fusion between pustules and it has a higher number of ribs on the head valve, lateral and postmucronal areas. The pustule morphology and number of ribs, of the lectotype is similar to specimens that García-Ríos (2003: fig. 77–81) figured from Puerto Rico. Overall, the PNAA specimens showed similarities with previously figured specimens from the Bahamas, Florida and Puerto Rico in the girdle scales and spicules, and in the morphology of the major lateral radula teeth (Ferreira 1978b, Lyons 1985, Kaas and Van Belle 1994, García-Ríos 2003).

Family Chitonidae Rafinesque, 1815

Subfamily Toniciinae Pilsbry, 1893

Genus *Tonicia* Gray, 1847

Tonicia schrammi (Shuttleworth, 1856)

Figures 6A–C, 7A–K

Material examined. Two specimens; 27.5 and 28.5 mm long, 14 and 14.2 mm wide. Cabaña CONANP (CNMO4992).

Description. Medium-sized chitons with an oval outline. Live specimens mostly pink, dark purple and white (Figure 6B), turning to orange when preserved; creamy with large dark brown spots (Figure 6A, C); girdle with narrow white bands, and rounded small spots scattered without any clear pattern. Head valve (Figure 7A) semi-circular and slightly notched; sculpture pattern smooth, with faint radial irregular knobs. Tail valve (Figure 7B) oval; mucro elevated and slightly postmedian; postmucronal area bear few knobs radially oriented to the mucro; antemucronal area smooth. Intermediate valves (Figure 7C) with strongly bluntly pointed apex. Lateral areas (Figure 7D) strongly indicated by a diagonal rib of semi rectangular knobs, also present on the posterior margin, which gives the appearance of dentations, and in between them a third rib with fewer knobs that are closer to the posterior margin. Ocelli arranged in irregular radial bands. Micraesthetes small, grouped with no apparent number and ar-

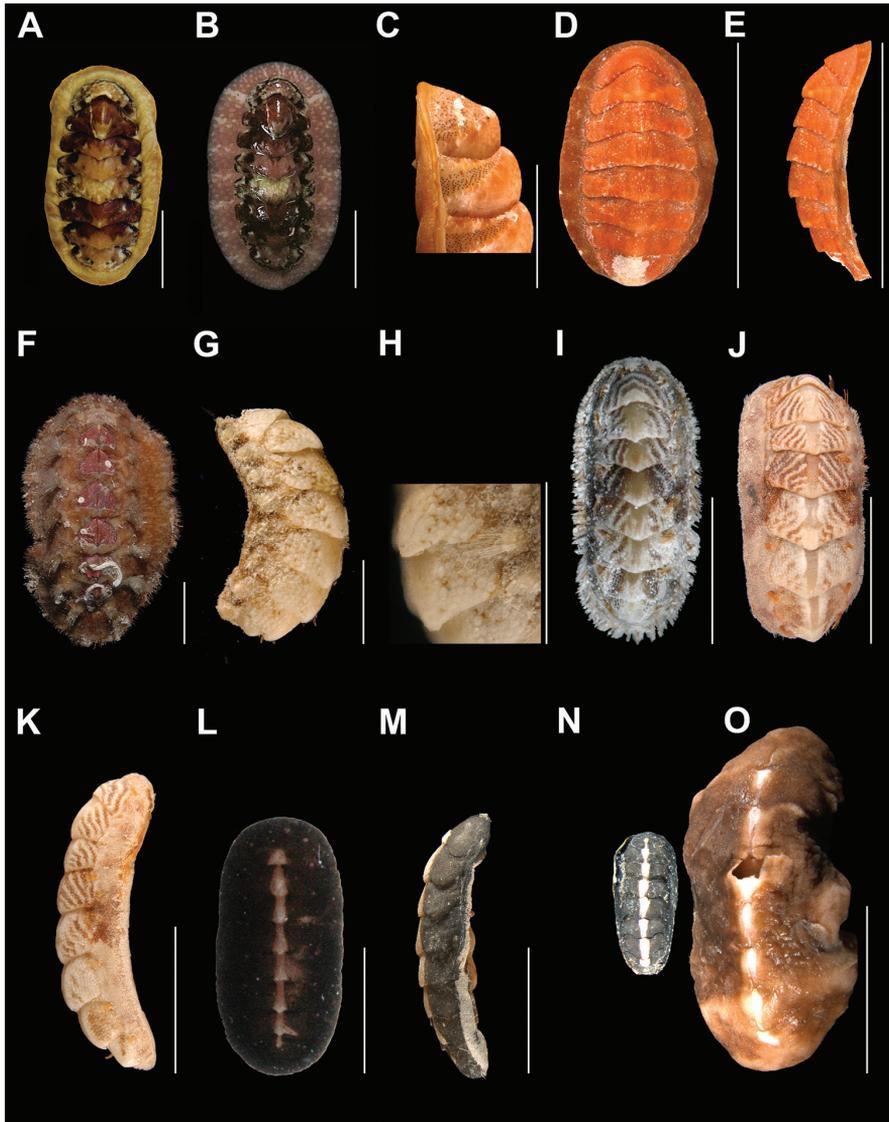


Figure 6. *Tonicia schrammi* (Shuttleworth, 1856), **A** preserved specimen, showing the color change **B** life specimen coloration from Cabaña CONANP (CNMO4992, 28.5 mm length) **C** same specimen in lateral view, SB = 1 cm. *Lepidochitona liozonis* (Dall & Simpson, 1901) **D** dorsal view and **E** lateral view of a specimen from Isla Perez (CNMO5002, 10 mm), SB = 1 cm. *Acanthochitona hemphilli* (Pilsbry, 1893) **F** dorsal view of a specimen from Laguna Arrecifal (CNMO4997, 34.8 mm length), SB = 1 cm. *Acanthochitona roseojugum* Lyons, 1988 **G** in dorsal view and **H** detail of valve IV and V in lateral view, of specimen from Isla Perez (CNMO4995, 3 mm length), SB = 1 mm. *Acanthochitona zebra* Lyons, 1988 **I** dorsal view of a life specimen **J** same specimen in preserved conditions **K** in lateral view of same specimen from Cabaña CONANP (CNMO4979, 9.2 mm length), SB = 5 mm. *Cryptoconchus floridanus* (Dall, 1889) **L** dorsal view of life specimen **M** lateral view of same specimen under preserved conditions from Isla Perez (CNMO4996, 9.3 mm length), SB = 5 mm **N** (CNMO4996) and **O** (CNMO5560, 20.3 × 8.3 mm length, Banco Chinchorro, Quintana Roo), shows the length comparison, SB = 1 cm.

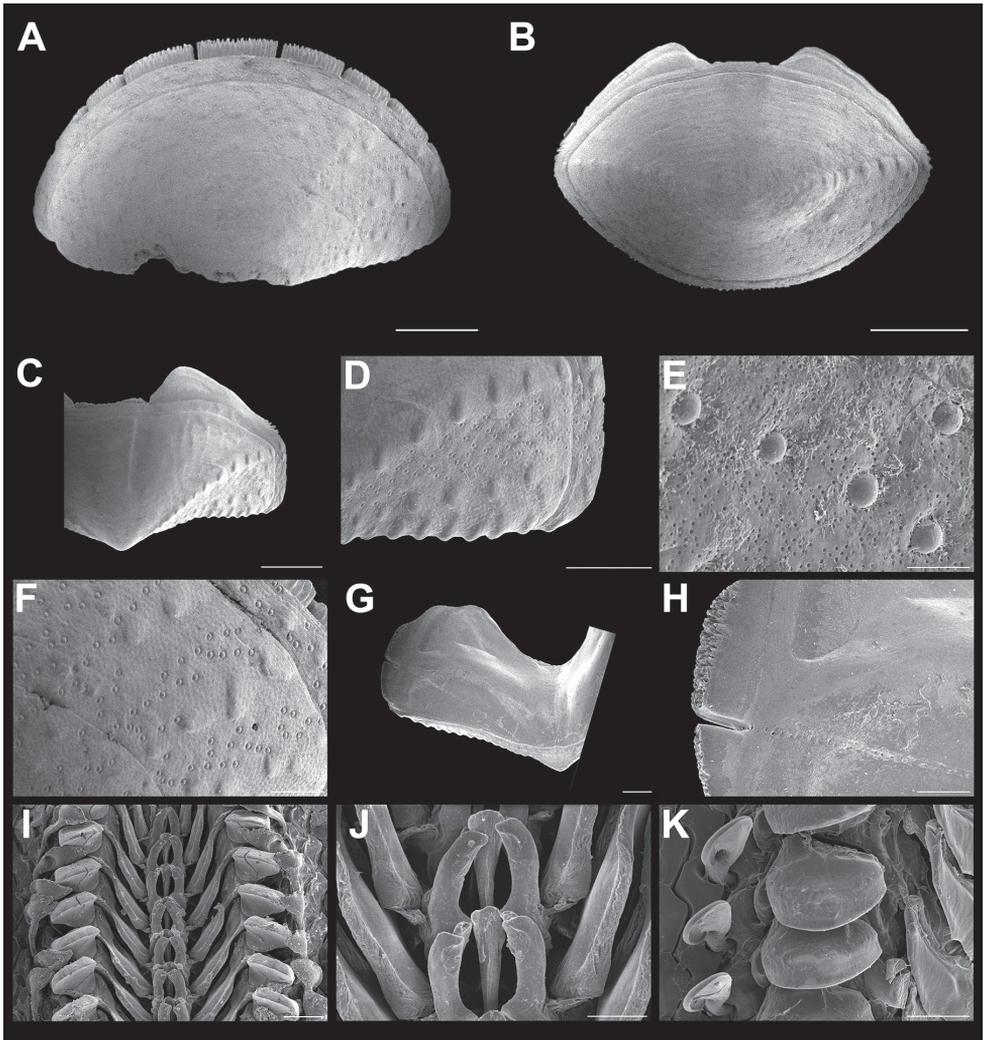


Figure 7. *Tonicia schrammi* (Shuttleworth, 1856). Scanning electron images of a specimen from Cabaña CONANP (CNMO4992, 27.5 mm length). **A** dorsal view of head valve (I), SB = 1 mm **B** dorsal view of tail valve (VIII), SB = 1 mm **C** dorsal view of intermediate valve IV, SB = 2 mm **D** detail of lateral area in dorsal view of the intermediate valve IV, SB = 1 mm **E** lateral area ocelli detail of intermediate valve IV, SB = 100 μ m **F** head valve (I) detail, showing the ocelli alignment, SB = 50 μ m. **G**, ventral view of intermediate valve IV, SB = 1 mm **H** insertion teeth and slit detail of intermediate valve IV in ventral view, SB = 50 μ m **I** radular teeth, SB = 100 μ m **J** central and minor lateral teeth detail, SB = 10 μ m **K** major lateral teeth detail, SB = 50 μ m.

rangement, others seem to be scattered (Figure 7E). Tegmentum with scattered small black rounded ocelli, forming radial irregular bands (Figure 7F). Girdle covered with tiny spicules. Apophyses short and wide, semi triangular shaped (Figure 7G). Articulation white and thick, insertion teeth hardly dentate, slit deep (Figure 7H); slit

formula 9–10/1/10–13. Radula (Figure 7I) with central teeth long and distally narrow, minor lateral tooth somewhat arched, long, smaller than central tooth, distally somewhat pointed (Figure 7J); major lateral tooth as one single, rounded, wide plate, not dentate (Figure 7K).

Habitat. Found in the intertidal on rocks and turtlegrass, *T. testudinum*.

Remarks. García-Ríos (2003: fig. 109) described Puerto Rico specimens, and figured the radula microstructure of a 21 mm specimen, which showed the medium tooth narrow and bent outward on its posterior end, and the minor lateral teeth somewhat straight. Our examination of a PNAA specimen of 28.5 mm length revealed the minor lateral tooth arched inwards, and the central tooth is rounded on its distal end (Figure 7J). Microstructure examination of PNAA specimen (28.5 mm) showed the ocelli aligned in irregular bans, somewhat in quincunx towards to the apex, and less abundant than the previous descriptions (Figure 7D, F).

The examination of one paralectotype (NMBE19115/5a) (Figure 14D), revealed a higher density of ocelli somewhat aligned in groups on the lateral areas, head valve and postmucronal area of tail valve. Kaas et al. (2006) described a specimen from Puerto Rico (La Paguera, Media Luna) with similar ocelli arrangement pattern and density. Our specimens showed less density of ocelli and although they appear to be aligned, their arrangement is more irregular (Figure 7D, F). The knowledge of this species in the Mexican Caribbean is limited, and only further studies will corroborate the morphologic distinctions of specimens from this area. In this study, we extend the distribution range of *T. schrammi* to the PNAA.

Suborder Acantochitonina Bergenhayn, 1930

Family Lepidochitonidae Iredale, 1914

Genus *Lepidochitona* Gray, 1821

Lepidochitona liozonis (Dall & Simpson, 1901)

Figures 6D–E, 8A–I

Material examined. One specimen of 10 mm long, 6 mm wide. Isla Perez (CNMO5002).

Description. Small-sized chiton, of elongate-oval shape. Tegmentum dark orange, mottled with small white spots, tail valve showing a large irregularly shaped white spot on the postmucronal area; girdle with irregular lighter and darker longitudinal bands (Figure 6D). Tegmentum micro-granular, smooth, usually with growth lines. Head valve (Figure 8A) semicircular; posterior margin “V” shaped and notched. Tail valve (Figure 8B), wider than long, semicircular, the antemucronal and postmucronal area are indicated by a weak diagonal ridge; mucro somewhat elevated, antemedian; postmucronal slope slightly concave. Intermediate valves (Figure 8C) broadly rectangular, side margins somewhat rounded, posterior margin convex, with a prominent beak; lateral areas not rosy, with a faint diagonal ridge line. Articulamentum thin and translucent; apophyses well separated, long and narrow; slit formula 10/1/12. Megalaesthetes large

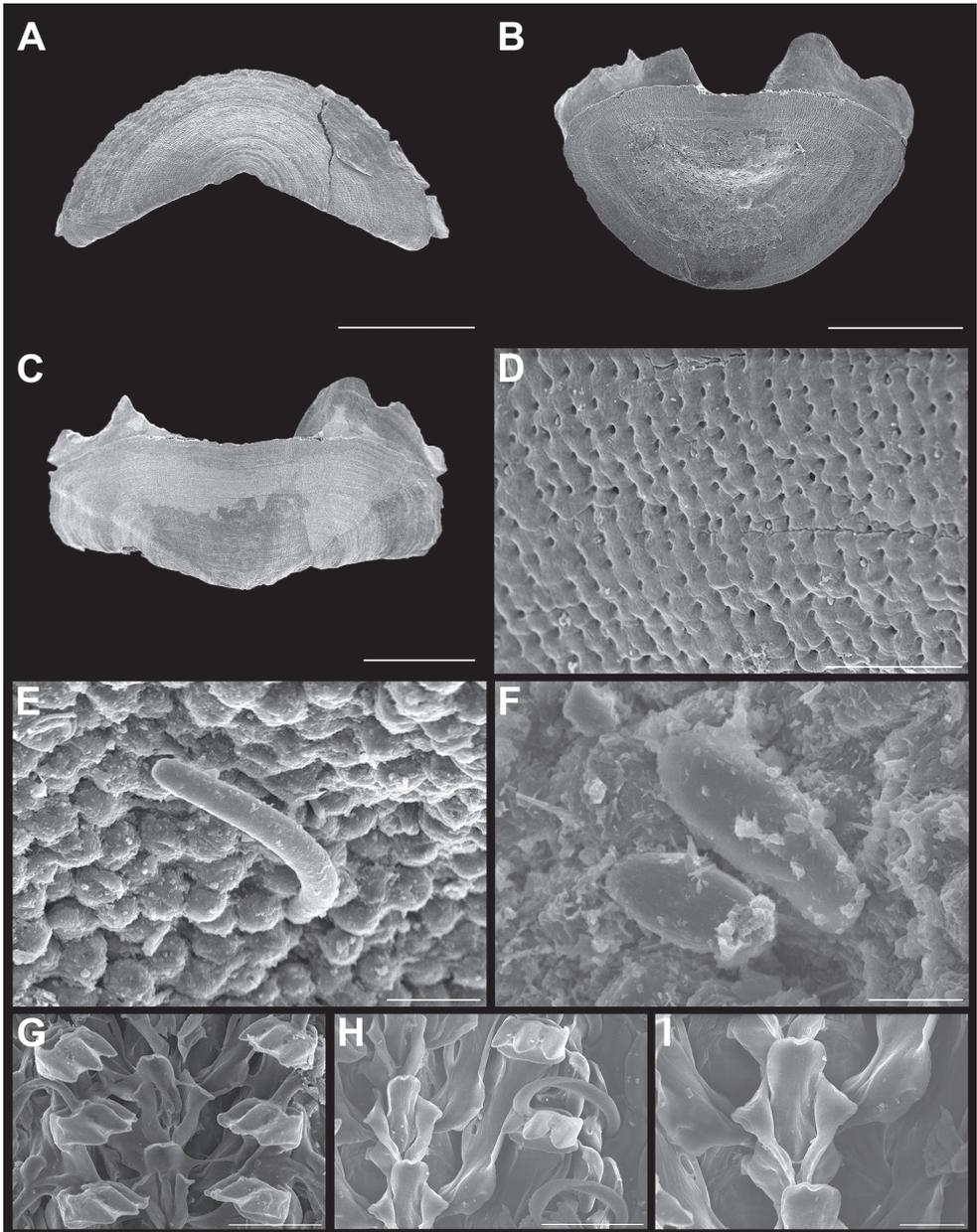


Figure 8. *Lepidochitona liozonis* (Dall & Simpson, 1901). Scanning electron images of a specimen from Isla Perez (CNMO5002, 10 mm length). **A** dorsal view of head valve (I), SB = 1 mm **B** dorsal view of tail valve (VIII), SB = 1 mm **C** dorsal view of intermediate valve IV, SB = 1 mm **D** detail of aesthetes of valve IV, SB = 100 μ m **E** girdle hyaline spicules, SB = 20 μ m **F** detail of girdle spicules, SB = 10 μ m **G** radular teeth, SB = 50 μ m **H** major lateral teeth detail, SB = 50 μ m **I** detail of central and minor lateral teeth, SB = 20 μ m.

(Figure 8D), arranged longitudinally, forming a depression on the tegmentum. Girdle covered with small, short, distally rounded spicules (Figure 8E, F), scattered with hyaline curved spicules (Figure 8E), arranged in groups of 2–3. Radula (Figure 8G) with a long, spatulate central tooth, distally wider, with its anterior end curved outwards; major lateral tooth tricuspid, the cusps around the same size (Figure 8H), the minor lateral tooth sub triangularly shaped, almost half the size of the central tooth (Figure 8I).

Habitat. Found in the intertidal on rocks, associated with crustose coralline red and brown algae.

Remarks. This species was considered by Ferreira (1985) as a synonym of *Lepidochitona beanii* (Carpenter, 1857). According to him, there were no particular differences between similar appearing specimens from the Caribbean or Eastern Pacific. However, in our opinion, there are major differences between them. As earlier noted by Kaas and Van Belle (1985), *L. liozonis* has an antemedian mucro, the apophyses are sinuated and somewhat elongated, and the girdle shows irregular slender spicules. In contrast, *L. beanii* bears a postmedian mucro, has shorter and semi-rectangular shaped apophyses, and hyaline long spicules interspersed and bunched at the sutures in groups of 3–4.

Recently, García-Ríos (2015) compared the morphologic features and DNA sequences (mitochondrial cytochrome oxidase subunit I or COI) of *L. liozonis* from its type locality (Puerto Rico, Culebra Island, Ensenada Honda) to specimens from Florida Keys, which were considered as variety “*tropica*” (Pilsbry 1940). His results showed that these have to be considered as two different species. *Lepidochitona pseudoliozonis* García-Ríos, 2015 from Florida Keys is characterized by its larger body size (average of 9.7 mm), the deep concave postmucronal slope, and the longer marginal spicules. The Puerto Rico specimens (representing *L. liozonis*) can be distinguished by their smaller body length (average of 7 mm), the postmucronal slope being almost straight to somewhat concave, and with shorter marginal spicules. The examination of the *L. liozonis* type specimen (USNM161920) (Figure 14B) revealed that the postmucronal slope of the tail valve is somewhat concave (Figure 6E), and the intermediate valves are carinated with a pointed apex. The PNAA specimens resemble the holotype and the specimens from Puerto Rico, both with a slightly concave postmucronal slope, which seems to be a morphologic feature that discriminates both species.

Family Acanthochitonidae Pilsbry, 1893

Genus *Acanthochitona* Gray, 1821

Acanthochitona hemphilli (Pilsbry, 1893)

Figures 6F, 9A–K

Material examined. Seven specimens; 7–38 mm long, 3.2–21 mm wide. Agregacion Meros (CNMO4939, CNMO4999), Cabezas entre Blanca y Pajaros (CNMO4940), Yate Acatl (CNMO4946), Precio Caribbean (CNMO4941), Laguna Arrecifal (CNMO4997).

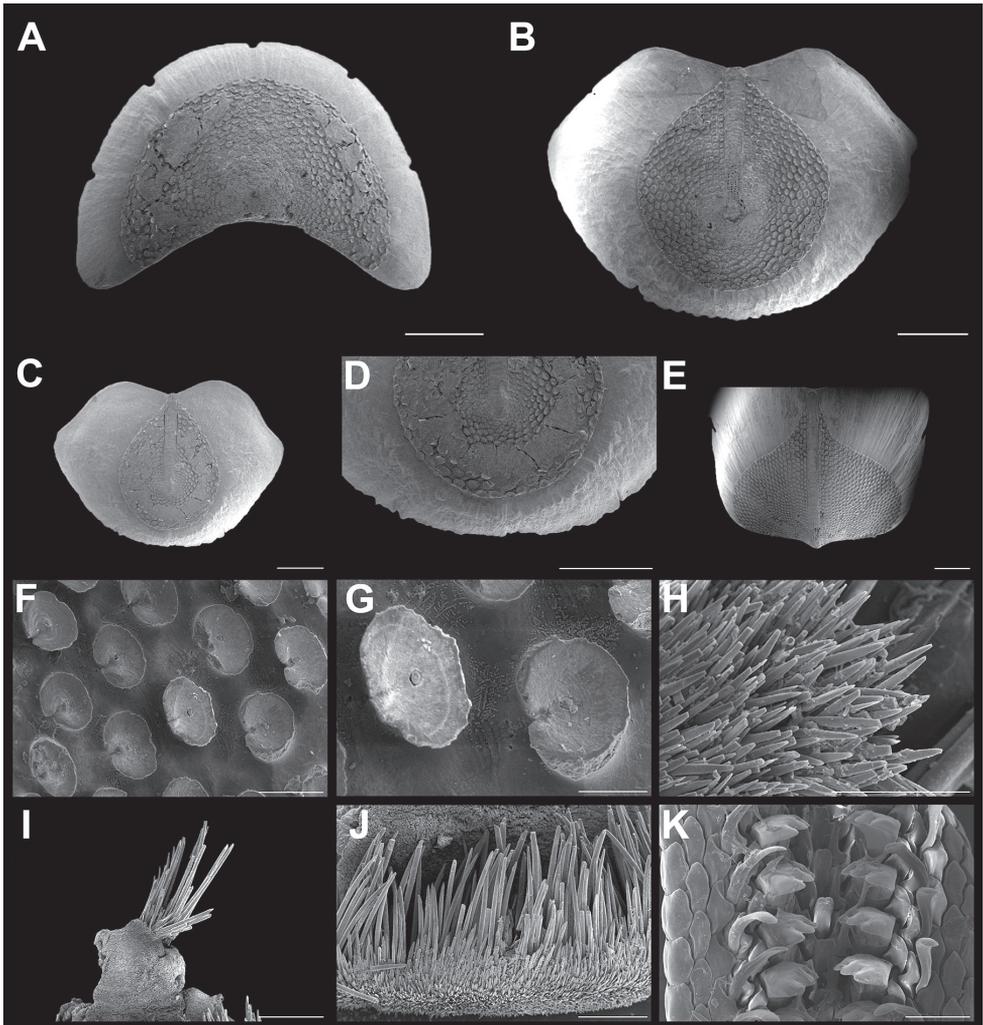


Figure 9. *Acanthochiton hemphilli* (Pilsbry, 1893). Scanning electron images of a specimen from Agregacion Meros (CNMO4939, 36.5 mm length). **A** dorsal view of head valve (I), SB = 1 mm **B** dorsal view of tail valve (VIII), SB = 1 mm **C** dorsal view of tail valve (VIII), of specimen from Laguna Arrecifal (CNMO4997, 38 mm length), SB = 1 mm **D** detail of articulation of tail valve (CNMO4997), SB = 1 mm **E** dorsal view of intermediate valve IV (CNMO4939), SB = 1 mm **F** pustules detail of tail valve (VIII), SB = 100 μ m **G** detail of pustules of intermediate valve IV, SB = 50 μ m **H** detail of girdle spicules, SB = 100 μ m **I** detail of girdle tuft, SB = 1 mm **J** detail of ventral spicules of girdle, SB = 0.50 mm **K** radular teeth, showing central and major lateral teeth, SB = 200 μ m.

Description. Large chitons, body of oval shape. Tegmentum mostly red and orange (Figure 6F). Head valve (Figure 9A) semi-rounded, posterior margin “V” shaped, with concave apex, not notched; the pustule formations fade towards apex. Tail valve

tegumentum drop shaped (Figure 9B); the pustules arranged concentrically; the postmedian somewhat elevated mucro not pointed (Figure 9B, C). Articulamentum solid, wide, well extending in all valves; wing-like shaped in the intermediate valves and the tail valve, with the slits short like a little opening and located posterior in the tail valve (Figure 9D); slit formula $5/1/2-1$. Intermediate valves (Figure 9E) with rounded sides; jugal area narrow, with a pointed apex. Sculpture of semi-reniform pustules, more oval than elongated, with one single aesthete located in the center of the pustule (Figure 9F, G). Girdle wide and covered with small, hyaline smooth spicules (Figure 9H). Ventral spicules long and somewhat curved (Figure 9J). Dorsal tufts with long hyaline spicules (Figure 9I). Radula (Figure 9K) with a tridentate mayor lateral tooth, cusps rounded, the central cusp a little longer than the outer ones; the central tooth of rectangular shape, spatulate, longer than the minor lateral tooth.

Habitat. Found from the intertidal to the shallow subtidal down to 12 m on rocks associated with crustose coralline red algae.

Remarks. The PNAA specimens have more rounded or kidney-shaped pustules that are distributed across all valves (Figure 9F). The slits are shallow or not deep in the intermediate valves. In the tail valve, one of them is regularly absent (Figure 9D). The lack of the second slit on the tail valve was observed in three specimens, although there was no indication of any damage to the girdle or the valves, which sometimes may cause deformities in the articulamentum development. The central tooth of the PNAA species is a long sub rectangular plate, which in contrast to specimens from Puerto Rico (García-Ríos 2003: figure 133), show a conspicuously elongate-rounded tooth.

Acanthochitona roseojugum Lyons, 1988

Figures 6G–H, 10A–G

Material examined. One juvenile specimen; 3 mm long, 1 mm wide. Isla Perez (CNMO4995).

Description. Small-sized chiton, of a broad oval shape; tegumentum creamy color, with dark and lighter brown small spots; girdle irregularly banded in olive green and white (Figure 6G, H). Valves arched, somewhat elevated, especially the tail valve. Head valve (Figure 10A) wider than long, posterior margin almost straight; pustules directed radially towards the apex, apex smooth. Tail valve wider than long; mucro elevated and shifted somewhat postmedian (Figure 10B). Intermediate valves (Figure 10C) with a wide, smooth jugum, anteriorly somewhat straight; apex strongly pointed; pustules directed radially towards the apex. Articulamentum wide, especially on the tail valve, apophyses wing-shaped; slit formula $5/1/2$. Tegumentum with sub-spatulate elongate pustules, with rounded edges, one single megal aesthete and two microaesthetes located at the pustule base (Figure 10D). Girdle covered with short and longer spicules (Figure 10E) and tufts with hyaline long needles (Figure 10F). The spicules are wider

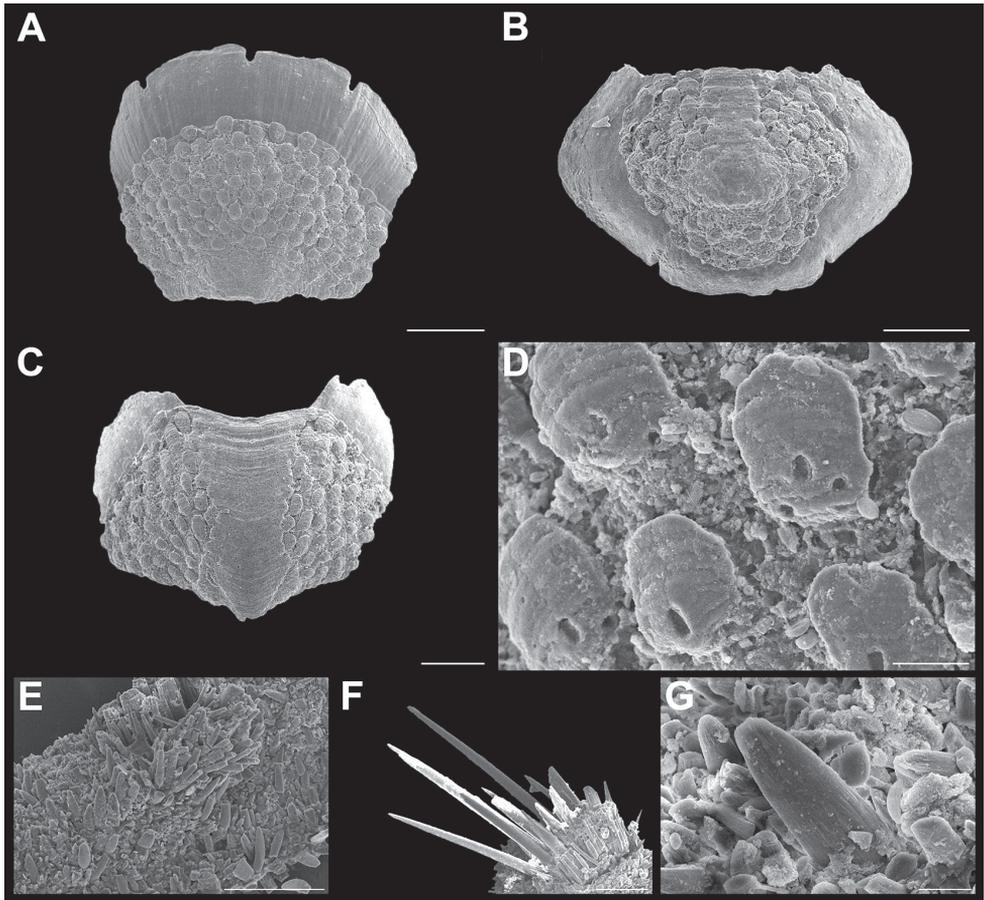


Figure 10. *Acanthochitona roseojugum* Lyons, 1988. Scanning electron images of a specimen from Isla Perez (CNMO4995, 3 mm length). **A** Dorsal view of head valve (I), SB = 200 μ m **B** dorsal view of tail valve (VIII), SB = 200 μ m **C** dorsal view of intermediate valve IV, SB = 200 μ m **D** detail of pustules of intermediate valve IV, SB = 20 μ m **E** girdle spicules, SB = 100 μ m **F** girdle tuft detail, SB = 100 μ m **G** detail of girdle spicules, SB = 10 μ m.

on the base and narrowing anteriorly; its apical area with a fine thin longitudinal striate (Figure 10G).

Habitat. Found in the shallow subtidal at 12 m on rocks, associated with crustose algae.

Remarks. The PNAAspecimen of *A. roseojugum* display a single sub central meg-aesthete and two micraesthetes near the pustule base, which coincide with the description of Lyons (1988). Lyons also remarked this species high similarity in the sculpture pattern with *A. andersoni* Watters, 1981, and he found it difficult to separate these species. He called the few characters he established to distinguish the species from each

other “subjective”. We found Lyons’ separation of these species to rely on only slight differences of pustule and valve morphology and body length. A more focused study is needed to clarify whether these nominal species are actually distinct species.

Acanthochitona zebra Lyons, 1988

Figures 6I–K, 11A–H

Material examined. Five specimens; 7.5–11.5 mm long, 3.2–7 mm wide. Laguna Arrecifal Desterrada (CNMO4945), Cabaña CONANP (CNMO4979), Laguna Desterrada (CNMO4993).

Description. Small-sized chitons, color mainly beige to creamy, with concentric bands in dark brown or green on head, tail valve and the lateropleural areas of intermediate valves (Figure 6I–K). Head valve (Figure 11A) semicircular, wider than long, posterior margin straight, apex slightly present. Tail valve (Figure 11B) smaller than head valve; mucro postmedian. Intermediate valves (Figure 11C) with tegmentum wider than long; apex pointy; jugum smooth and wider anteriorly. Insertion plate curved, short on its sides; apophyses long and anteriorly elevated wing-shaped in intermediate valves (Figure 11D); sub-rectangular in tail valve; slits in intermediate valves and in the tail valve are hardly present; slit formula 5/1/2. Tegmentum covered with sub-spatulate pustules, wider on their posterior end and somewhat inflated on their central area (Figure 11E). Girdle in living specimens wide, mostly cream-white colored with dark brown or olive-green, irregular longitudinal bands; covered with small spicules (Figure 11F, G), flattened, elongated and strongly ribbed (7–8 ribs) spicules, the ribs reach and join the spicule apex (Figure 11G); tufts reduced or less dense, with long hyaline spicules (Figure 11F). Radula (Figure 11H) with a pointed tricuspid major lateral tooth, the cusps are of almost the same size; central teeth sub-rectangular or spatulate anteriorly curved outwards.

Habitat. Found from the intertidal to the shallow subtidal around 12 m, on living corals, rocks and turtlegrass, *T. testudinum*.

Remarks. Lyons (1988) described morphological variation in this species (figure 118–120, and 121–127 respectively) from Tamarind Beach reef in Grand Bahamas, Dry Tortugas Florida and Puerto Rico. According to those figures, it seems that the Bahamas specimen (figure 118–120, of 10 mm length) showed a wider tegmentum in IV, and a remarkably elongated head valve. A PNAA specimen (11.2 mm) showed similarities with those specimens from Florida (Lyons 1988: figure 125, 11 mm), particularly in its rounded tegmentum, which seems to be typical in specimens of nearly the same length, and which is also similar to the type specimen (USNM859319) (15 mm). This specimen is also characterized by a somewhat rounded outline of the tegmentum (Figure 14A). Closer examination of the pustules of the PNAA specimens revealed them to have a somewhat inflated surface on their center (Figure 11E). Lyons (1988) did not call attention to this character state but the pustules are similar in his figures.

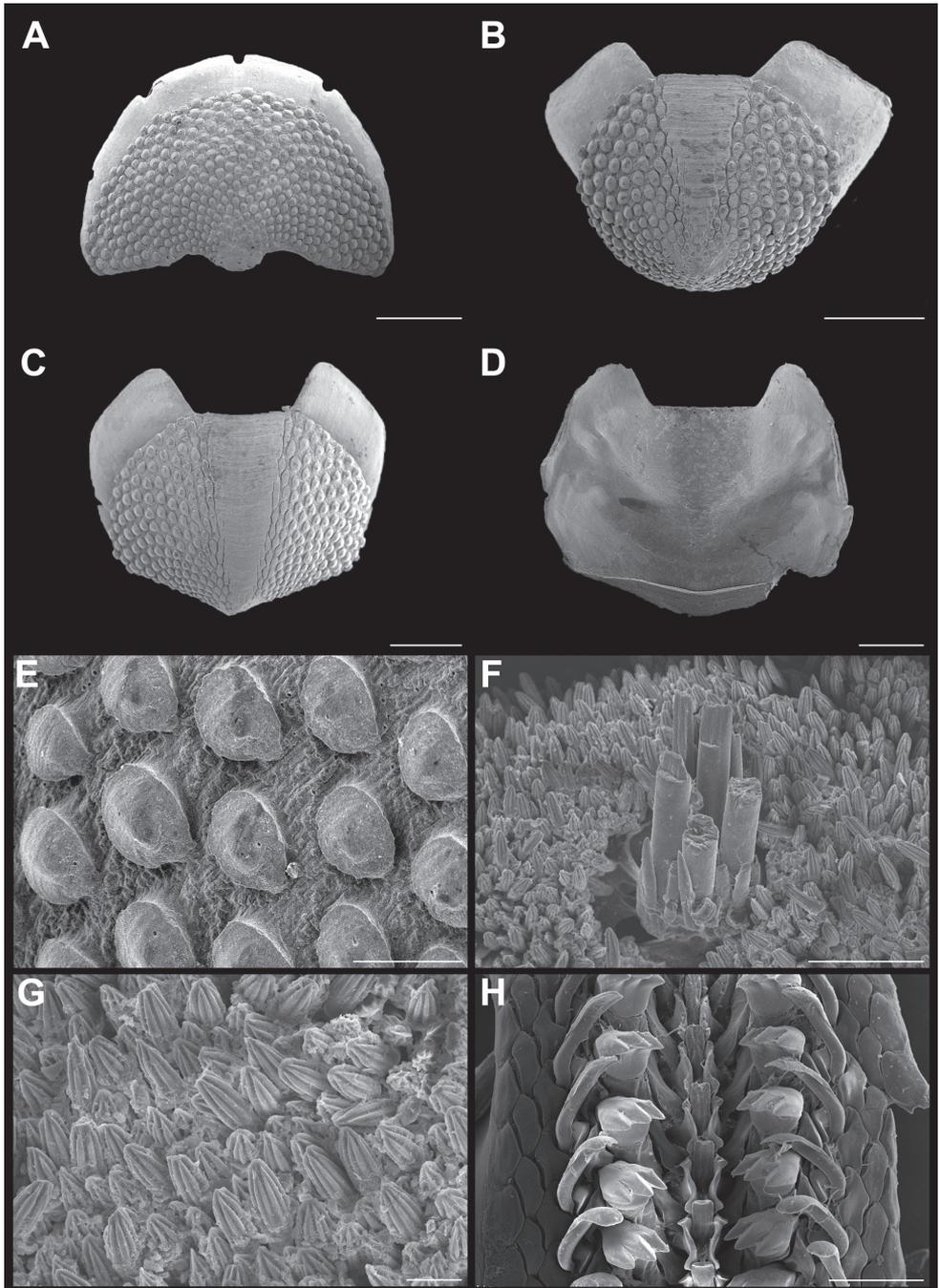


Figure 11. *Acanthochitona zebra* Lyons, 1988. Scanning electron images of a specimen from Laguna Desterrada (CNMO4993, 9.7 mm length). **A** dorsal view of head valve (I), SB = 500 μ m **B** dorsal view of tail valve (VIII), SB = 500 μ m **C** dorsal view of intermediate valve IV, SB = 500 μ m **D** ventral view of intermediate IV, SB = 500 μ m **E** intermediate valve IV pustules detail, SB = 100 μ m **F** girdle spicules and tuft, SB = 100 μ m **G** girdle spicules detail, SB = 20 μ m **H** radular teeth, SB = 100 μ m.

Genus *Cryptoconchus* Blainville MS, Burrow, 1815***Cryptoconchus floridanus* (Dall, 1889)**

Figures 6L–O, 12A–F, 13A–H

Material examined. Two specimens; 7.1–9.3 mm long, 3.0–4.2 mm wide. Isla Perez (CNMO4996).

Description. Small-sized chitons, of oval body shape, somewhat elongated. Color dark brown to black, tegmentum white or creamy (Figure 6L–O). Valves covered by a smooth girdle; tegmentum very reduced; only the jugal area is exposed. Occasionally, tegmentum developing pustule formations, roundish or in irregular polygon shapes, opposed to oval, with a single megaesthete located on the pustule base. Head valve (Figure 12A) with a sub-quadrant outline, not notched, the posterior margin slightly concave; tegmentum semicircular and raised, flattened on its base; usually smooth, it can show small, irregularly shaped semi-oval pustules, which are larger anteriorly (Figure 13B), and arranged in a concentric pattern around the apex, covering most of the dorsal tegmentum surface (Figure 13A). Intermediate valves (Figure 12D, E), with a pointed apex; jugum smooth, slightly wider anteriorly; tegmentum when present reduced to two longitudinal narrow areas, adjacent to the jugum, and located near to the apex (Figure 13C), with small, longitudinally orientated and often irregularly rounded protruding (Figure 13D); jugum smooth with numerous megal aesthetes, distributed on its posterior end. Tail valve wider than long; jugal area narrow; mucro postmedian (Figure 12C); tegmentum (when present) bulb-shaped (Figure 13E); in juvenile specimens, the postmucronal area somewhat depressed, and slits missing (Figure 12B). Tegmentum around the mucro very limited, can bear a few pustule-like somewhat rounded to completely irregular shaped forms; the jugal area near to the mucro shows numerous megal aesthetes with no apparent arrangement (Figure 13E). Articulamentum wide, and especially in head valve, slits are somewhat deeply “u”-shaped; intermediate valves with two short and shallow slits (Figure 12F), almost absent in juveniles (Figure 12D), apophyses wide and wing-shaped; articulamentum of tail valve anteriorly wide, with short apophyses, with two “u”-shaped slits, located on the base of the valve; slit formula 5/1/2. Girdle smooth, constituted of mantle tissue, no elements present (Figure 13F). Radula (Figure 13G) with a central semi-wedge shaped tooth, rounded on its apical end and pointed posteriorly; major lateral tooth with four cusps, the outermost cusp only half of the size of the others, wider and broadened anteriorly (Figure 13H).

Habitat. Found in the shallow subtidal to 12 m on rocks and dead coral, associated with crustose coralline red and green algae.

Remarks. The reduced tegmentum area and its black nude girdle make the identification of this species quite unequivocal. The examination of the morphology of a juvenile (7.1 × 3.0 mm) PNAA specimen revealed the lack of slits and tegmentum pustules. In a somewhat larger animal (9.3 × 4.2 mm), the slits and pustules could be observed in all valves (explained above). Remarkably, the pustules on the head valve

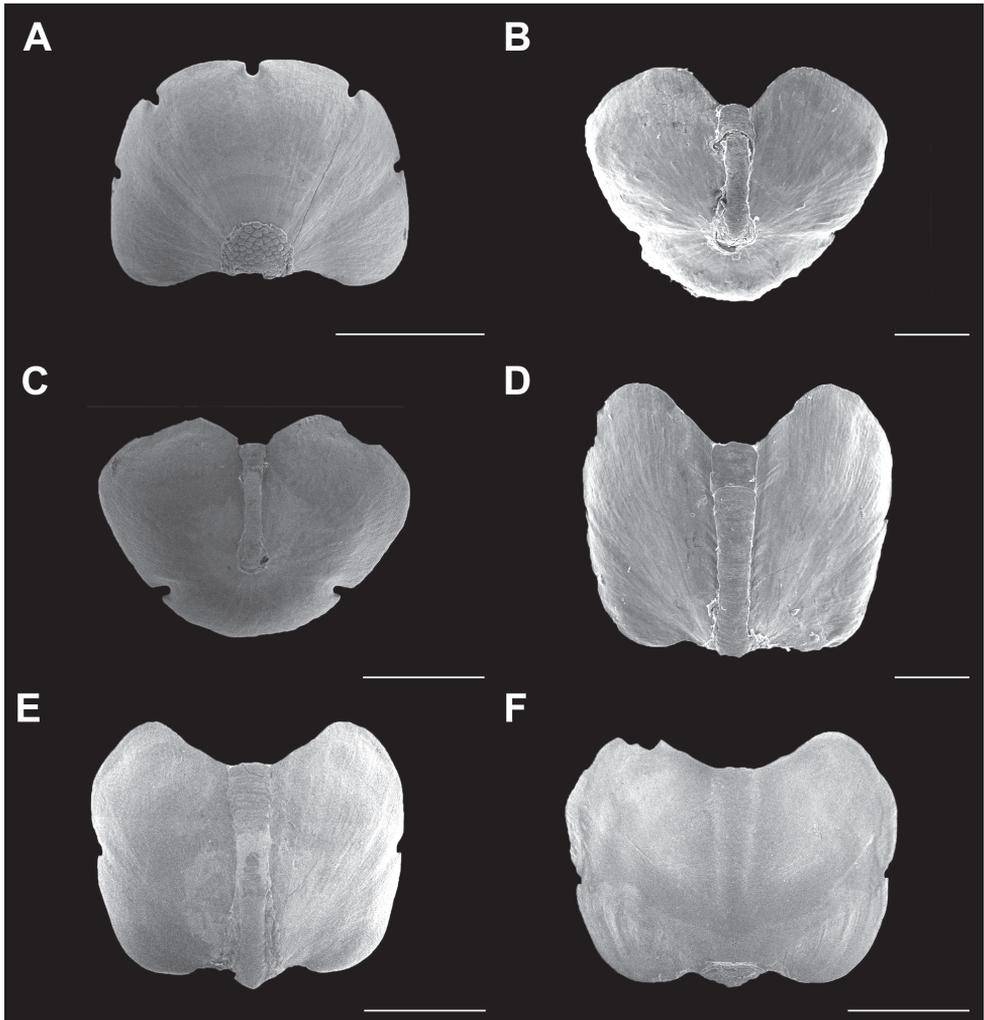


Figure 12. *Cryptoconchus floridanus* (Dall, 1889). Scanning electron images of a specimen from Isla Perez (CNMO4996, 9.3 mm length). **A** dorsal view of head valve (I), SB = 500 μm **C** dorsal view of tail valve (VIII), SB = 500 μm **E** dorsal view of intermediate valve IV, SB = 100 μm **F** ventral view of intermediate valve IV. Juvenile specimen from Isla Perez (CNMO4996, 7.1 mm length) **B** dorsal view of tail valve (VIII), SB = 100 μm **D** dorsal view of intermediate valve IV, SB = 100 μm .

cover most of its area, whereas on the intermediate and the tail valve they are less numerous and more irregular in shape than on the head valve. Lyons (1988: figure 148, 149) figured some intermediate valves of a specimen of 10.7 mm length from Vaca Key, Monroe County, Florida with rudimentary pustules near the jugal area, which strongly resemble PNAAspecimens. On the contrary, this condition was not observed in Puerto Rico specimens (García-Ríos 2003).

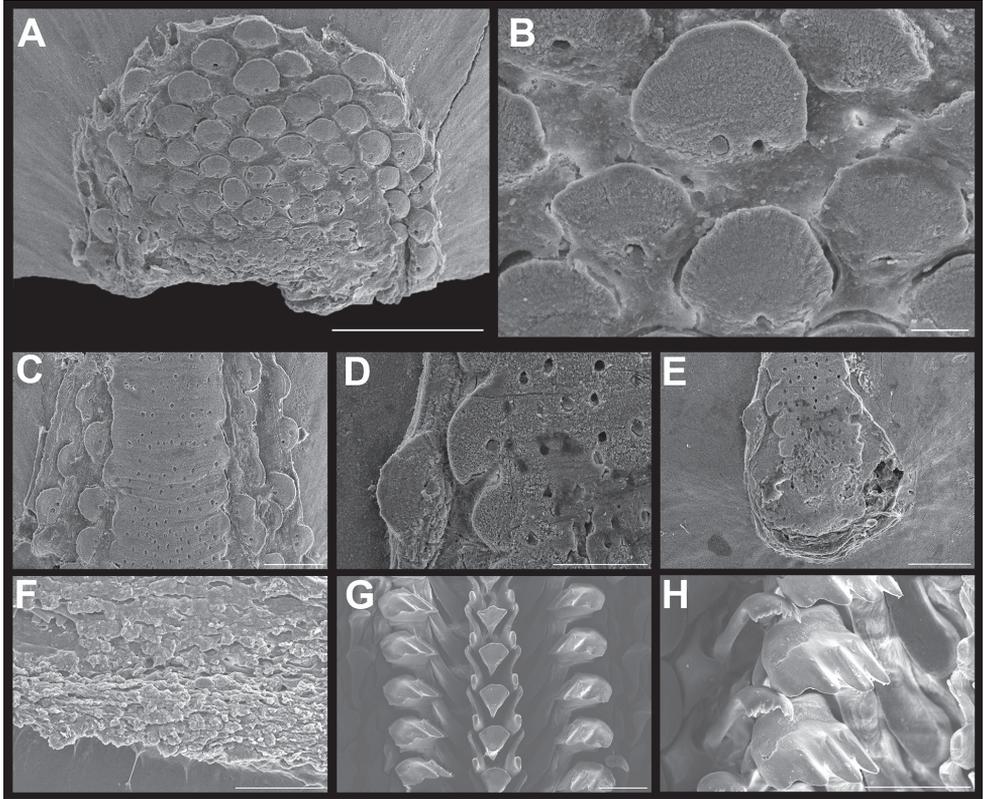


Figure 13. *Cryptoconchus floridanus* (Dall, 1889). Scanning electron images of specimen from Isla Perez (CNMO4996, 9.3 mm length). **A** tegmentum detail, showing the pustules on the head valve (I), SB = 200 μ m **B** head valve pustules detail, SB = 200 μ m **C** jugal area of intermediate valve IV, showing the pustule formation, SB = 200 μ m **D** detail of pustules on jugal area of intermediate valve IV, SB = 200 μ m **E** tail valve jugum of tail valve (VIII), SB = 200 μ m **F** girdle detail, SB = 100 μ m **G** radular teeth, SB = 100 μ m **H** major lateral teeth detail, SB = 50 μ m.

The examination of a larger *C. floridanus* (CNMO5560, 20.3 \times 8.3 mm) (Figure 6O) from Banco Chinchorro revealed a lack of pustules and little tegmentum development at all. Our observations suggest that some chitons might develop tegmentum, including pustules, but this in the observed specimens was not related to chiton size. The Banco Chinchorro specimen of *C. floridanus* is one of the largest animals recorded from Mexico, after the Puerto Rico species of 21 mm length (García-Ríos 2003: figure 153), which also lacks of tegmentum formations. Regarding the radula, the fourth cusp of the major lateral tooth seems to be distinctive for the PNAA specimens, while the Puerto Rico specimen had only three cusps. The differences observed in our specimens compared to those from Puerto Rico, and the similarities with the PNAA and Florida Keys specimens is interpreted here to be due to high variability within a widespread species.

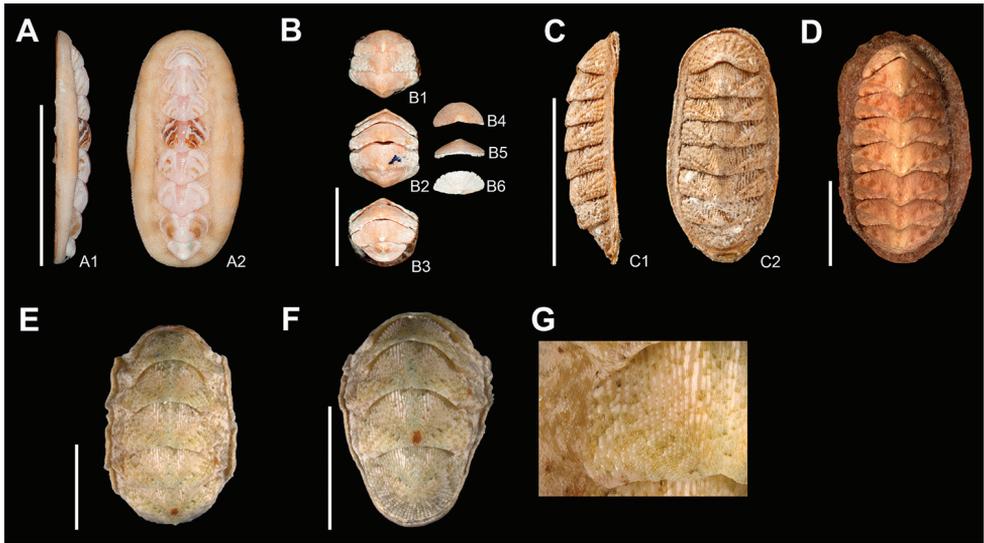


Figure 14. *Acanthochitona zebra* Lyons, 1988, **A** holotype (USNM859319), from Silver Cove Canal Freeport, Grand Bahama Island, specimen of 15 mm length; A1, in lateral view; A2, in dorsal view, SB = 10 mm. *Lepidochitona liozonis* (Dall & Simpson, 1901) **B** holotype (USNM161920), from Culebra Island, Ensenada Honda, Puerto Rico, specimen of 13.5 mm length; B1, curled chiton in dorsal view showing intermediate valves II-IV; B2, curled chiton in dorsal view showing intermediate valves IV-V; B3, curled chiton in dorsal view showing intermediate valves VI-VIII. Disarticulated valves; B4, head valve in dorsal view; B5, head valve in frontal view; B6, head valve in ventral view, SB = 5 mm. *Calloplax janeirensis* (Gray, 1828) **C** lectotype (NHMUK 1977041/2), from Brazil Rio de Janeiro, specimen of 16.2 mm length. C1, in lateral view and C2, in dorsal view, SB = 15 mm. *Tonicia schrammi* (Shuttleworth, 1856) **D** dorsal view of a paralectotype (NMBE19115/5a), from West Indies, Guadeloupe, specimen of 29 mm length, SB = 10 mm. *Stenoplax floridana* (Pilsbry, 1892), from Banco Chinchorro, Quintana Roo (CNMO5557) **E** specimen of 26.7 mm length, in dorsal view showing intermediate valves III-VII, SB = 5 mm **F** same specimen in dorsal view, showing intermediate valves VI-VIII, SB = 5 mm **G** detail of intermediate valve IV in dorsal view, showing the pustule formation near the diagonal ridge.

Discussion

This study reports nine chiton species, belonging to five families and seven genera, in which Acanthochitonidae is the best represented with four species. PNAAC chitons are characteristic for carbonate-rich habitats (Lyons and Moretzsohn 2009) and mainly associated with a rocky substrate in subtidal depths, with the exception of *I. erythronotus* found on dead coral. *Tonicia schrammi*, *C. janeirensis* and *L. liozonis* were exclusively reported from the intertidal, and *Acanthochitona* species showed more affinity to subtidal depths. We suspect that the low abundances recorded for *L. liozonis*, *T. schrammi* and *C. floridanus* and *A. roseojugum* in the original surveys, which mainly focused on other invertebrate groups, and all chiton material included in this paper was collected as bycatch.

Our research from PNAAC produced *Tonicia schrammi* as the only representative of Chitonidae, and extends its distribution to the Gulf of Mexico. Other members of this

family, specifically members of the genus *Chiton*, have been reported as widespread in the Caribbean (Bullock 1988) but were absent from our samples. This is probably due to the predominance of coral substrates and low rock formations with low tide activity in the PNNA habitats, whereas most species of *Chiton* are common in the intertidal of rocky shores.

A high morphological variability could be observed in the valve sculpture of *C. janeirensis* and *C. floridanus*, and in the central and minor lateral teeth in the radula of *T. schrammi*, *A. hemphilli*, and *C. floridanus*, which also show a higher similarity with specimens from the Florida Keys than with specimens from Puerto Rico and the Bahamas. Morphological differences were also identified within the same species from other regions within the Caribbean. We found a great accordance between *A. andersoni* and *A. roseojugum* descriptions, with very few valve and pustule character states that allow to separate both species. Further studies including a DNA analysis are needed to clarify the taxonomic status of these two taxa.

Acanthochitona hemphilli showed the most striking variation when comparing it to specimens from other areas, particularly in the repetitive lack of the second slit on tail valve with no apparent damage. Although it is known that members of Acanthochitonidae follow the general trend of tegmentum reduction and the extension of the articulamentum laminae, the loss of slits in the sutural laminae of *A. hemphilli* seems to represent a natural pattern within *Acanthochitona* s.s.

A study of the morphological variability within species of the Acanthochitonidae can be performed by comparison with García-Ríos (2003), who fully reviewed the species presented here and figured mostly specimens from Puerto Rico. *Cryptoconchus floridanus* from the Florida Keys (Saito 2004: figure 7A–F) had similar radular teeth morphology to specimens from Puerto Rico, with a sub-spatulate, distally wider central tooth and a tricuspid major lateral tooth. Instead, PNAA specimens revealed wedge-shaped central tooth and the major lateral with a fourth smaller outer cusp; which requires further investigation and the examination of more specimens.

Lyons (1988) described *Acanthochitona* species from the Caribbean and from few areas of Central America, focused exclusively on pustule morphology and aesthete number and position. Later, Watters (1990) also focused on the same pustule elements in the Eastern Pacific *Acanthochitona* species. Finally, García-Ríos (2003) included the radula and girdle elements to characterize Puerto Rican chitons, supplying a large compilation of SEM images that allow a much better understanding of the taxonomic structures of Caribbean species. However, in the major contributions dealing with *Acanthochitona* there was a tendency to omit other morphological characters and to limit the detailed description of a species exclusively to tegmentum sculpturing. This is the case of *A. zebra*, whose valves structure (dorsal and ventral) were described in detail (Lyons 1988), but with few other details of its morphology. We figured *A. zebra* girdle spicules and radular teeth for the first time, which are somewhat oval long and strongly ribbed, with few hyaline spicules in the girdle tufts, and the central tooth is sub-rectangular and the major lateral tooth is tricuspid.

The comparison of PNAA chiton diversity with that of other areas was challenging due to the limited number of specimens available for the study, and the lack of good images of morphological structures in the existing literature. We have included SEM images of radular and girdle features described here for the first time, especially for *Acanthochitona* species.

Saito (2004) also stressed the lack of radula information in most of the chiton studies, and he proposed a more refined study of the radular teeth. However, our examination of the central radular teeth revealed consistently high intraspecific variability for species of *Acanthochitona*. Still, we agree with Saito's suggestion that it is desirable to generate a full set of information on the character states of the radula, as well as the girdle elements to increase the effectiveness of comparison within and between species; and we also coincide with other authors that more specimens are needed to be examined from different localities to verify or falsify previous species records.

Despite a long history of taxonomic mollusk research in the Caribbean, the chiton fauna of Mexican shores in the Yucatan Peninsula and its surroundings remains far from well known. We predict that future studies will extend the distribution range of other Caribbean species to include the PNAA reefs or their vicinity in the Gulf of Mexico.

Museums' collections

We are grateful for the prompt assistance on photograph the type specimens to: W. Moser curator of the Invertebrate Zoology collection of the United States National Museum of Natural History Smithsonian Institution, Washington D.C. and the technical assistance provided by Y. Villiacampa. To Ms. A. Salvador, curator of marine Mollusca at the British Museum of Natural History of London and to K. Webb from the NHMUK Photographic Unit.

Acknowledgements

We thank to the Ecology research group of UMDI-Sisal UNAM that supported the fieldwork, especially to R. Garza, A. Gallardo, F. Mex, P. Westendarp, Q. Hernández, and E. Lemus. To the personal of SEMAR for assistance on transportation and from Perez Island, CONANP and SCT teams for accommodation. To E. Naranjo from Instituto de Biología, UNAM for house holding the PNAA chitons in the Colección Nacional de Moluscos, UNAM and for providing to the first author space in her laboratory. To D.J. Eernisse from California State, University of Fullerton, C. García-Ríos from Universidad de Puerto Rico Humacao and R.N. Clark associate of Santa Barbara Museum of Natural History, for their valuable comments and suggestions to improve this paper. To B. Mendoza-Garfias from the Laboratorio de la Biodiversidad I, IBUNAM for promptly processed and greatly captured our SEM material. To S. Guzmán from the Laboratorio de la Biodiversidad II, IBUNAM for her technical as-

sistance on the photograph laboratories. To Y. Ornelas from Instituto Ciencias del Mar y Limnología, UNAM for assisting with part of the SEM images. To M. Reguero from Instituto Ciencias del Mar y Limnología for space in her laboratory and for sharing literature. To E. Neubert of Natural History Museum Bern, Switzerland for sharing *T. schrammi* paralectotype image and data. The chiton material presented in this study was collected following Mexican regulations under the collecting permits DGPA/04966/140508.1175 and DGPA/05808/040609.1684). This work was partially funded by Programa de Biodiversidad Marina de Yucatan (BDMY) through a CONABIO project NE018 and the Harte Research Institute for the Gulf of Mexico Studies, to the third author, and by PAPIME-UNAM PE207210, CONACyT-SEMARNAT 108285 for the second author.

References

- Arce N, García-Ríos CI (2015) Crecimiento alométrico en valvas de *Stenoplax* spp. Simposio de Flora y Fauna del Caribe. Departamento de Biología, Universidad de Puerto Rico en Humacao. <https://doi.org/10.13140/RG.2.1.3330.8244>
- Boudreaux WW (1987) Comparisons of molluscan reef flat assemblages from four reefs of the Campeche Bank, Yucatan, Mexico. M.S. non-thesis project, Corpus Christi State University, Corpus Christi, Texas, 47 pp.
- Bullock RC (1981) Two new species of *Acanthochitona* from the new world (Polyplacophora: Cryptoplacidae). *The Nautilus* 95(4): 171–177.
- Bullock RC (1985) The *Stenoplax limaciformis* (Sowerby, 1832) Species complex in the New World (Mollusca: Polyplacophora: Ischnochitonidae). *The Veliger* 27: 291–307.
- Bullock RC (1988) The Genus *Chiton* in the New World (Polyplacophora: Chitonidae). *The Veliger* 31(3/4): 141–191.
- Bullock RC, Franz CJ (1994) A preliminary taxonomic survey of the chitons (Mollusca: Polyplacophora) of Isla de Margarita, Nueva Esparta, Venezuela. *Memoria* 54: 9–50.
- Bullock RC, Franz CJ, Buitrago J (1994) A report on a collection of chitons (Mollusca: Polyplacophora) dredged near Isla Coche, Nueva Esparta, Venezuela. *Memoria* 54: 77–93.
- Chavez EA, Hidalgo E, Izaguirre MA (1985) A comparative analysis of Yucatan Coral Reefs. *Proceeding of the Fifth International Coral Congress Tahiti* 6: 355–361.
- Ekdale AA (1974) Marine molluscs from the shallow-water environments (0–60 meters) off the northeast Yucatan coast, Mexico. *Bulletin of Marine Science* 24: 639–668.
- Ferreira JA (1978a) The Chiton species described by C.B Adams, 1845 from Jamaica. *Bulletin of Marine Science* 28: 81–91.
- Ferreira JA (1978b) The genus *Calloplax* Thiele, 1909 (Mollusca: Polyplacophora) in the Americas. *Bulletin of the Southern California Academy of Sciences* 77: 56–64.
- Ferreira AJ (1982) A new species of *Calloplax* (Mollusca: Polyplacophora) in the eastern Pacific. *Veliger* 24: 321–324.
- Ferreira JA (1985) Chiton (Mollusca: Polyplacophora) fauna of Barbados, West Indies, with the description of a new species. *Bulletin of Marine Science* 36: 189–219.

- Fosberg FR (1961) A brief study on the cays of Arrecife Alacran, a Mexican Atoll. Atoll Research Bulletin 93: 1–25. <https://doi.org/10.5479/si.00775630.93.1>
- García-Ríos CI (2003) Los Quitones de Puerto Rico. Editorial Isla Negra, San Juan Puerto Rico, 209 pp.
- García-Ríos CI (2015) *Lepidochitona pseudoliozonis*, una nueva especie de quiton (Polyplacophora: Ischnochitonidae) del norte del Caribe. Revista de Biología Tropical Vol. 63(2): 369–384. <https://doi.org/10.15517/rbt.v63i2.14862>
- González MA, Chávez EA, de la Cruz G, Torruco D (1991) Distribution patterns of gastropods and bivalves at the Yucatán Peninsula, Mexico. Ciencias Marinas 17(3): 147–172.
- Hicks DW, Barrera NC, Tunell Jr W (2001) Ecological distribution of shallow-water Mollusca on the Alacran reef, Campeche Bank, Yucatan, Mexico. Texas Conchologist 38(1): 7–30.
- Irisarri I, Eernisse DJ, Zardoya R (2014) Molecular phylogeny of *Acanthochitonina* (Mollusca: Polyplacophora: Chitonida): three new mitochondrial genomes, rearranged gene orders and systematics, Journal of Natural History. <https://doi.org/10.1080/00222933.2014.963721>
- Kaas P (1972) Polyplacophora of the Caribbean region. Studies on the fauna of Curacao and other Caribbean Islands, Martinus Nijhoff. The Hague 41: 1–162.
- Kaas P, Van Belle R (1985) Monograph of Living Chitons (Mollusca: Polyplacophora). Vol 2. Suborder Ischnochitonina. Ischnochitonidae. Schizoplacinae, Callochitoninae and Lepidochitoninae. Brill/Backhuys, Leiden, 198 pp.
- Kaas P, Van Belle RA (1987) Monograph of Living Chitons (Mollusca: Polyplacophora). Vol 3. Suborder Ischnochitonidae. Chaetopleurinae and Ischnochitoninae. Addition to vols. 1 and 2. Brill/Backhuys, Leiden, 302 pp.
- Kaas P, Van Belle RA (1990) Monograph of Living Chitons (Mollusca: Polyplacophora). Vol 4. Suborder Ischnochitonina: Ischnochitonidae: Ischnochitoninae. (cont.). Addition to vols. 1, 2 and 3. Brill/Backhuys, Leiden, 315 pp.
- Kaas P, Van Belle RA (1994) Monograph of Living Chitons (Mollusca: Polyplacophora). Vol 5. Suborder Ischnochitonina: Ischnochitonidae: Ischnochitoninae (concluded); Callistoplacinae; Mopaliidae. Addition to vols. 1–4. Brill/Backhuys, Leiden, 407 pp.
- Kaas P, Van Belle RA (1998) Catalogue of Living chitons (Mollusca: Polyplacophora), 2nd revised edition. Backhuys, publishers, Leiden, 204 pp.
- Kaas P, Van Belle RA, Strack HL (2006) Monograph of Living Chitons (Mollusca: Polyplacophora). 6. Suborder Ischnochitonina (concluded): Schizochitonidae & Ischnochitonidae. Additions to Volumes 1–5. Brill EJ I. Leiden – New York – Koln.
- Lyons WG (1985) *Chaetopleura staphylophera* (Polyplacophora: Chaetopleuridae), a new species from the Southeastern United States and Bahamas. The Nautilus 99(2–3): 35–44.
- Lyons WG (1988) A review of Caribbean Acanthochitonidae (Mollusca: Polyplacophora) with descriptions of six new species of *Acanthochitona* Gray, 1821. American Malacological Bulletin 6(1): 79–114.
- Lyons WG, Moretzsohn F (2009) Polyplacophora (Mollusca) of the Gulf of Mexico. In: Felder DL, Camp DK (Eds) Gulf of Mexico-Origins, Waters and Biota. Biodiversity. Texas A&M University Press, College Station, Texas, 569–578.

- Ortigosa D, Lemus-Santana E, Simões N (2015) New records of opisthobranchs (Gastropoda: Heterobranchia) from Arrecife Alacranes National Park, Yucatan, Mexico. *Marine Biodiversity Records* 8, e117. <https://doi.org/10.1017/S1755267215000925>
- Pilsbry HA (1940) On The Life Habits Of Some Tropical Fresh-Water Mussels By Fritz Haas. *Nautilus* 53(3), pl 12, figure 4.
- Pilsbry HA (1892–1894) Polyplacophora. In Tryon Jr GW (Ed.) *Manual of Conchology* 14 (53–54): 1–128 (1992), 14 (55–56): 129–350 (1993–1994).
- Reyes-Gómez A (2004) Chitons in Mexican Waters. *Bolletino Malacologico* 5: 69–82.
- Reyes-Gómez A, Salcedo-Vargas MA (2002) The recent Mexican chiton (Mollusca: Polyplacophora) species. *The Festivus* 34: 17–27.
- Rice WH, Kornicker LS (1962) Mollusks of Alacran Reef, Campeche Bank, Mexico. *Institute of Marine Science* 8: 366–403.
- Rice WH, Kornicker LS (1965) Mollusks from the deeper waters of the northwestern Campeche Bank, Mexico, *Publications of the Institute of Marine Science* 10: 108–172.
- Saito H (2004) Phylogenetic significance of the radula in chitons, with special reference to the Cryptoplacoidea (Mollusca: Polyplacophora). *Bollettino Malacologico* 5: 83–104.
- Sanvicente-Añorve L, Solís-Weiss V, Ortigosa J, Hermoso-Salazar M, Lemus-Santana E (2012a) Opisthobranch fauna from the National Park Alacranes Reef, southern Gulf of Mexico. *Cahiers du Biologie Marine* 53: 447–460.
- Sanvicente-Añorve L, Hermoso-Salazar M, Ortigosa J, Solís-Weiss V, Lemus-Santana E (2012b) Opisthobranch assemblages from a coral reef system: the role of habitat type and food availability. *Bulletin of Marine Science* 88(4): 1061–1074. <https://doi.org/10.5343/bms.2011.1117>
- Sirenko B (2006) New outlook on the system of chitons (Mollusca: Polyplacophora). *Venus* 65(1–2): 27–49.
- Smith AG, Ferreira AJ (1977) Chiton fauna of the Galápagos Islands. *Veliger* 20 (2): 82–97.
- Thiele J (1909–1910) Revision des Systems der Chitonen. Teil I. *Chun's Zoologica* 22(56): 1–70 (1909), 2: 71–132 (1910).
- Van Belle RA (1983) The systematic classification of the chitons (Mollusca: Polyplacophora). *Informations de la Société Belge de Malacologie*, 11:1–178.
- Vokes HE, Vokes EH (1983) Distribution of shallow-water marine Mollusca, Yucatan Peninsula, Mexico. *Tulane University*, 54 pp.
- Watters T (1981) Two New species of *Acanthochitona* from the New World (Polyplacophora: Cryptoplacidae). *The Nautilus* 95: 171–177.
- Watters T (1990) A review of the recent Eastern Pacific Acanthochitoninae (Mollusca: Polyplacophora: Cryptoplacidae) with the description of a New Genus, *Americhiton*. *The Veliger* 33(3): 241–271.
- Wiley GN, Circé RC, Tunnell Jr W (1982) Mollusca of the rocky shores of East Central Veracruz State, Mexico. *The Nautilus* 96(2): 55–61.

Appendix

Summary of chiton species occurring within the Atlantic coast of Mexico, the species distribution ranges are indicated north to south, first continental localities followed by Islands.

Class Polyplacophora Gray, 1821

Order Chitonida Thiele, 1910

Suborder Chitonina Thiele, 1910

Family Ischnochitonidae Dall, 1889

***Ischnochiton striolatus* (Gray, 1828)**

Type locality. Brazil, Río de Janeiro; between Bogue Inlet, North Carolina and Santa Catarina Islands (Kaas and Van Belle 1990).

Additional localities. USA (Florida Keys), Mexico (Yucatan, Quintana Roo); Cuba, Jamaica, Puerto Rico, St. John, St. Croix, Antigua, Guadeloupe, Dominica, Martinique, Grenada, Tobago, Bonaire, Klein Bonaire, Aruba, Colombia, Trinidad (Kaas 1972, Ferreira 1985, Reyes-Gómez and Salcedo-Vargas 2002, García-Ríos 2003, Lyons and Moretzsohn 2009).

***Ischnochiton erythronotus* (C. B. Adams, 1845)**

Type locality. Jamaica (Kaas and Van Belle 1990).

Additional localities. USA (Bonefish Key and Garden Key, Florida), Mexico (PNAA, Quintana Roo: Cozumel), Belize, Honduras; Bahamas, Cuba, Jamaica, Puerto Rico, St. Thomas, St. Eustatius, Guadeloupe, Barbados, Dominican Republic, Virgin Islands, Cayman Islands (Kaas 1972, Ferreira 1978a as *Chiton erythronotus*, 1985, Kaas and Van Belle 1990, Reyes-Gómez and Salcedo-Vargas 2002, García-Ríos 2003, Lyons and Moretzsohn 2009, present study).

***Ischnochiton pseudovirgatus* Kaas, 1972**

Type locality. Boca Lagoon, Curacao (Kaas and Van Belle 1990).

Additional localities. USA (Florida: Jupiter and St. Lucie); Mexico (Yucatan); Curacao, Trinidad, Barbados (Ferreira 1985, Kaas and Van Belle 1990, Lyons and Moretzsohn 2009).

***Stenoplax floridana* (Pilsbry, 1892)**

Type locality. Key West, Florida (Kaas and Van Belle 1987).

Additional localities. USA (Florida Keys), Mexico (Yucatan), Honduras, Panama, Colombia; Cuba, West Caribbean (Kaas & Van Belle, 1987, Lyons and Moretzsohn 2009).

***Stenoplax bahamensis* Kaas & Van Belle, 1987**

Type locality. Arthur's Town, Cat Island, Bahamas (Kaas and Van Belle 1987).

Additional localities. USA (Florida Keys), Mexico (Yucatan, **PNAA**, Quintana Roo), Honduras; Bahamas, Cuba, Jamaica, Hispaniola, Isla de San Andres (as *S. producta* in Bullock 1985, Kaas and Van Belle 1987, Lyons and Moretzsohn 2009, present study).

***Stenoplax boogii* (Haddon, 1886)**

Type locality. West of Isla Plata, Colombia (Kaas and Van Belle 1987).

Additional localities. Western Atlantic: USA (Florida), Belize, Colombia, Brazil (Los Testigos, Fernando de Noronha and Ceara to Alagoas); Bermudas, Bahamas, Puerto Rico, Cayman Islands, Virgin Islands, Aruba. Eastern Pacific: Mexico (Cabo San Lucas), Colombia, Ecuador, Peru, Costa Rica, Panama (Kaas 1972, Ferreira 1985, Kaas and Van Belle 1987, Reyes-Gómez and Salcedo-Vargas 2002, García-Ríos 2003, Lyons and Moretzsohn 2009).

Family Callistoplacidae Pilsbry, 1893

***Calloplax janeirensis* (Gray, 1828)**

Type locality. Brazil Rio de Janeiro (Kaas and Van Belle 1994).

Additional localities. USA (Florida), Mexico (Yucatan, **PNAA**, Quintana Roo: Cozumel), Venezuela (Puerto Mara, Quetepec, Guiria, Carupano, Santa Fe, Coche Island and Margarita Island), Brazil (Porto Van Belle); Bahamas, Puerto Rico, Virgin Islands (San Martin, Saba, Dominica, Trinidad) (Ferreira 1978b, Kaas and Van Belle 1994, Bullock and Franz 1994, Bullock et al. 1994, Reyes-Gómez and Salcedo-Vargas 2002, García-Ríos 2003, as *Chaetopleura janeirensis* in Lyons and Moretzsohn 2009, present study).

Family Chitonidae Rafinesque, 1815***Chiton tuberculatus* Linnaeus, 1758**

Type locality. Gambier, New Providence, Bahamas Island (Bullock 1988).

Additional localities. USA (Florida: Boca Raton), Mexico (Yucatan, Quintana Roo: Isla Mujeres), Venezuela (Isla de Margarita); Bermuda, Puerto Rico, Trinidad (Ferreira 1985, Bullock 1988, Reyes-Gómez and Salcedo-Vargas 2002, García-Ríos 2003, Lyons and Moretzsohn 2009).

***Chiton squamosus* Linnaeus, 1764**

Type locality. Robins Bay, St. Mary, Jamaica (Bullock 1988).

Additional localities. Mexico (Veracruz, Yucatan, Quintana Roo); Bahamas, Cuba, Jamaica (St. Mary Robin Bay), Grenada; (Bullock 1988, Reyes-Gómez and Salcedo-Vargas 2002, García-Ríos 2003, Lyons and Moretzsohn 2009).

***Chiton marmoratus* Gmelin, 1791**

Type locality. Unknown (Bullock 1988).

Additional localities. Mexico (Veracruz, Yucatan, Quintana Roo: Isla Mujeres), Panama; Costa Rica, Honduras, Venezuela; Bahamas, Cuba, Jamaica, Puerto Rico, Dominican Republic, Barbados, Guadeloupe, Grand Cayman, St. Thomas, St. Croix, Curacao, St. John, Saba, Antigua, St. Eustatius, Montserrat, Granada, Trinidad, Tobago, Bonaire (Klein Bonaire), Aruba (Kaas 1972, Ferreira 1985, Bullock 1988, Reyes-Gómez and Salcedo-Vargas 2002, García-Ríos 2003, Lyons and Moretzsohn 2009).

***Chiton viridis* Spengler, 1797**

Type locality. St. Croix, Virgin Islands (Bullock 1988).

Additional localities. USA (Florida Keys), Mexico (Yucatan, Quintana Roo), Panama, Colombia, Venezuela; Bahamas, Cuba, Puerto Rico, Barbados, St. Thomas, St. Croix, Grand Cayman, Curacao, Aruba Dominican Republic, Antigua St. Lucia, San Andres Island, Trinidad, Tobago Bonaire (Kaas 1972, Ferreira 1985, Bullock 1988, Reyes-Gómez and Salcedo-Vargas 2002, García-Ríos 2003, Lyons and Moretzsohn 2009).

***Acanthopleura granulata* (Gmelin, 1791)**

Type locality. Western Atlantic (Ferreira 1985).

Additional localities. USA (Florida), Mexico (Quintana Roo: Cozumel), Honduras, Nicaragua, Costa Rica, Panama; Bahamas, Cuba, Jamaica, Puerto Rico, Haiti,

St. Martin, Curacao, St. John, St. Croix, St. Barts, St. Eustatius, St. Kitts, Antigua, Guadeloupe, Granada, Tobago, Grand Cayman, Trinidad, Dominican Republic, Trinidad, Bonaire, Dominican Republic (Kaas 1972, Ferreira 1985, Reyes-Gómez and Salcedo-Vargas 2002, García-Ríos 2003).

***Toncia schrammi* (Shuttleworth, 1856)**

Type locality. Guadeloupe Island (Kaas et al. 2006).

Additional localities. USA (Florida), Mexico (PNAA), Honduras, Colombia; Bermuda, Bahamas, Cuba, Jamaica, Puerto Rico, Grand Cayman, Virgin Islands, Bonaire, Barbados, Aruba, Curacao, Guadalupe Island (Kaas 1972, Ferreira 1985, García-Ríos 2003, Kaas et al. 2006, Lyons and Moretzsohn 2009, present study).

Family Lepidochitonidae Iredale, 1914

***Lepidochitona liozonis* (Dall & Simpson, 1901)**

Type locality. Ensenada Honda, Isla Culebra, Puerto Rico (Kaas and Van Belle 1985).

Additional localities. USA (Florida), Mexico (Yucatan, PNAA, Quintana Roo), Colombia; Bermuda, Bahamas, Cuba, Puerto Rico, Barbados (Kaas and Van Belle 1985, García-Ríos 2003, Lyons and Moretzsohn 2009, present study).

Family Mopaliidae Dall, 1889

***Ceratozonia squalida* (C. B. Adams, 1845)**

Type locality. Jamaica (Kaas and Van Belle 1994).

Additional localities. USA (Florida), Mexico (Quintana Roo: Cozumel), Colombia, Venezuela; Cuba, Bahamas, Jamaica, Puerto Rico, Barbados, Martinique, Grand Cayman Island, St. Vincent, St. John, Saba, St. Eustatius, Montserrat, Grenada, Trinidad, Tobago, Curacao, Aruba, Trinidad, Dominican Republic (Kaas 1972, Ferreira 1978a, 1985, Kaas and Van Belle 1994, Reyes-Gómez and Salcedo-Vargas 2002, García-Ríos 2003, Lyons and Moretzsohn 2009).

Family Acanthochitonidae Pilsbry, 1893

***Acanthochitona hemphilli* (Pilsbry, 1893)**

Type locality. Key West, Florida (Lyons 1988).

Additional localities. USA (Florida), Mexico (Yucatan, **PNAA**, Quintana Roo), Belize, Honduras; Bahamas, Cuba Puerto Rico; Jamaica, Aruba (Lyons 1988, Reyes-Gómez and Salcedo-Vargas 2002, García-Ríos 2003, Lyons and Moretzsohn 2009, present study).

***Acanthochitona pygmaea* Pilsbry, 1893**

Type locality. Cedar Keys, Florida (Lyons 1988).

Additional localities. USA (Florida: Cedar Keys), Mexico (Campeche, Yucatan, Quintana Roo); Bermuda, Bahamas, Cuba, Puerto Rico, Virgin Islands, Saba (Lyons 1988, García-Ríos 2003, Lyons and Moretzsohn 2009).

***Acanthochitona roseojugum* Lyons, 1988**

Type locality. Bartlett Hill, Eight Mile Rock, Grand Bahama Island (Lyons 1988)

Additional localities. USA (Florida, Dry Tortugas), Mexico (**PNAA**, Quintana Roo), Honduras; Bahamas, Cuba (Lyons 1988, García-Ríos 2003, Lyons and Moretzsohn 2009, present study).

***Acanthochitona zebra* Lyons, 1988**

Type locality. Silver Cove Canal, Freeport, Grand Bahama Island (Lyons 1988).

Additional localities. USA (Florida Keys, Dry Tortugas), Mexico (Yucatan, **PNAA**, Quintana Roo), Belize; Bahamas, Cuba Puerto Rico, Aruba, Curacao (Lyons 1988, García-Ríos 2003, Reyes-Gómez 2004, Lyons and Moretzsohn 2009, present study).

***Acanthochitona andersoni* Watters, 1981**

Type locality. St. Vincent, Lesser Antilles (Bullock 1981).

Additional localities. USA (Florida), Mexico (Quintana Roo, Yucatan), Panama, Venezuela; Bahamas, Cuba, Netherlands Antilles, (as *Americhiton andersoni* in Watters 1981, Lyons 1988, Reyes-Gómez and Salcedo-Vargas 2002, García-Ríos 2003, as *Americhiton andersoni* in Lyons and Moretzsohn 2009).

***Cryptoconchus floridanus* (Dall, 1889)**

Type locality. Cape, Florida (Lyons 1988).

Additional localities. USA (Florida Keys, Dry Tortugas), Mexico (Yucatan, **PNAA**); Bahamas, Cuba, Jamaica, Puerto Rico, Cayman Islands, Aruba, Bonaire (Lyons 1988, García-Ríos 2003, Reyes-Gómez 2004, Lyons and Moretzsohn 2009, present study).

Two new species of *Leptosyllus* from Korea (Copepoda, Harpacticoida, Paramesochridae)

Jinwook Back¹, Wonchoel Lee²

1 Department of Taxonomy and Systematics, National Marine Biodiversity Institute of Korea, Seocheon, 325-902, Korea **2** Department of Life Science, College of Natural Sciences, Hanyang University, Seoul 133-791, Korea

Corresponding author: Wonchoel Lee (wlee@hanyang.ac.kr)

Academic editor: D. Defaye | Received 30 July 2015 | Accepted 8 March 2017 | Published 3 April 2017

<http://zoobank.org/574FD12F-ED4A-41ED-8389-F24564971F37>

Citation: Back J, Lee W (2017) Two new species of *Leptosyllus* from Korea (Copepoda, Harpacticoida, Paramesochridae). ZooKeys 665: 37–57. <https://doi.org/10.3897/zookeys.665.6150>

Abstract

Two new species of *Leptosyllus* are described from the subtidal zone of Korea. Both species were assigned to the subgenus *Leptosyllus* (*Leptosyllus*) T. Scott, 1894, based on following three characters: two-segmented rami of P1, absence of endopod on P2 and P3, and presence of one-segmented endopod of P4. *L. (L.) pundius* **sp. n.** is most closely related to *L. (L.) punctatus* Mielke, 1894, however clearly distinguishable from it based on mandibular exopod with two setae, shape of P6, and caudal seta III ornamented with spinules in the new species. *L. (L.) koreanus* **sp. n.** is clearly distinguishable from its congeners by the second segment of P1 endopod armed with one element, male baseoendopod of P5 with one seta, and one segmented endopod of mandibular palp. The world distribution and updated key to the species of the genus *Leptosyllus* are provided.

Keywords

Copepoda, Harpacticoida, Korea, *Leptosyllus*, Paramesochridae, taxonomy

Introduction

Although the marine biodiversity of Korea is very high according to a recent estimation (Costello et al. 2010), many small interstitial organisms, including harpacticoid copepods, still remain unknown. Harpacticoid copepods play an important role in the benthic food web, and are an important source of biodiversity in Korea. Thus far, 88 harpacticoid species (58 genera and 23 families) including planktonic, free-living

benthic, and invertebrate-associated species have been reported from Korean waters (Song et al. 2012).

Paramesochrid harpacticoids, with their reduced appendages and vermiform body shapes, successfully inhabit subtidal and intertidal sandy bottoms (Boxshall and Halsey 2004). Many free-living genera of the family Paramesochridae have adapted to living on various sandy sediments irrespective of depth and salinity (Plum and George 2009). For example, *Emertonia clausi* Pointer & Veit-Köhler, 2013 was collected from the deep sea (Pointner et al. 2013) while *Remanea naksanensis* Back, Lee & Huys, 2011 was collected from brackish water (Back et al. 2011). So far, nine species belonging to four genera in the family Paramesochridae have been discovered in Korea (Back and Lee 2014).

Thomas Scott (1894) proposed the genus *Leptopsyllus* and fixed *Leptopsyllus typicus* T. Scott, 1894 as the type and presented a generic diagnosis and description of this species. Lang (1944) created the new genus *Paraleptopsyllus* based on the one-segmented P3 endopod. In Kunz's (1962) revision of the family Paramesochridae, the author proposed nine genera including four new genera, *Apodopsyllus*, *Intermedopsyllus* (accepted as *Wellsopsyllus* (*Intermedopsyllus*) Huys, 2009), *Kliopsyllus* Kunz, 1962 (accepted as *Emertonia* Wilson, 1932), and *Scottopsyllus* Kunz, 1962 (accepted as *Wellsopsyllus* (*Scottopsyllus*) Apostolov & Marinov, 1988), based on the segmentation of the legs. Subsequently, each species originally placed in *Leptopsyllus* was allocated to a suitable genus. However, Kunz (1981) revised the family Paramesochridae and treated the genus *Paraleptopsyllus* as subgenus. Especially, Huys (2009) proposed the correcting name and authorship of subgenus *Intermediopsyllus* Huys, 2009 in accordance with ICZN Art.16, because Kunz (1962) contravened ICZN Art.13.3. As a result, the genus *Leptopsyllus* comprises two subgenera, *Leptopsyllus* T. Scott, 1894 and *Paraleptopsyllus* Lang, 1944 and the genus *Leptopsyllus* currently consists of 11 valid species (Wells 2007). Until now, only one species, *Leptopsyllus* (*Paraleptopsyllus*) *arcticus* (Lang, 1936), has been assigned to the subgenus *Paraleptopsyllus*.

A survey of harpacticoid copepods from subtidal zones in Korea resulted in the discovery of two new species belonging to *Leptopsyllus* (*Leptopsyllus*). Here these two species are described and an updated key to species of the genus is provided.

Materials and methods

Specimens were collected from sediments in the subtidal zone near Pung Island off the west coast of Korea (*Leptopsyllus* (*Leptopsyllus*) *pundius* sp. n.), and Maemul Island (*Leptopsyllus* (*Leptopsyllus*) *koreanus* sp. n.) off the south coast of Korea. Sediments were collected using a grab (surface area 0.1 m²) and fixed with 5% buffered formalin. Copepods were extracted from the sediment samples using the Ludox method (Burgess 2001) and preserved in 70% ethanol. Dissected specimens were mounted on several slides separately using lactophenol as a mounting medium. Slides were sealed with transparent nail varnish. Observations were made using a microscope (Olympus BX51) equipped with differential interference contrast and a drawing tube.

The descriptive terminology of Huys et al. (1996) was adopted. Abbreviations used in the descriptions are:

- A1** antennule;
A2 antenna;
ae aesthetasc;
exp exopod;
enp endopod;
P1–P6 first to sixth thoracopod;
exp (enp)-1 (2, 3) to denote the proximal (middle, distal) segment of a three-segmented ramus;
CR caudal ramus.

Specimens were deposited in the National Marine Biodiversity Institute of Korea (**MABIK**). Scale bars in figures are in μm .

Systematics

Family Paramesochridae Lang, 1944

Genus *Leptopsyllus* (*Leptopsyllus*) T. Scott, 1894

Updated genus diagnosis. Paramesochridae. Body cylindrical, depressed dorsoventrally; with distinct separation between prosome and urosome; rostrum fused with cephalothorax. Caudal ramus with 5–7 setae. Antennule 7- or 8-segmented in female, subchirocer in male. Antennary exopod 1-segmented (except for *L. (L.) dubatyi*, 2-segmented) with 3–5 setae. Maxilla with 3 endites on syncoxa; endopod 1-segmented. Maxilliped with elongate basis; endopod 1- or 2-segmented. P1 biramous, 2-segmented endopod and exopod. P2 uniramous; without endopod; with 3-segmented exopod, except for *L. (L.) abyssalis* with 2-segmented exopod. P3 uniramous; without endopod, except for *L. (P.) arcticus* with 1-segmented endopod; with 3-segmented exopod, except for *L. (L.) abyssalis* with 2-segmented exopod. P4 biramous; with 1-segmented endopod; with 3-segmented exopod, except for *L. (L.) abyssalis* with 2-segmented exopod. P1–P4 armature formulae:

	Exopod	Endopod
P1	0.022	0.020
P2	0[1] ¹ .0[1] ² .011	
P3	0.0[1] ² .011	
P4	0.0.011	010

¹ *L. (L.) paratypicus*

² *L. (L.) paratypicus*, *L. (L.) celticus*

Exopod of P5 armed with 3 setae in both sexes.

Sexual dimorphisms in A1, P5, P6 and genital segment.

Type species. *Leptopsyllus (Leptopsyllus) typicus* T. Scott, 1984

Additional species. *L. (L.) paratypicus* Nicholls, 1939; *L. (L.) reductus* Lang, 1948; *L. (L.) harveyi* Wells, 1963; *L. (L.) elongatus* Drzycimski, 1967; *L. (L.) dubatyi* Soyer, 1974; *L. (L.) abyssalis* Becker, Noodt & Schriever, 1979; *L. (L.) platyspinosus* Mielke, 1984; *L. (L.) punctatus* Mielke, 1984; *L. (L.) celticus* Bodin & Jackson, 1987; *L. (L.) pundius* sp. n.; and *L. (L.) koreanus* sp. n.

***Leptopsyllus (Leptopsyllus) pundius* sp. n.**

<http://zoobank.org/D56A6D69-3919-4719-899A-889C1023E935>

Figs 1–4

Type locality. Republic of Korea, Pung Island (Korean name Pungdo): subtidal zone, 37°5'21.46"N, 126°24'27.10"E (depth: 30 m, sand).

Materials examined. Holotype 1♀ (MABIK CR00235287) dissected on four slides. Sampled by a grab on a fishing boat on 16 Feb 2008.

Diagnosis. Description of female. Total body length 390 µm (Fig. 1A); largest width measured at posterior margin of cephalic shield: 67 µm; body cylindrical, slightly depressed dorsoventrally; urosome gradually tapering posteriorly; whole body very hyaline. Rostrum triangular, fused with cephalic shield; with 2 small sensilla. Cephalothorax bell-shaped; pleural areas weakly developed and posterolateral angles rounded; posterior margin smooth, without distinct hyaline frill.

Genital field located mid-ventrally halfway the length of the genital double-somite; copulatory pore located near posterior border of genital field and covered by small process (Fig. 2D); P6 represented by transverse plate with 1 bare seta (Fig. 2D); penultimate somite with well-developed pseudoperculum; anal operculum not developed.

CR (Fig. 1C). Parallel, about 2.7–3.0-times as long as greatest width, conical, distal margin blunt; each ramus armed with 6 setae (seta I not observed and probably vestigial); seta II bare; setae III stout, bearing spinule-like elements; seta IV pinnate; seta V pinnate, longest; seta VI shortest and pinnate; seta VII bi-articulate at base and arising from inner dorsal surface.

A1 (Fig. 2A). 8-segmented, short, robust; seg-1 longest; seg-4 sub-cylindrical process armed with long slender seta fused basally to aesthetasc; seg-6 armed with 1 slender bare seta arising from ventral sub-cylindrical process; armature formula: 1–[1 pinnate], 2–[8 bare + 1 pinnate], 3–[5 bare + 2 pinnate], 4–[2 bare + (1 + ae)], 5–[1 bare], 6–[3 bare], 7–[2 bare], 8–[5 bare + acrothek]; apical acrothek consisting of well-developed aesthetasc fused basally to 2 slender, naked setae.

A2 (Fig. 2B). 4-segmented, comprising coxa, basis, and free 2-segmented enp; coxa small and bare; basis approximately 2.2 times as long as maximum width, without

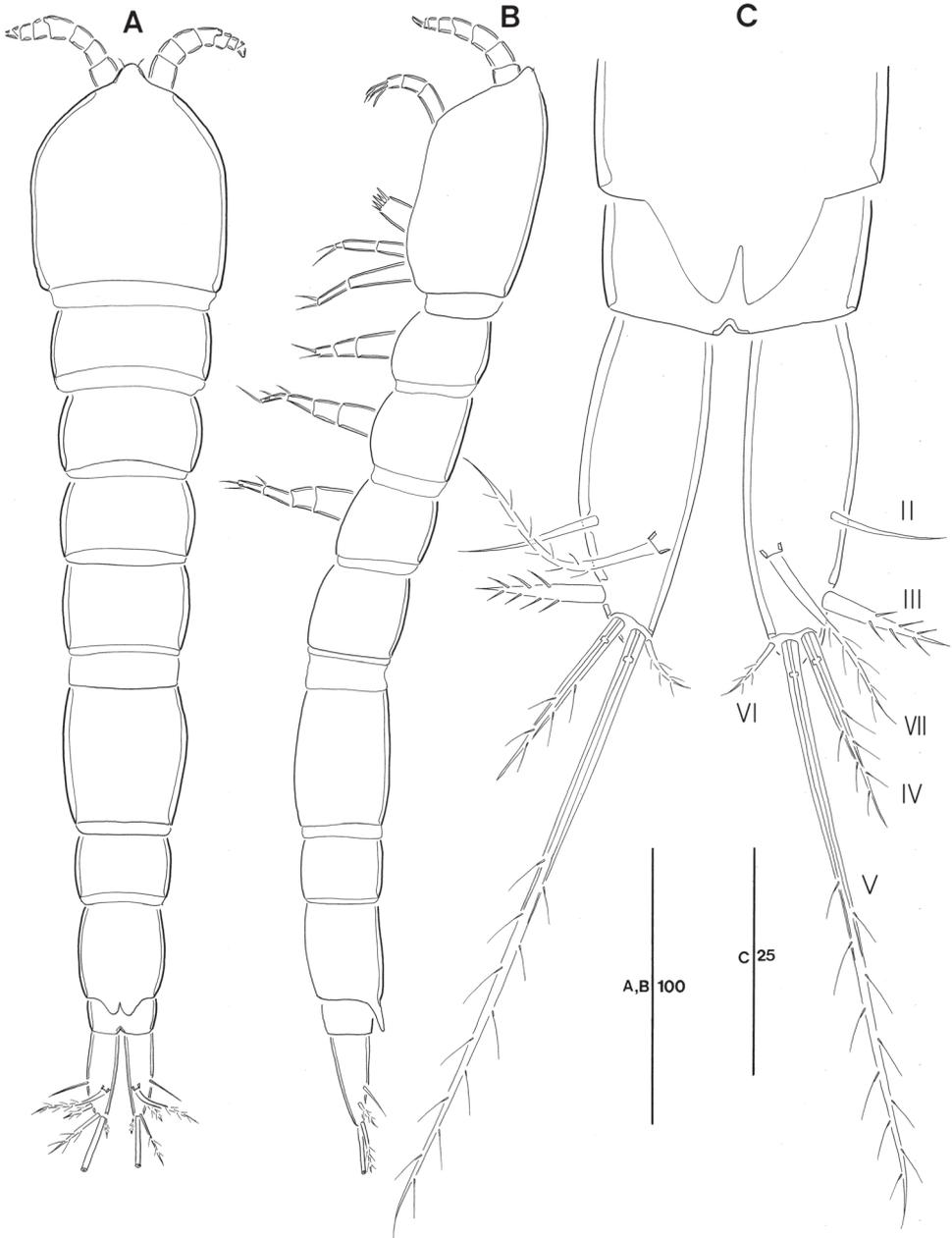


Figure 1. *Leptopsyllus (Leptopsyllus) pundius* sp. n. (♀). **A** habitus, dorsal **B** habitus, lateral **C** pseudopericulum, anal somite, and caudal rami, dorsal. Scale bars are in microns.

any surface ornamentation; exp 1-segmented, with 2 lateral bare and 2 distal modified setae; proximal endopodal segment with 1 pinnate abexopodal seta; distal endopodal segment armed with 2 bare short spines laterally, 1 naked and 2 spine-like setae in

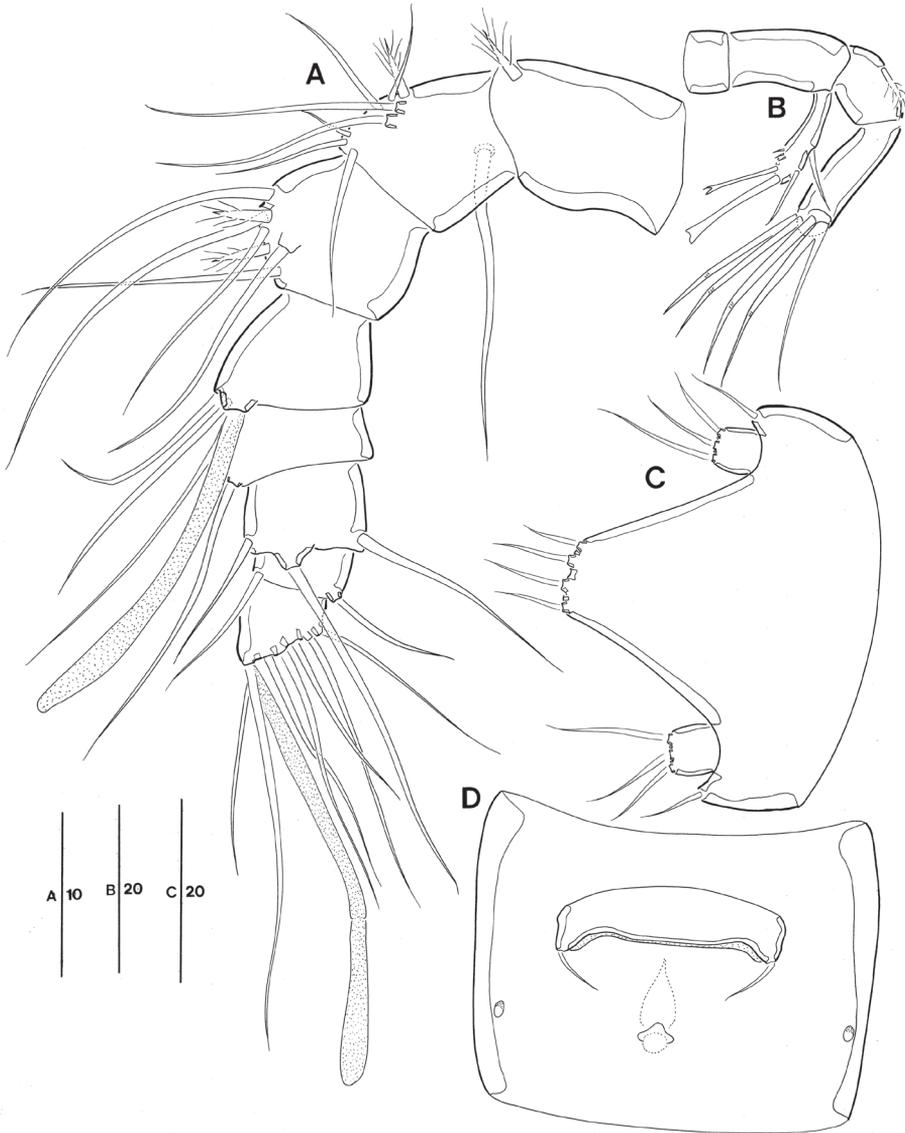


Figure 2. *Leptopsyllus (Leptopsyllus) pundius* sp. n. (♀). **A** antennule **B** antenna **C** P5 **D** P6 and genital field. Scale bars are in microns.

middle of segment, 3 geniculate setae around distal margin, and 1 longest geniculate seta fused at base with 1 bare seta.

Mandible (Fig. 3A). Coxa with well-developed gnathobase bearing 1 pinnate seta at dorsal corner and 6 major spinous overlapping teeth; palp biramous, comprising basis, 1-segmented exp and 2-segmented enp; basis widening distally, with 3 bare setae; exp with 2 distal setae; enp long; enp-1 same as long as exp, with 2 bare setae; enp-2 with 5 basally fused setae at apex.

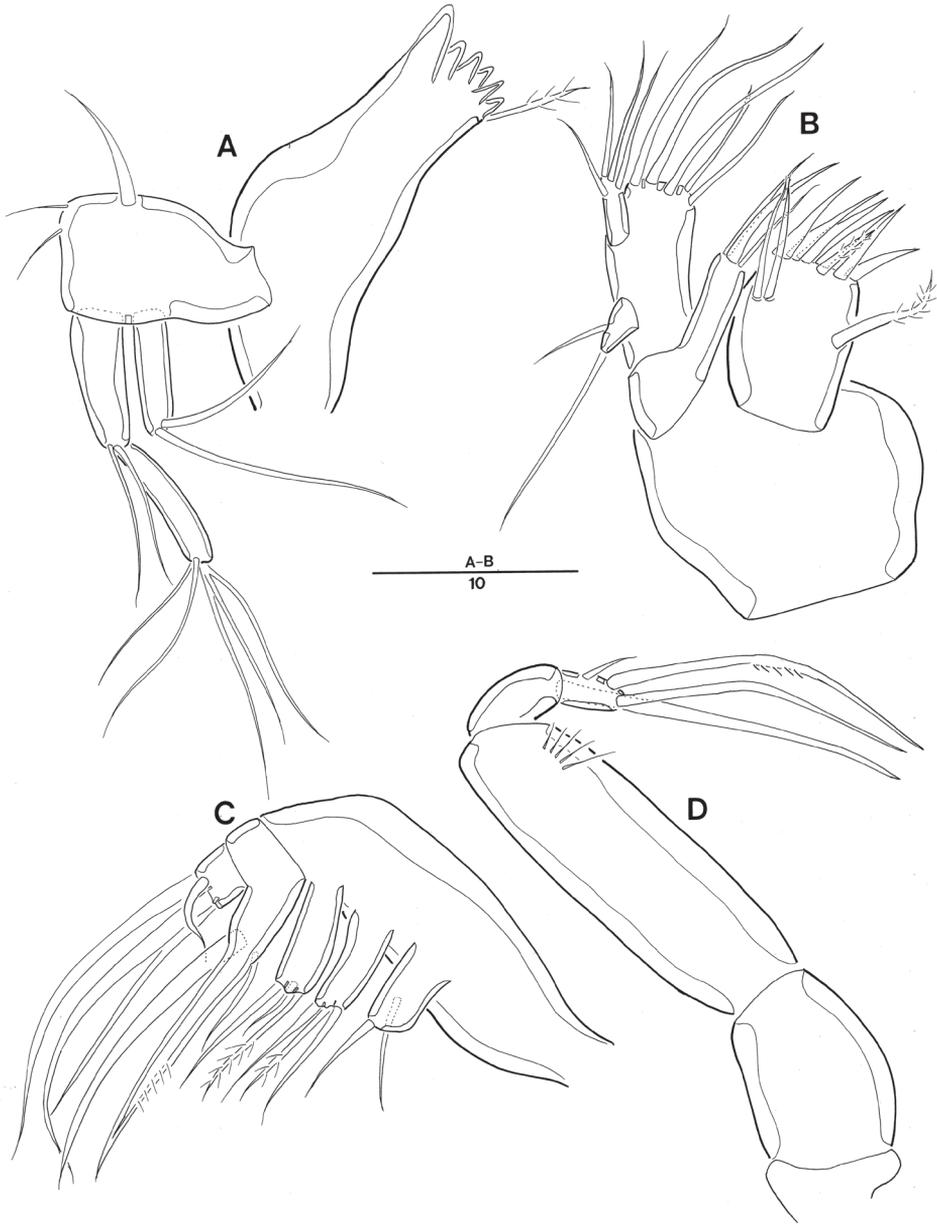


Figure 3. *Leptosyllus* (*Leptosyllus*) *pundius* sp. n. (♀). **A** mandible **B** maxillule **C** maxilla **D** maxilliped. Scale bars are in microns.

Maxillule (Fig. 3B). Praecoxal arthrite well-developed, with 6 spines, 2 pinnate setae, and 2 juxtaposed slender setae; coxa with cylindrical endite bearing 3 distal bare setae; basis cylindrical; endites fused, collectively bearing 5 distal bare setae; exp 1-segmented, small, with 2 bare setae; enp 1-segmented, with 4 bare setae distally.

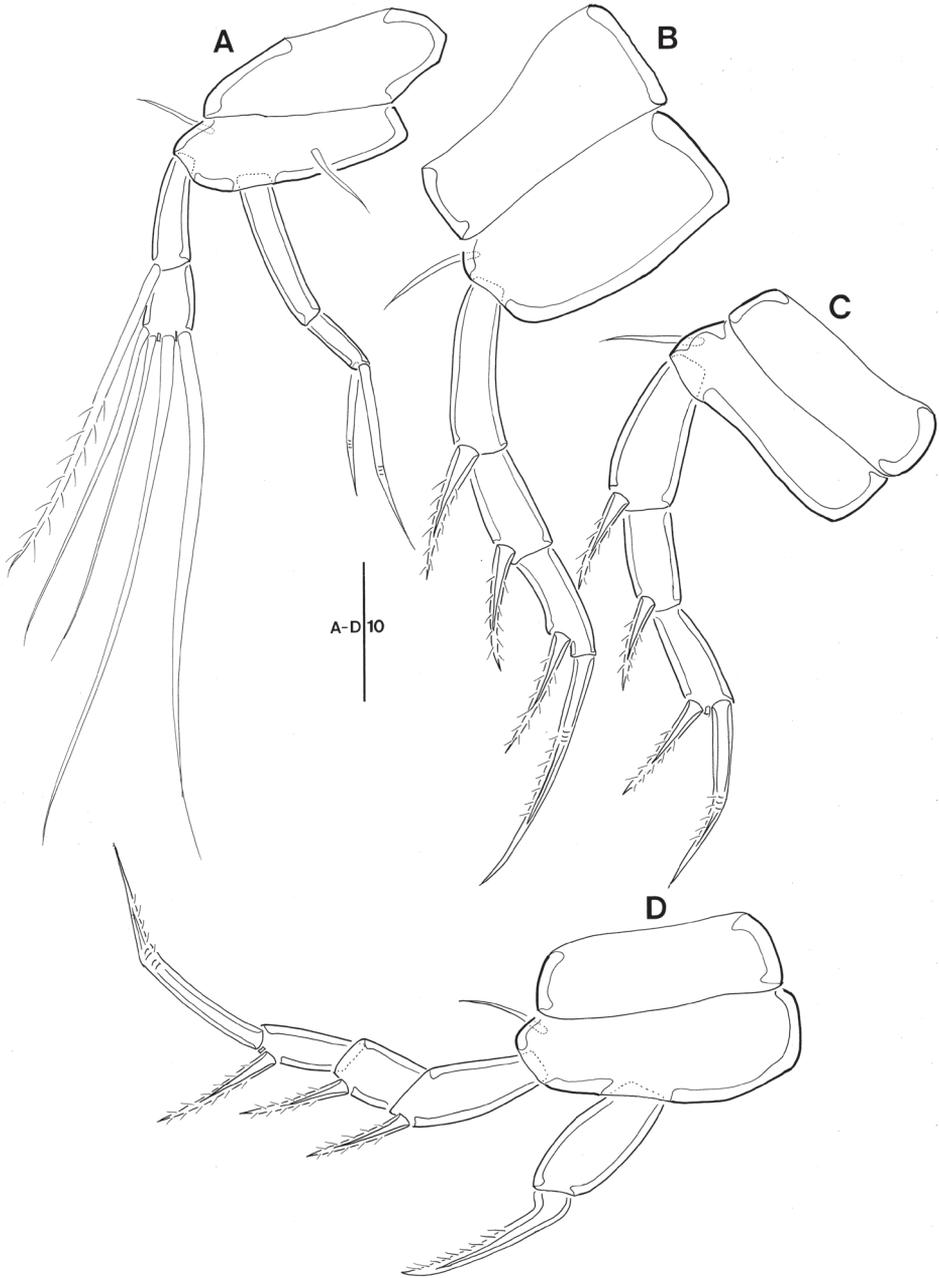


Figure 4. *Leptopsyllus (Leptopsyllus) pundius* sp. n. (♀). **A** P1 **B** P2 **C** P3 **D** P4. Scale bars are in microns.

Maxilla (Fig. 3C). Syncoxa with 3 cylindrical endites; praecoxal endite with 2 bare setae; proximal and distal coxal endite with 1 pinnate and 2 bare setae each; allobasis with 2 strong claws and 1 bare seta; enp 1-segmented, with 5 bare setae apically.

Maxilliped (Fig. 3D) comprising syncoxa, basis and 2-segmented enp; syncoxa without element; basis with 1 row of spinules sub-distally; enp-1 with 1 stout seta on distal margin; enp-2 with 1 bare and 2 geniculate setae.

P1 (Fig. 4A). Coxa bare; basis with 1 bare seta on proximal inner margin and 1 small bare outer seta; exp shorter than enp; exp-1 about 1.6 times longer than exp-2, with 1 pinnate seta near outer distal corner; exp-2 with 4 long bare setae distally; enp-1 unornamented, elongate, and approximately 2.3 times as long as enp-2; enp-2 small, with 2 geniculate setae apically.

P2, P3 (Fig. 4B, C). Coxa bare; basis without any surface ornamentation; outer margin with 1 bare seta; exp 3-segmented; exp-1 and -2 with 1 outer pinnate spine; exp-3 with 1 pinnate outer spine and 1 geniculate seta; enp absent.

P4 (Fig. 4D). Coxa bare; basis with 1 bare seta; exp 3-segmented; exp-1 and -2 with 1 outer spine; exp-3 with 1 outer spine and 1 geniculate seta; enp as long as exp-1, with 1 strong spine distally.

Armature formula as follows:

	Exopod	Endopod
P1	0.022	0.020
P2	0.0.011	
P3	0.0.011	
P4	0.0.011	010

P5 (Fig. 2C) with medially fused baseoendopods and discrete exps; baseoendopod with 1 basal seta; endopodal lobes elongate, closely pressed to each other, with 2 bare apical setae each; exp small, with 3 bare setae, innermost one longest.

Description of male. Unknown.

Etymology. The specific name refers to the type locality of the new species, Pung Island, Korea.

***Leptosyllus (Leptosyllus) koreanus* sp. n.**

<http://zoobank.org/98FAF7F8-CC51-4EAF-9D2D-6EF13672A363>

Figs 5–8

Type locality. Republic of Korea, Maemul Island (Korean name : Maemuldo), subtidal zone off 37° 37'43.38"N, 128° 46'24.51"E (depth: 50 m, muddy sand).

Material examined. Holotype 1♂ (MABIK CR00235288) dissected on four slides. Sampled by a grab on a fishing boat on 23 Feb 2011.

Diagnosis. Description of female. Unknown.

Description of male. Total body length 575 µm; largest width measured at posterior margin of cephalic shield: 105 µm (Fig. 5A); body cylindrical and slightly depressed dorsoventrally; urosome gradually tapering posteriorly; sensilla present as illustrated in Fig. 5A–C; body somites connected by well-developed arthrodial membranes. Rostrum small, fused with cephalic shield; with 2 sensilla (Fig. 5D). Cepha-

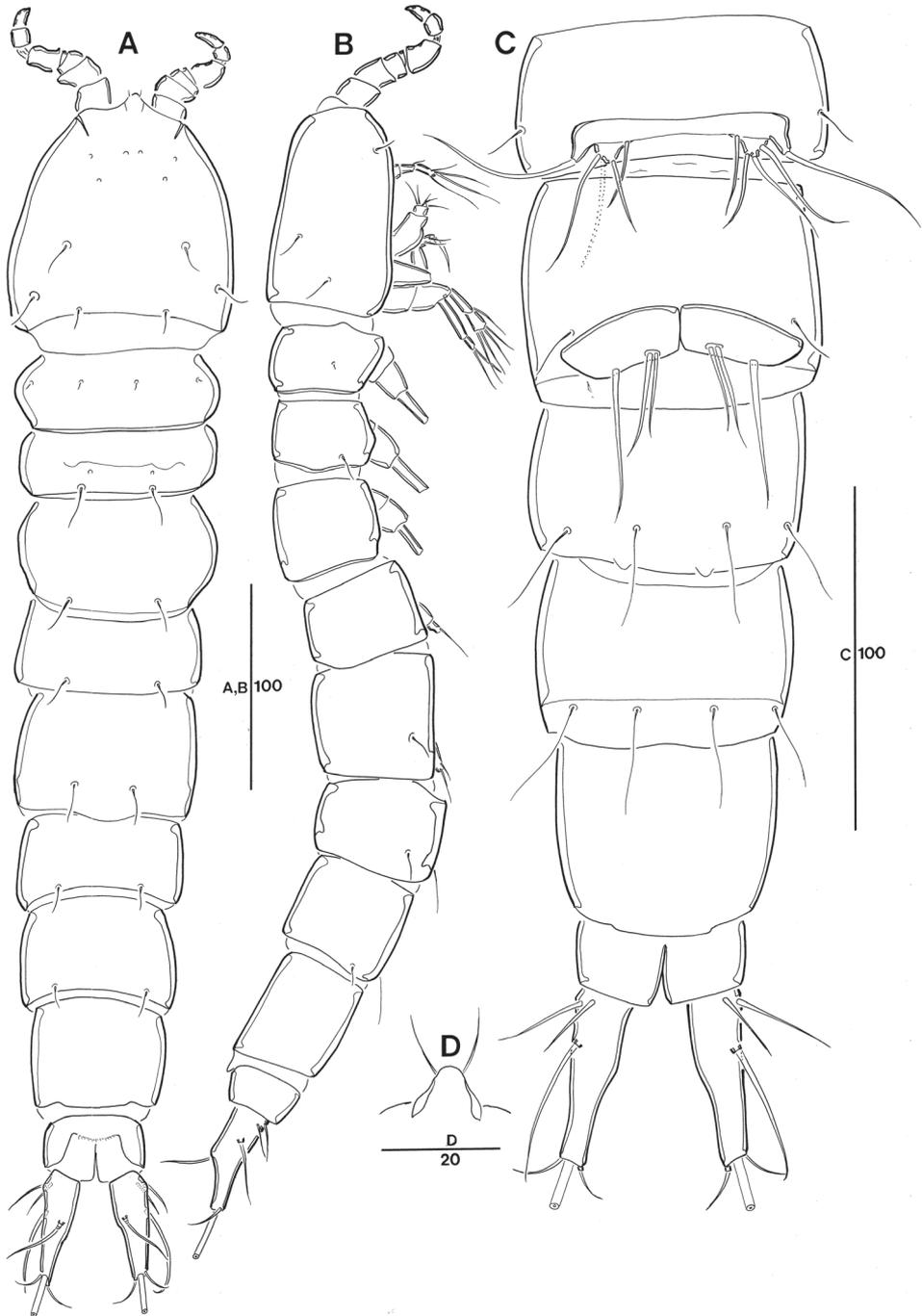


Figure 5. *Leptopsyllus (Leptopsyllus) koreanus* sp. n. (♂). **A** habitus, dorsal **B** habitus, lateral **C** urosome, ventral **D** rostrum. Scale bars are in microns.

lothorax (Fig. 5A, B) bell-shaped, smooth posterior margin, with few sensilla; pleural areas weakly developed and posterolateral angles rounded; posterior margin smooth, without distinct hyaline frill. Anal somite (Figs 5A, 6A₁) with developed spinulose operculum.

CR (Fig. 6A₁, A₂). Parallel, about 3.1-times as long as greatest width, conical, distal margin rounded; each ramus armed with 7 setae; seta I bare, situated rather ventrally; setae II and III bare, situated laterally; seta IV shortest, bare; seta V longest, about 3 times as long as the caudal ramus; seta VI bare, composite, consisting of proximal process and distal seta; setae IV–VI displaced onto dorsal surface of ramus; seta VII tri-articulate at base and arising from inner dorsal surface.

A1 (Fig. 6B₁–B₅) 7-segmented, short, robust, subchirocer; seg-1 with row of spinules along sub-distal margin; seg-5 swollen; armature formula: 1–[1 bare], 2–[9 bare + 1 pinnate], 3–[7 bare + 1 pinnate], 4–[2 bare], 5–[9 bare + 2 pinnate + (1 + ae)], 6–[2 bare], 7–[12 bare + 1 pinnate]; visible apical acrothek not present.

A2 (Fig. 6C₁, C₂) 4-segmented, comprising coxa, basis, 2-segmented enp, and 1-segmented exp; coxa small and bare; basis approximately 3.1-times as long as maximum width, ornamented with row of spinules along inner margin; exp inner distal corner forming spinous projection with 2 lateral and 2 distal naked setae; proximal endopodal segment with 1 pinnate abexopodal seta; distal endopodal segment ornamented with 2 rows of spinules horizontally, with 2 spine-like setae, 1 pinnate seta sub-apically (Fig. 6C₂), 4 geniculate setae around distal margin, and 1 longest geniculate seta fused at base with 1 longest seta.

Mandible (Fig. 7A₁, A₂). Coxa with well-developed gnathobase bearing 1 bare seta at the dorsal corner and 6 overlapping teeth; palp biramous, comprising basis, 1-segmented exp and enp; basis with 1 pinnate seta and ornamented with row of spinules near base of seta; exp small, with 2 bare setae; enp long with 2 lateral setae in middle and 5 basally fused setae at apex.

Maxillule (Fig. 7B). Praecoxal arthrite well-developed, with 7 spines, 1 pinnate seta, and 2 juxtaposed slender setae on anterior surface; coxa with cylindrical endite bearing 1 claw and 2 naked setae; basis cylindrical; endites fused, with 5 naked setae; exp 1-segmented, small, with 2 pinnate setae; enp 1-segmented, elongate, rectangular, with 6 naked setae around apex.

Maxilla (Fig. 7C). Syncoxa with 3 endites; praecoxal endite with 1 pinnate and 1 naked setae; proximal and distal coxal endite with 3 naked setae; allobasis with 1 uni-pinnate strong claw, 1 bare claw, 1 accessory seta, and 1 bare seta near base of enp; enp 2-segmented; enp-1 with 2 bare setae; enp-2 with 3 bare setae apically.

Maxilliped (Fig. 7D) 3-segmented, comprising syncoxa, basis and 1-segmented endopod; syncoxa with 1 bare seta; elongate basis ornamented with 3 spinules in middle; enp 2.5 times as long as wide, with 2 naked seta laterally, 1 apical seta, 1 curved stout claw, and 1 accessory on claw.

P1 (Fig. 8A). Basis without outer seta, with 1 bare seta on proximal inner margin; exp shorter than enp; exp-1 with 1 long uni-pinnate seta near outer distal corner, ornamented with row of spinules along outer margin and with long spinules on inner

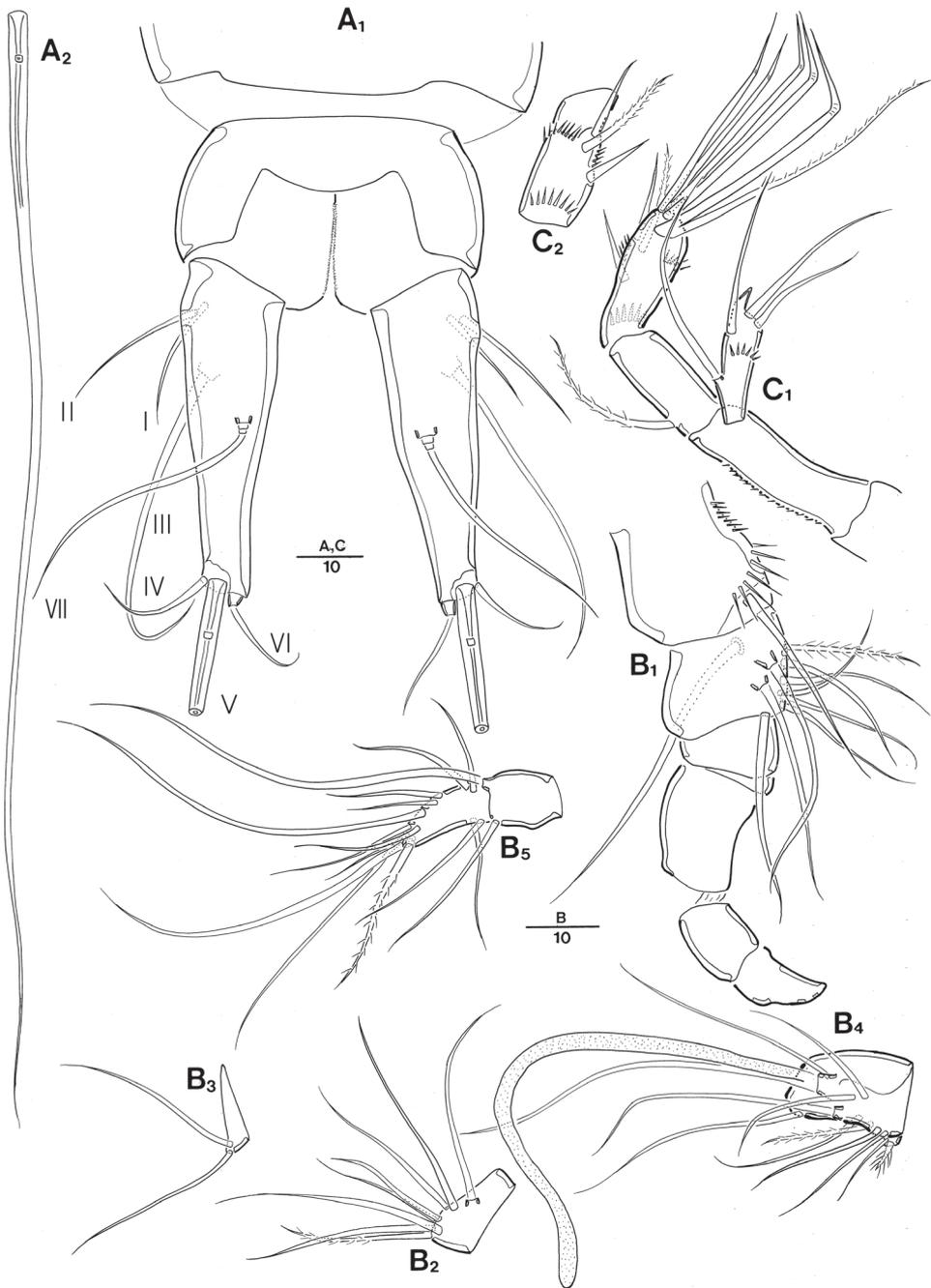


Figure 6. *Leptopsyllus (Leptopsyllus) koreanus* sp. n. (♂). **A₁**, anal somite and caudal ramus, dorsal **A₂**, seta V **B₁**, segments-1 and -2 of antennule **B₂**, segment-3 **B₃**, segment-4 **B₄**, segment-5 **B₅**, segments-6 and -7 **C₁**, antenna **C₂**, endopod-2 of antenna, lateral. Scale bars are in microns.

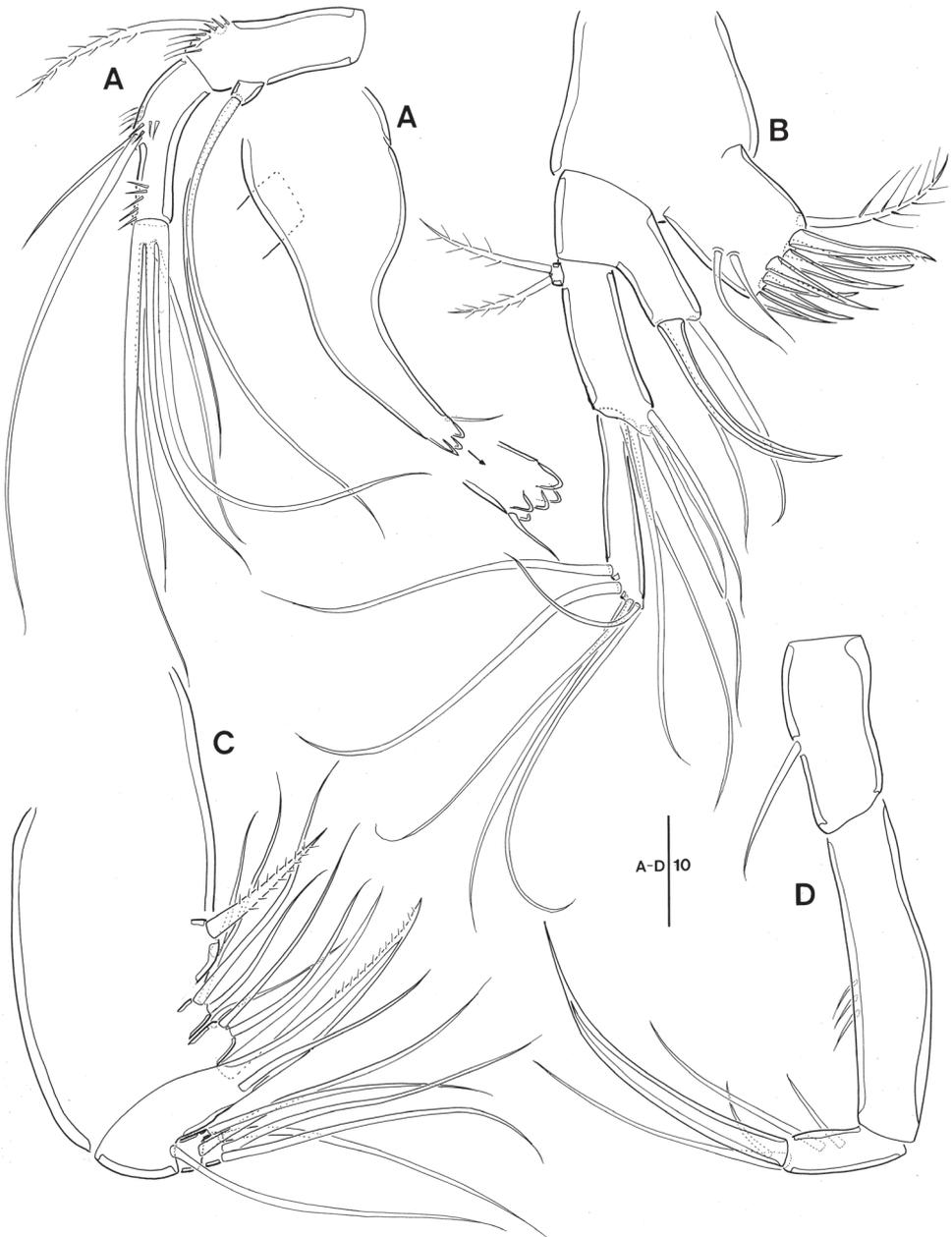


Figure 7. *Leptopsyllus (Leptopsyllus) koreanus* sp. n. (♂). **A₁** gnathobase of mandible **A₂** mandibular palp **B** maxillule **C** maxilla **D** maxilliped. Scale bars are in microns.

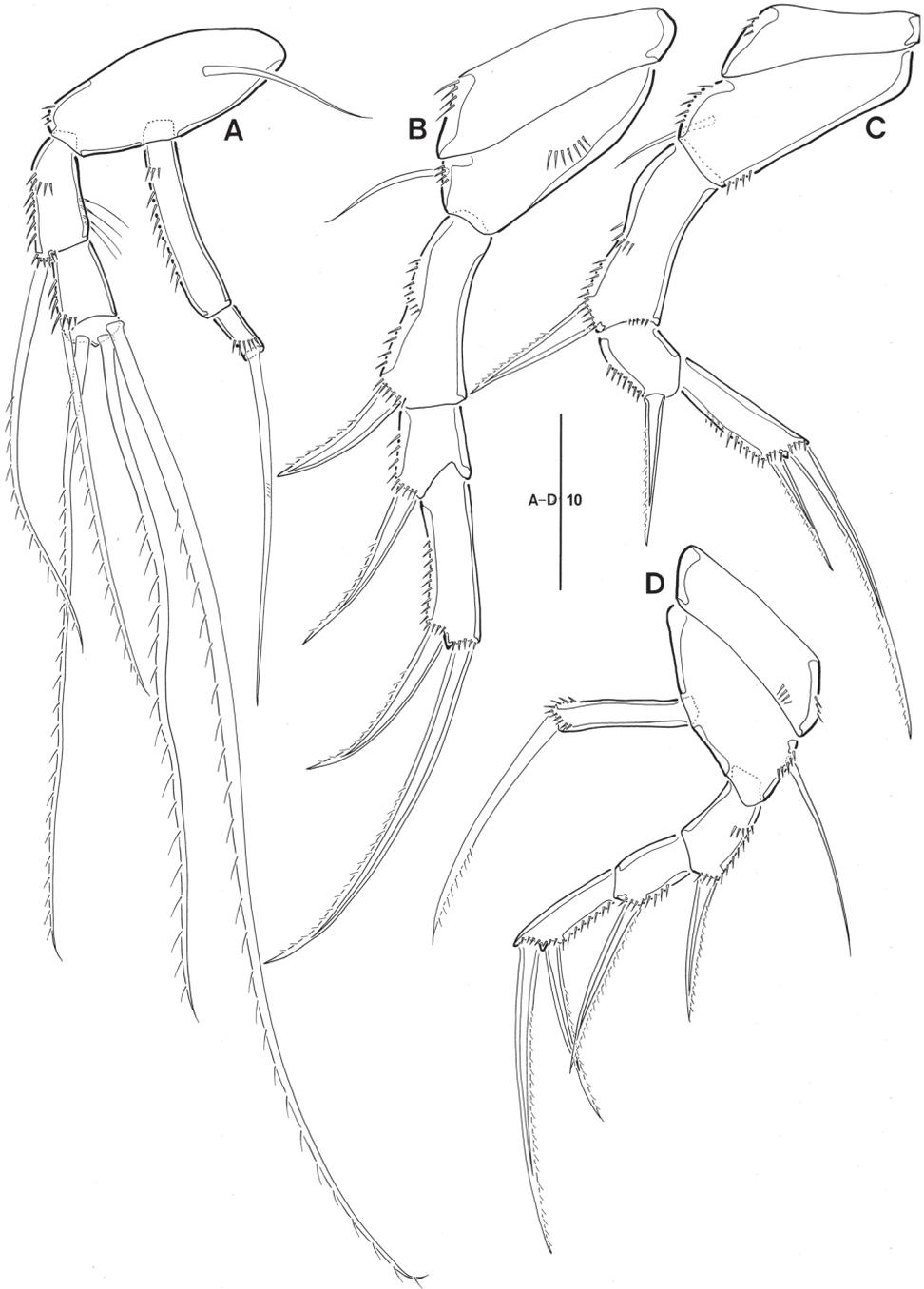


Figure 8. *Leptosyllus (Leptosyllus) koreanus* sp. n. (♂). **A** P1 **B** P2 **C** P3 **D** P4. Scale bars are in microns.

margin; exp-2 with 4 long uni-pinnate setae; enp-1 elongate and approximately 3.5 times as long as enp-2 and ornamented with row of spinules along outer margin; enp-2 small, with 1 geniculate seta.

P2, P3 (Fig. 8B, C). Coxa ornamented with rows of spinules as figured; basis with 1 outer bare seta and ornamented with row of spinules on inner and outer margin; exp 3-segmented; exp-1 longest, with 1 outer uni-pinnate spine; exp-2 shortest, with 1 outer uni-pinnate spine; exp-3 sub-rectangular, with 2 pinnate spines; enp absent.

P4 (Fig. 8D). Coxa ornamented with 2 rows of spinules; basis with 1 outer seta; exp 3-segmented; exp-1 and -2, with 1 outer uni-pinnate spine; exp-3 with 2 uni-pinnate spines; enp represented by elongate segment with 1 spine-like seta.

Armature formula as follows:

	Exopod	Endopod
P1	0.022	010
P2	0.0.011	
P3	0.0.011	
P4	0.0.011	010

P5 (Fig. 5C). Exopod and baseoendopod not fused; baseoendopod with 1 outer basal seta, endopodal lobes confluent with 1 seta each; exp small, triangular, with 3 naked setae.

P6 (Fig. 5C) symmetrical, with 2 bare setae arising from small protrusion on inner part of P6, and 1 outer longest bare seta.

Etymology. The specific name refers to the type locality of the new species in Korea.

Discussion

General status and zoogeography of the genus *Leptopsyllus* T. Scott, 1894

Since the genus *Leptopsyllus* was proposed by Scott T (1894) based on the reduction of legs, several species have been described in *Leptopsyllus*. Though many species were originally assigned to the genus *Leptopsyllus*, some of them were moved to new genera according to new classifications based on leg characteristics (reduced or absent). Boxshall and Halsey (2004) proposed the number of species in each genus and the key to genera based on Kunz (1981), Huys (1987), and Cottarelli and Forniz (1994). As a result, the genus *Leptopsyllus* currently consists of 13 valid species including the two new species described in this study. However, the complete descriptions of mouthparts are lacking for many species, because of the small body size of these organisms. In addition, the abundant of species in *Leptopsyllus* is usually low. Unfortunately, we founded only one female of *L. (L.) pundius* sp. n. and one male of *L. (L.) koreanus* sp. n. during the study.

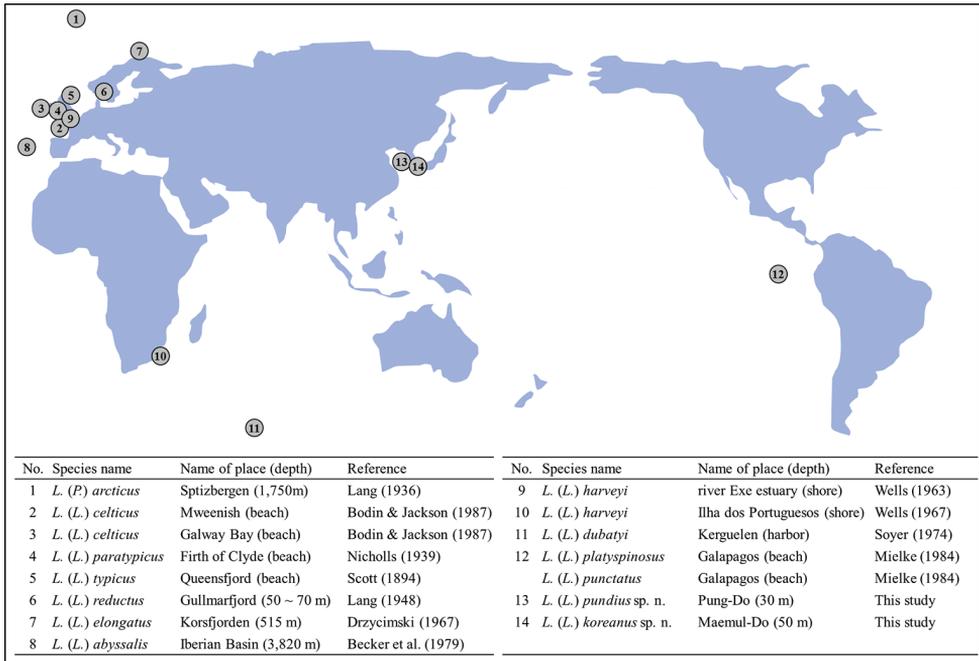


Figure 9. Distribution of genus *Leptopsyllus* and number of specimens based on original papers.

Until now, many species belonging to genus *Leptopsyllus* have been found mainly in Europe in Atlantic Ocean (Fig. 9). Most species are distributed along the coast including islands intertidal zone, but three species, *Leptopsyllus (Paraleptopsyllus) arcticus* (Lang, 1936), *L. (L.) elongates* Drzycimski, 1967, and *L. (L.) abyssalis* Becker, Noodt & Schriever, 1979, were collected from deep sea (deeper than 200 m). Belonging to the family Paramesochridae, species of *Leptopsyllus* are well known for living in sandy bottom, however, some species were found in muddy sediment (Lang, 1948; Drzycimski, 1967; Plum and George, 2009). In this study, *L. (L.) pundius* sp. n. is found in the sandy sediment, while *L. (L.) koreanus* was collected from muddy sand sediment. In conclusion, species belonging to the genus *Leptopsyllus* are thought to inhabit a variety of sediments and depths.

Relationships between two new species and their congeners

The two new species are placed in the genus *Leptopsyllus* T. Scott, 1894 based on the absence of an endopod on P2 and P3, P4 endopod armed with one apical seta, and presence of two setae/spines on the distal segments of the exopods on P2–P4. The two new species are placed in subgenus *Leptopsyllus* on account of the absence of P3 endopod because the discrepancy in the diagnostic characters between the subgenera *Leptopsyllus* T. Scott, 1894, and *Paraleptopsyllus* Lang, 1944 is presence or not of P3 endopod.

Table 1. Morphological characters of *Leptopsyllus* (*Leptopsyllus*). Four groups were distinguished by the feature of the female P5.

Group	Species name	Body Size Female (Male)	A2 No. of exp seg. (total No. of setae)	Swimming legs										P5	
				P1	P2		P3		P4			Exp. separation	Benp. develope (No. of setae)		
				Exp-2	Exp-1	Exp-2	Exp-2	Exp-2	Exp-3	Exp-1	Exp-2				
1	<i>abyssalis</i>	730	1(5)	011	0	021	021	021	·	010	·	F	N(0)		
	<i>reductus</i>	500	?(4)	011	0	0	0	?	?	0	010	F	N(0)		
2	<i>plainspinosus</i>	400–440 (360)	1(4)	011	0	0	0	0	0	011	·	S	N(0)		
	<i>celticus</i>	380–400	1(4)	011	0	1	1	0	021	010	·	F	D(2)		
3	<i>dubatyi</i>	400–445	2(4)	011	0	0	0	0	011	010	·	S	D(0)		
	<i>harveyi</i>	420	1(3)	011	0	0	0	0	021	010	·	S	D(0)		
4	<i>punctatus</i>	290–390 (280–380)	1(4)	011	0	0	0	0	011	010	·	S	D(2)		
	<i>typicus</i>	700	1(4)	011	?	?	0	0	011	0	010	S	D(2)		
Unknown	<i>pundius</i> sp. n.	390	1(4)	011	0	0	0	0	011	010	·	S	D(2)		
	<i>elongatus</i>	(900)	1(5)	010	0	0	0	0	011	010	·	?	?		
Unknown	<i>paratypicus</i>	(360)	1(4)	011	1	1	1	0	011	010	·	male only	male only		
	<i>koreanus</i> sp. n.	(575)	1(4)	010	0	0	0	0	011	010	·	male only	male only		

* No.: number, seg.: segment, S: separated, F: fused, D: developed, N: not developed, Unknown : P5 of female were not described in the species of the group

Leptopsyllus (*L.*) *pundius* sp. n. is closely related to *L.* (*L.*) *punctatus* Mielke, 1984 based on combination of three characters: (1) body length, (2) one segment of A2 exopod with 4 setae, (3) P5 exopod separated with the baseoendopod, and 4) the baseoendopod well developed armed with 2 setae (Table 1). However, *L.* (*L.*) *pundius* sp. n. can be differentiated from the congener by (1) the one-segmented mandibular exopod armed with two setae; whereas *L.* (*L.*) *punctatus* has four setae on the exopod of the mandible (Table 1), (2) P6 with one element, and (3) caudal seta III is stout, decorated with spinules. In addition, the structure of the rostrum with a pair of small sensillae of the new species is also unique character in the genus *Leptopsyllus*. Several species, (*Caligopsyllus primus* Kunz, 1975, *Diarthrodella ergeneae* Sonmez, Karaytug & Sak, 2015, *Emertonia clausi* Pointer & Veit-Köhler, 2013, *L.* (*L.*) *punctatus*, *L.* (*L.*) *pundius* sp. n.; *L.* (*L.*) *koreanus* sp. n., and *Scottopsyllus* (*S.*) *praecipuus* Veit-Köhler, 2000) in Paramesochridae have a couple of sensillae on the rostrum. However, rostrum structure in other congeners of the genus *Leptopsyllus* was ignored or is unknown due to the small size of these species.

The description of *L.* (*L.*) *koreanus* sp. n. is based on a single male specimen. Although we are not able to compare *L.* (*L.*) *koreanus* sp. n. with its congeners based on female characters, the new species has clear morphological differences from its congeners: (1) single seta on the second segment of the P1 endopod; only one species in the subgenus *Leptopsyllus*, *L.* (*L.*) *elongates* Drzycimski, 1967, shares this character with *L.* (*L.*) *koreanus*, (2) a single seta on the baseoendopod of P5 in male; this is a unique character in the subgenus *Leptopsyllus*, and (3) one-segmented endopod of the mandibular palp; *L.* (*L.*) *koreanus* sp. n. shares this character with *L.* (*L.*) *platypinosus* Mielke, 1984. The caudal ramus in the genus *Leptopsyllus* is conical and its distal margin is bluntly pointed; however, caudal seta formula varies among congeners. *Leptopsyllus* (*L.*) *koreanus* sp. n. clearly has caudal seta I, although this seta is obscure in other congeners. Both new species have a tri-articulated seta VII, while *L.* (*L.*) *punctatus* and *L.* (*L.*) *platypinosus* have a bi-articulated seta VII arising from a chitinous outgrowth on the dorsal surface. However, the caudal rami and setae of other species in *Leptopsyllus* have not been described in detail in other previous studies.

Four distinctive groups within the genus *Leptopsyllus* can be recognized based on the shape of the female P5 (Table 1): (1) the exopod and baseoendopod fused without developed baseoendopodal lobes (*L.* (*L.*) *abyssalis* Becker, Noodt & Schriever, 1979 and *L.* (*L.*) *reductus* Lang, 1948), (2) the exopod and baseoendopod not fused, without developed endopodal lobes (*L.* (*L.*) *platypinosus*), (3) the exopod and baseoendopod fused, with developed endopodal lobe (*L.* (*L.*) *celticus* Bodin & Jackson, 1987), (4) the exopod and baseoendopod not fused, with developed endopodal lobes (*L.* (*P.*) *arcticus* (Lang, 1936), *L.* (*L.*) *typicus* T. Scott, 1894, *L.* (*L.*) *dubatyi* Soyer, 1974, *L.* (*L.*) *harveyi* Wells, 1963, *L.* (*L.*) *punctatus*, and *L.* (*L.*) *pundius* sp. n.). In the case of the seta formula of P5 exopod, all female species in the genus have three setae. Unfortunately, *Leptopsyllus* (*L.*) *elongatus*, *L.* (*L.*) *paratypicus* Nicholls, 1939, and *L.* (*L.*) *koreanus* sp. n. are cannot be assigned to any of the four groups because they have been described based on the male specimen. More studies will be necessary to prove the relationship among four groups including female and male P5.

Key to the species of the genus *Leptopsyllus*

The latest key proposed by Bodin & Jackson (1987) includes nine species of *Leptopsyllus*, and does not include the two species *L. (P.) arcticus* and *L. (L.) abyssalis*. Because only the males of some species have been described, the extent of sexual dimorphism in mouthparts or P1–P4 was not known. An updated key is developed on the basis of selected characteristics from the original description that identifies species within the genus *Leptopsyllus*.

- | | | |
|----|--|---|
| 1 | P3 endopod 1-segmented | (Subgenus <i>Paraleptopsyllus</i>) ... <i>L. (P.) arcticus</i> |
| – | P3 endopod absent | (Subgenus <i>Leptopsyllus</i>) ...2 |
| 2 | P2–P4 exopod 2-segmented..... | <i>L. (L.) abyssalis</i> |
| – | P2–P4 exopod 3-segmented..... | 3 |
| 3 | Distal segment of P1 endopod with 1 seta | 4 |
| – | Distal segment of P1 with 2 elements | 5 |
| 4 | A2 exopod with 5 setae; caudal ramus with 5 setae | <i>L. (L.) elongatus</i> |
| – | A2 exopod with 4 setae; caudal ramus with 7 setae ... | <i>L. (L.) koreanus sp. n.</i> |
| 5 | Middle segments of P2 and P3 exopod with 1 inner element..... | 6 |
| – | Middle segment of P2 and P3 exopod without inner element..... | 7 |
| 6 | Male exopod of P5 with 3 setae | <i>L. (L.) paratypicus</i> |
| – | Male exopod of P5 with 4 setae | <i>L. (L.) celticus</i> |
| 7 | A2 exopod 2-segmented..... | <i>L. (L.) dubatyi</i> |
| – | A2 exopod 1-segmented..... | 8 |
| 8 | A2 exopod with 3 setae | <i>L. (L.) harveyi</i> |
| – | A2 exopod with 4 setae | 9 |
| 9 | P5 endopodal lobe flattened..... | 10 |
| – | P5 endopodal lobe well developed | 11 |
| 10 | P5 exopod separated, caudal seta III modified..... | <i>L. (L.) platyspinosus</i> |
| – | P5 exopod fused with baseoendopod | <i>L. (L.) reductus</i> |
| 11 | Each P5 baseoendopodal lobe divided in middle; P1 exp-1 with 2 outer setae..... | <i>L. (L.) typicus</i> |
| – | Each P5 baseoendopodal lobe without median incision; P1 exp-1 with 1 outer seta | 12 |
| 12 | Caudal seta III stout and decorated with spinules defined at base; each side of P6 with 1 seta | <i>L. (L.) pundius sp. n.</i> |
| – | Caudal seta III cylindrical, decorated with long spinules; each side of P6 with 3 setae..... | <i>L. (L.) punctatus</i> |

Acknowledgements

This research was supported by Securement, Analysis and Evaluation of Marine Invertebrate Bioresources (MABIK 20w17M00600) sponsored by the National Marine Biodiversity Institute of Korea.

References

- Back J, Lee W (2014) Two new species of the genus *Wellsopsyllus* (Copepoda; Harpacticoida; Paramesochridae) from the Yellow Sea. *Zootaxa* 3895: 346–366. <https://doi.org/10.11646/zootaxa.3895.3.2>
- Back J, Lee W, Huys R (2011) A new species of *Remanea* Klie, 1929 (Copepoda: Harpacticoida: Paramesochridae) with a redescription of the type species. *Journal of Natural History* 45: 2939–2964. <https://doi.org/10.1080/00222933.2011.622057>
- Becker KH, Noodt W, Schriever G (1979) Eidonomie und Taxonomie abyssaler Harpacticoida (Crustacea, Copepoda) Teil II. Paramesochridae, Cylindropsyllidae und Cletodidae. *Meteor Forsch-Erg* 31: 1–37.
- Bodin P, Jackson D (1987) A new species of *Leptopsyllus* (Copepoda: Harpacticoida: Paramesochridae) from northern Brittany and the west coast of Ireland, with a key to the genus. *Proceedings of the Royal Irish Academy* 87B: 93–99.
- Boxshall GA, Halsey SH (2004) An introduction to copepod diversity. The Ray Society, London, 2000 pp.
- Burgess R (2001) An improved protocol for separating meiofauna from sediments using colloidal silica sols. *Marine Ecology Progress Series* 214: 161–165. <https://doi.org/10.3354/meps214161>
- Costello MJ, Coll M, Danovaro R, Halpin P, Ojaveer H, Miloslavich P (2010) A Census of marine biodiversity knowledge, resources, and future challenges. *Plos One* 5: e12110. <https://doi.org/10.1371/journal.pone.0012110>
- Cottarelli V, Forniz C (1994) *Meiopsyllus marinae*: a new genus and a new species of Paramesochridae from the meiobenthos of Asinara and S. Pietro Islands (Sardinia). *Annali Museo Civico Storia Naturale Giacomo Doria* 90: 577–589.
- Drzycimski I (1967) Zwei neue Harpacticoida (Copepoda) aus dem westnorwegischen Küstengebiet. *Sarsia* 30: 75–82. <https://doi.org/10.1080/00364827.1967.10411103>
- Huys R (1987) *Paramesochra* T. Scott 1892 (Copepoda, Harpacticoida): a revised key, including a new species from the SW Dutch coast and some remarks on the phylogeny of the Paramesochridae. *Hydrobiologia* 144: 193–210. <https://doi.org/10.1007/BF00005554>
- Huys R (2009) Unresolved cases of type fixation, synonymy and homonymy in harpacticoid copepod nomenclature (Crustacea: Copepoda). *Zootaxa* 2183: 1–99.
- Huys R, Gee JM, Moore CG, Hamond R (1996) Synopses of the British Fauna (New Series) No. 51. Marine and brackish water harpacticoid copepods, Part 1. Field Studies Council, Shrewsbury, 352 pp.
- Kunz H (1962) Revision der Paramesochridae (Crust. Copepoda). *Kieler Meeresforschungen* 18: 245–257.
- Kunz H (1981) Beitrag zur Systematik der Paramesochridae (Copepoda, Harpacticoida) mit Beschreibung einiger neuer Arten. *Mitteilungen aus dem Zoologischen Museum der Universität Kiel* 1: 1–33.
- Lang K (1936) Copepoda Harpacticoida. Swedish Antarctic Expedition 1901–1903, Further Zoological Results 3: 1–68.

- Lang K (1944) Monographie der Harpacticiden (Vorläufige Mitteilung). Almqvist & Wiksells, Uppsala, 39 pp.
- Lang K (1948) Monographie der Harpacticiden. Håkan Ohlsson, Lund, 2 vols, 1682 pp.
- Mielke W (1984) Interstitielle Fauna von Galapagos. XXXI. Paramesochridae (Harpacticoida). *Microfauna Marina* 1: 63–147.
- Nicholls AG (1939) Some newsand-dwelling copepods. *Journal of the Marine Biological Association of the United Kingdom* 23: 327–341. <https://doi.org/10.1017/S0025315400013928>
- Pointner K, Kihara TC, Glatzel T, Veit-Köhler G (2013) Two new closely related deep-sea species of Paramesochridae (Copepoda, Harpacticoida) with extremely differing geographical range sizes. *Marine Biodiversity* 43: 293–319. <https://doi.org/10.1007/s12526-013-0158-3>
- Plum C, George KH (2009) The paramesochrid fauna of the Great Meteor Seamount (North-east Atlantic) including the description of a new species of *Scottosyllus* (*Intermedosyllus*) Kunz (Copepoda: Harpacticoida: Paramesochridae). *Marine Biodiversity* 39: 265–289. <https://doi.org/10.1007/s12526-009-0022-7>
- Scott T (1894) Additions to the fauna of the Firth of Forth. Part VI. Reports of the Fishery Board for Scotland 12: 231–271.
- Song SJ, Park J, Kwon B-O, Ryu J, Khim JS (2012) Ecological checklist of the marine brackish-water harpacticoid copepod fauna in Korean waters. *Zoological Studies* 51: 1397–1410.
- Soyer J (1974) Harpacticoides (Crustacés Copépodes) de l'archipel de Kerguelen. 1. Quelques formes mesopsammiques. *Bulletin du Muséum National d'Histoire Naturelle, Zoologie* 168: 1169–1223.
- Wells JBJ (1963) Copepoda from the littoral region of the estuary of the River Exe (Devon, England). *Crustaceana* 5: 10–26. <https://doi.org/10.1163/156854063X00020>
- Wells JBJ (1967) The littoral Copepoda (Crustacea) of Inhaca Island, Mozambique. *Transactions of the Royal Society of Edinburgh* 67: 189–358. <https://doi.org/10.1017/S0080456800024017>
- Wells JBJ (2007) An annotated checklist and keys to the species of Copepoda Harpacticoida (Crustacea). *Zootaxa* 1568: 1–872.

New record for the genus *Platymessa* Mello-Leitão, 1941 in Colombia, with the description of a new species (Opiliones, Cosmetidae)

Conchita A. Pinzón-M.¹, Victor R. Townsend, Jr.², Neis Martínez-H.¹

1 Departamento de Biología, Universidad del Atlántico, Km 7 vía a Puerto Colombia, Barranquilla, Colombia

2 Department of Biology, Virginia Wesleyan College, 1584 Wesleyan Drive, Norfolk, Virginia 23502, USA

Corresponding author: Victor R. Townsend, Jr. (vtownsend@vwc.edu)

Academic editor: A. Kury | Received 29 November 2016 | Accepted 14 March 2017 | Published 3 April 2017

<http://zoobank.org/10A79215-338A-473E-B1D0-55D7000CCE6F>

Citation: Pinzón-M CA, Townsend VR Jr, Martínez-H N (2017) New record for the genus *Platymessa* Mello-Leitão, 1941 in Colombia, with the description of a new species (Opiliones, Cosmetidae). ZooKeys 665: 59–70. <https://doi.org/10.3897/zookeys.665.11371>

Abstract

The genus *Platymessa* Mello-Leitão, 1941 is represented by two species in the Andes of Colombia: *P. h-inscriptum* Mello-Leitão, 1941 and *P. ectroxantha* Mello-Leitão, 1941. *Platymessa victoriae* Pinzón-M. & Townsend, **sp. n.** is described on the basis of somatic morphological characters and the structure of the penis. The placement of this new species in the genus *Platymessa* is based upon multiple characters including the outline of dorsal scutum, the presence of a blunt spine on coxa IV, having short and strong legs with femora III and IV having five longitudinal rows of small tubercles, the shape of the basitarsomeres of male leg I, the distribution and relative sizes of the marginal setae on the ventral plate of the penis, and the morphology of the chelicerae and cheliceral sockets. In contrast to other members of the genus, *P. victoriae* has a pair of triangular tubercles on scutal area III, lacks paired paramedian tubercles on scutal area V, and does not have a ladder mask color pattern on the dorsal scutum. The description of this species expands the distribution of the genus to north of the Oriental Cordillera in the Cesar Department of Colombia.

Keywords

Platymessa victoriae sp. n., Cesar Department, Colombia

Introduction

The family Cosmetidae Koch, 1839 is distributed from the southern U.S. to Argentina and with over 700 species, it is the second largest family of harvestman in the suborder Laniatores (Medrano and Kury 2016). Cosmetid harvestmen also are one of the best represented families of laniatorean harvestmen in the Neotropics (Kury and Pinto-da-Rocha 2007). The major distinguishing feature of cosmetid harvestmen is the lateral compression of the tibiae of the pedipalps that partially cover the chelicerae at rest (Pinto-da-Rocha 2011). The genus *Platymessa* Mello-Leitão, 1941 was originally diagnosed using characters based upon the Roewerian system, including the morphology of tarsus I and the ornamentation of the dorsal scutum. Two species were described from the Colombian Andes, *P. h-inscriptum* Mello-Leitão, 1941 and *P. nigrolimbata* Mello-Leitão, 1941. A third species, *P. transversalis*, was described by Roewer (1963) but has been subsequently transferred to the genus *Chusgonobius* Roewer, 1952 by Medrano and Kury (2016). Recently, Medrano and Kury (2016) used several characters to redescribe *Platymessa* including those based upon the shape of the dorsal scutum, the presence of a pair of paramedian granules on scutal area V, armature of coxa IV, and the morphology of the legs. Medrano and Kury (2016) also redescribed *P. h-inscriptum* as the type species of the genus and considered *P. nigrolimbata* as a junior synonym of *P. h-inscriptum*. In addition, Medrano and Kury (2016) transferred *Brachylibitia ectroxantha* Mello-Leitão, 1941 to the genus *Platymessa* proposing the new combination of *Platymessa ectroxantha*. In this paper, we propose the recognition of a third Colombian species in the genus *Platymessa* Mello-Leitão, 1941 on the basis of several characters including those based upon penis morphology. This is the first record of the genus for northern Colombia.

Methods

We examined 15 males and 28 females collected from the type locality (see below). Specimens were photographed with a Leica MC-120 HD digital camera attached to a Leica S8AP0 stereomicroscope and then processed with the software CombineZP. The illustrations were made with the aid of stereomicroscope with a camera lucida, Wild type 308700, Heerbrugg Switzerland. The illustrations of the penis were made from photographs taken with an optical Leica CME microscope and the software Inkscape version 0.91. The map was made with ArcGIS.

The shape of the dorsal scutum was described using the system proposed by Kury et al. (2007). We used the nomenclature for the macrosetae of the ventral plate of the penis that was proposed by Kury and Villarreal (2015), but refer to MS C3 as D1 and D1 as D2 (following system discussed in Medrano and Kury 2016). Terminology used for the description of the fields of microsetae on the ventral plate of the penis is based upon Kury (2016). Color names and codes follow Ridgway (1912). All of the measurements are in mm. Abbreviations: Cx; coxa, CW: carapace width, CL: carapace

length, DSW: dorsal scutal width, Fe: femur, DSL: dorsal scutal length, ICN: Instituto de Ciencias Naturales, Mt: metatarsus, MS: macrosetae, Pa: patella, Ta: tarsus, Ti: tibia, Tr: trochanter, TBL: total body length, UA: Universidad del Atlántico, UNAL: Universidad Nacional de Colombia.

Taxonomy

Cosmetidae C.L. Koch, 1839

Platymessa Mello-Leitão, 1941

Platymessa Mello-Leitão, 1941: 167; Roewer 1963: 52; Kury 2003: 81 (type species *Platymessa H-inscripta* Mello-Leitão, 1941, by original designation).

Platimessa [incorrect original spelling]: Mello-Leitão 1941: 167.

Brachylibitia Mello-Leitão, 1941: 166; Kury 2003: 38 [junior subjective synonym of *Cynorta* C.L. Koch, 1839 by Goodnight & Goodnight (1953: 38); synonymy disclaimed by Kury (2003: 38)]; Medrano & Kury 2016: 54-57 [Junior synonym of *Platymessa* Mello-Leitão 1941; type species: *Brachylibitia ectroxantha* Mello-Leitão, 1941, by original designation].

Platymessa victoriae Pinzón-M. & Townsend, sp. n.

<http://zoobank.org/43268445-8D44-481B-A1DC-6AEAEACFBDD0>

Diagnosis. This species differs from *P. h-inscriptum* and *P. ectroxantha* by the presence of multiple blunt tubercles in scutal area I, paired triangular tubercles in scutal area III, the absence of a pair of larger paramedian granules on dorsal scutal area V, lacking a ladder mask color pattern on the dorsal scutum, and instead having a V-shaped color pattern on the cephalic groove and a transverse line in the groove between areas III-IV on the dorsal scutum.

Type locality. Colombia, Cesar Department, Municipality of Manaure Balcón del Cesar, páramo de Sabana Rubia, 10°22'8.6"N; 72°53'33.6"W, 3200 m of elevation, 29 October 2015. C. Pinzón-M.

Type material. Holotype (ICN-AO-1030). Adult male preserved in 96% ethanol, penis in a microvial with 70% ethanol. Original label: "CO, Cesar, Manaure, Páramo de Sabana Rubia, 10°22'8.6"N; 72°53'33.6"W, 29 October 2015. The holotype, allotype and paratypes will be deposited in the Collection of the Arachnida at the Instituto de Ciencias Naturales (ICN-AO), National University of Colombia (ICN). Collector: C. Pinzón-M.

Paratypes. 21 individuals (10 ♂ ICN-AO-1032, ICN-AO-1033, ICN-AO-1034, ICN-AO-1035, ICN-AO-1036, ICN-AO-1037, ICN-AO-1038, ICN-AO-1039, ICN-AO-1040, ICN-AO-1041 and 11 ♀ ICN-AO-1042, ICN-AO-1043, ICN-

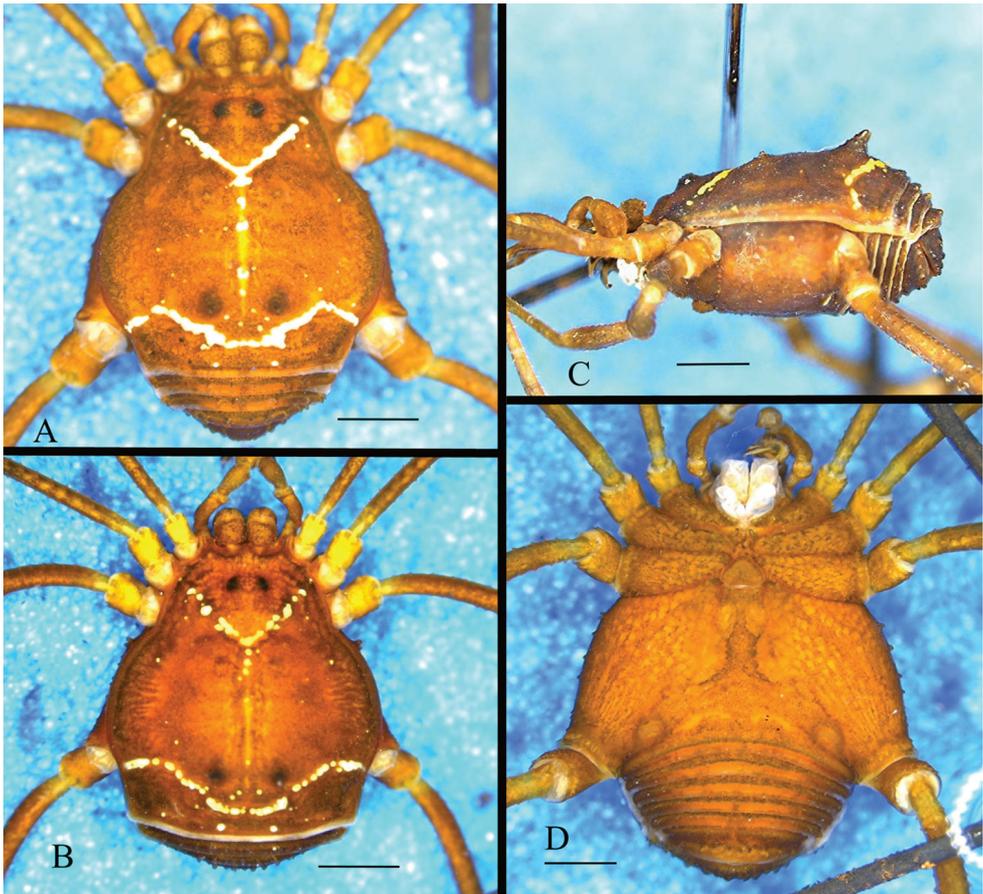


Figure 1. *Platymessa victoriae* sp. n. **A** Habitus, dorsal view (male holotype, ICN-AO-1030) **B** Habitus, dorsal view (female allotype, ICN-AO-1031) **C** Habitus lateral view (male holotype) **D** Ventral view (male holotype). Scale bar: 1mm.

AO-1044, ICN-AO-1045, ICN-AO-1046), Colombia, Cesar, Manaure, October 29, 2015. Collected with the holotype. 22 individuals (5 ♂ and 17 ♀), Colombia, Cesar, Manaure, March 12, 2016. Same data as the holotype.

Etymology. The new species is named to honor the memory of María Victoria Pinzón M.

Description of the male holotype. Measurements: CL: 1,34mm; DSW: 4,17mm CW 2,31mm; DSL: 4mm; Fe: 1,4; 2,9; 2,6; 3,3 mm. Ti: 1,1; 2,6; 1,5; 1,9 mm. **Dorsum** (Figs 1A, C–D and 2): Dorsal scutum β shaped, body slightly convex posteriorly, cheliceral sockets shallow flanked by subsquare lateral projections and separated by a short triangular median projection. Lateral borders with granules on the protrusion of the dorsal scutum, posterior border with a row of small and scarce granules. Free tergites each with one row of round tubercles. Ocularium with a slight median depression, covered with granules arranged proportionally towards each of the eyes.



Figure 2. *Platymessa victoriae* sp. n. (male holotype, ICN-AO-1030). Habitus, dorsal view. Scale bar: 1 mm.

Dorsal scutum in area I with a pair of relatively large blunt tubercles and many smaller granules; area III with a pair of strongtriangular tubercles that are tilted backwards. Anal operculum with tubercles of medium size. V-shaped color pattern on the cephalic groove and a transverse, discontinuous, substraight line behind the triangular tubercles on area III in the groove between areas III-IV. **Pedipalps** (Fig. 3A-C). Trochanter with a subdistal seta; femur at the dorsal border with a keel and the ventral border with a row of 8 tubercles of variable size; tibia with an ectal laminar projection wider to distal

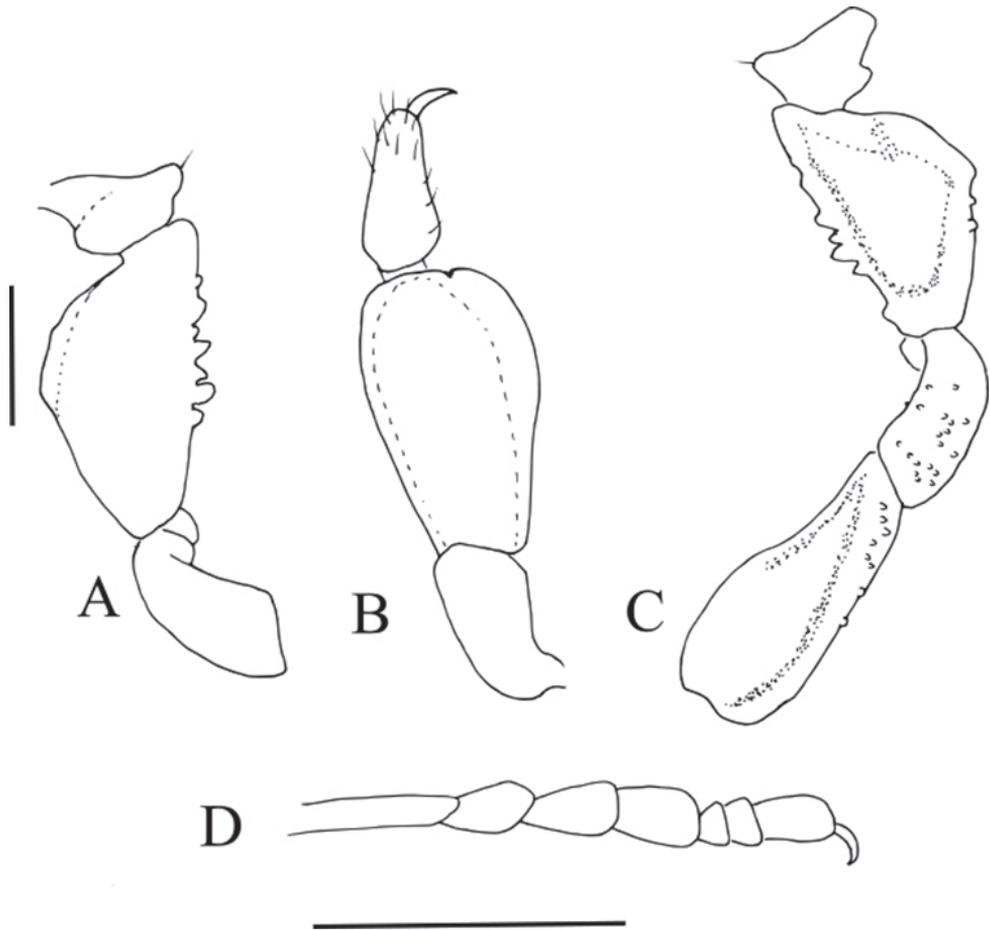


Figure 3. *Platymessa victoriae* sp. n. (male paratype, ICN-AO-1032) **A** Left pedipalp, Tro, Fe and Pa in ectal view **B** Same, Ti and Ta in dorsal view **C** Same in mesal view **D** Left basitarsus I in prolateral view. Scale bar: 1 mm.

part and in inner side, the projection is smaller and the same size lengthwise; tarsus with scarce setae on the dorsal surface. **Chelicerae.** Basichelicerite with a row of tubercles on the posterior border, the dorsal surface has small granules. Fixed finger with a row of six teeth which decrease in size towards the distal part, moveable finger with a row of 12 small denticles that are equal in size. **Legs.** Coxa IV with a distal prodorsal projection, ventrally with a subdistal blunt tubercle smaller than the prodorsal, *clavus inguinis* present. Femora of legs I and II substraight with some granules, III and IV slightly curved, in general, densely granulated, with five longitudinal rows of tubercles, the ventral tubercles are larger (Fig. 4A–E); patellae I–IV granulated; tibiae of legs III and IV slightly granulated; tarsi I with basitarsus inflated; tarsal formula: 5 (3); 9–9 (3); 7–7 (3); 7–7 (3). **Genitalia** (Fig. 5A–C). Ventral plate subrectangular, the basal region

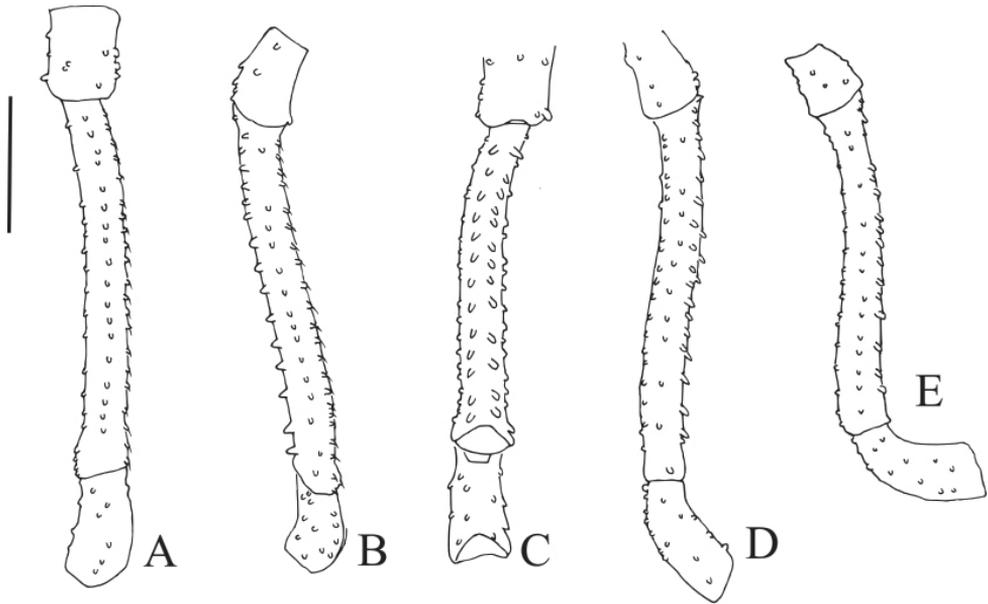


Figure 4. *Platymessa victoriae* sp. n. (male paratype, ICN-AO-1032) Left leg IV. **A** Fe in dorsal view **B** Same, in prolateral view **C** Same, in ventral view **D** Same, in retrolateral view **E** Left leg III, Fe in retrolateral view. Scale bar: 1mm.

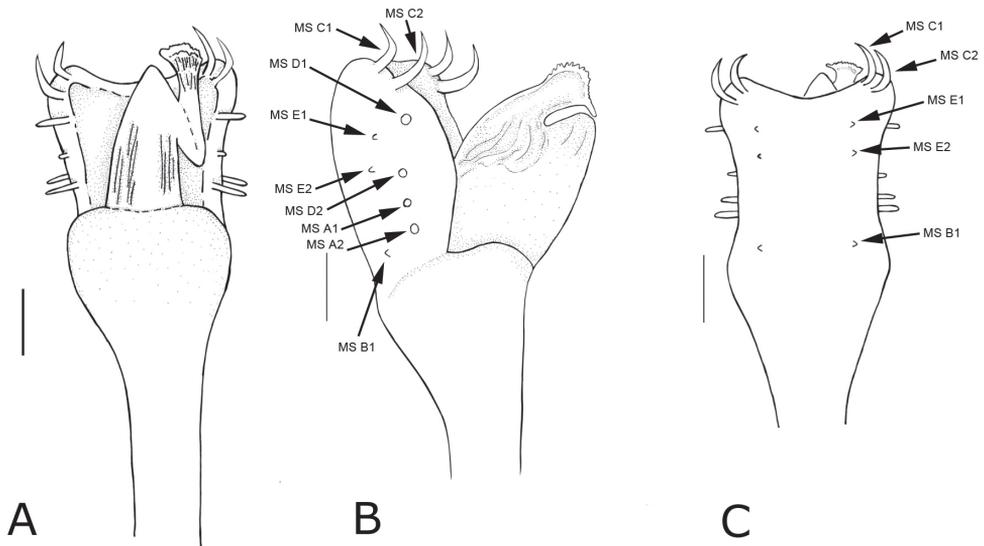


Figure 5. *Platymessa victoriae* sp. n. Penis, distal (male paratype, ICN-AO-1033). **A** Dorsal view **B** Lateral view **C** Ventral view. Locations of paired marginal setae (MS) on the ventral plate are indicated by arrows. MS C1 and C2 occur on the laterodistal margin. MS E1, E2 and B1 occupy the most ventral position and MS D1, D2, A1 and A2 are aligned on the dorsolateral border of the ventral plate. Scale bar: 0.01 mm.

is narrower than the distal, the lateral margins are subparallel and the distal margin is concave. Truncus apically thickened. On the lateral edges of the distal part of the ventral plate are two pairs of MS - C1 and C2, are strongly curved and flattened; there are two pairs of MS D1 and D2, D1 is well-developed, straight and cylindrical and shorter than C1 and C2 and MS D2 is reduced and cylindrical and occurs dorsally between MS A and C. In the basal part of the ventral plate there are two pairs of MS, A1 and A2 are both well-developed, cylindrical and anchored laterally to the ventral plate, although MS A1 is slightly more dorsal and remains aligned with the MS C1, C2 and D1 and with A2. On the ventral surface are located two pairs of MS, E1 and E2 located at the height of MS D1, both are reduced and aligned with a single pair of MS B1 located ventrally near the apical part of the truncus. On the ventral plate, the microsetae occur in the corners and extend on the lateral margins towards the proximal part of the ventral plate without touching each other. The midfield lacks microsetae. The distribution of microsetae is similar to that observed for *P. h-inscriptum* (Medrano and Kury, 2016).

Female allotype (Fig. 1B). Very similar to the male. Measurements: CL: 1,2mm; DSL: 2,5mm; AW: 1,6mm; DSW: 3,5mm; Fe: 1,4; 2,7; 2,1; 2,7 mm. Ti: 0,9; 2,1; 1,4; 1,9 mm.

Sexual dimorphism. Basitarsus I inflated in males (Fig. 3D), the tubercles of the femora and tibiae of legs III and IV are larger in males than in females, in general the tubercles on legs I-IV are larger in males. The dorsal scutum is almost α shape in males and γ shape in females; *clavus inguinis* and the body size of females is larger than that of males.

Table 1. *Platymessa victoriae* sp. n. Measurements of the legs and pedipalp of the male holotype.

	Leg I	Leg II	Leg III	Leg IV	Pedipalp
Co	0,9	1,22	1,42	2,8	0,2
Tr	0,4	0,6	0,6	0,8	0,6
Fe	1,4	2,9	2,6	3,3	0,7
Pa	0,7	1,1	0,9	0,9	0,5
Ti	1,1	2,6	1,5	1,9	1,1
Mt	1,8	3,5	2,7	3,6	
Ta	1,3	2,57	1,6	1,6	0,55

Table 2. *Platymessa victoriae* sp. n. Measurements of the legs of the female allotype.

	Leg I	Leg II	Leg III	Leg IV	Pedipalp
Tr	0,46	0,68	0,71	0,62	0,66
Fe	1,8	3,5	2,73	3,4	1,04
Pa	0,6	1,02	0,88	1,02	0,82
Ti	1,11	2,86	1,65	2,36	1,09
Mt	1,34	3,19	2,19	3,54	
Ta	1,14	2,46	1,4	1,62	0,47

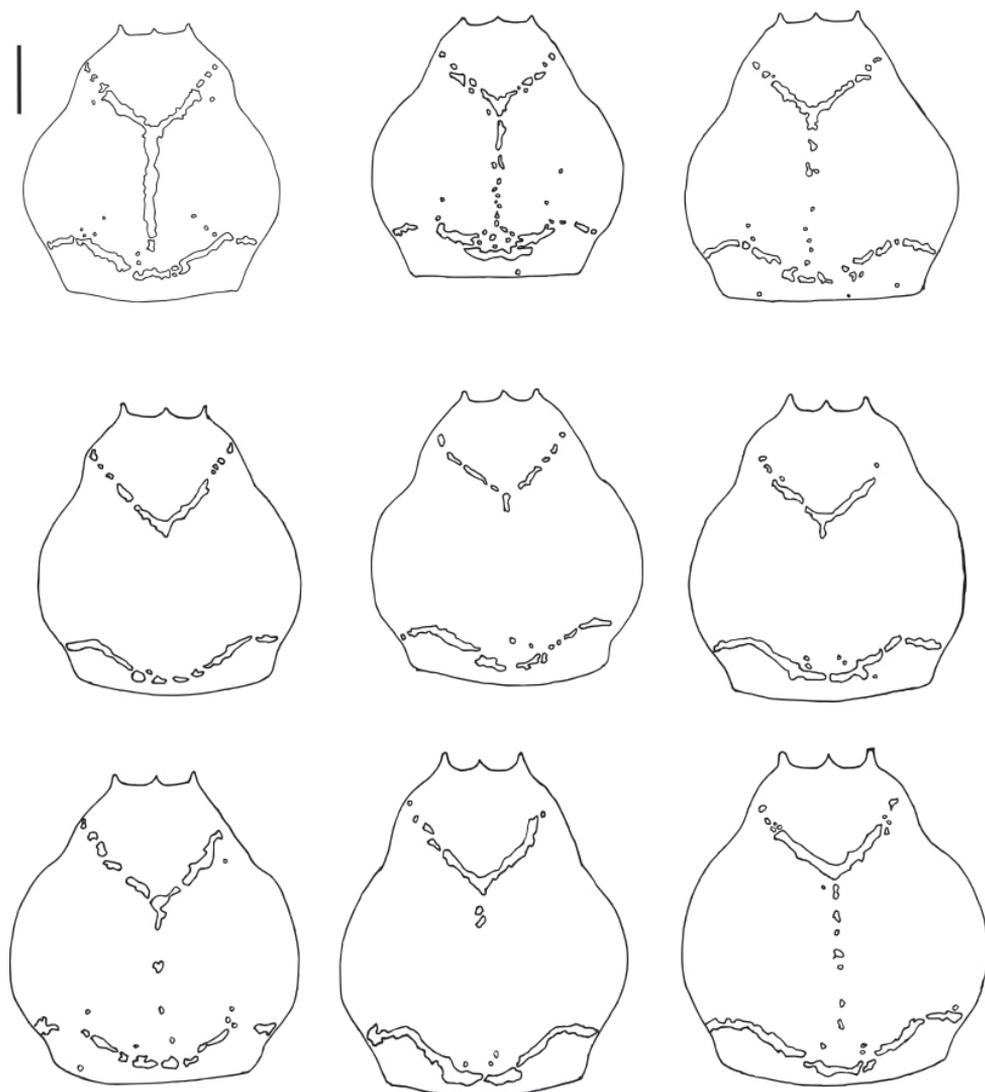


Figure 6. *Platymessa victoriae* sp. n. (male paratypes, ICN-AO-1032, ICN-AO-1034, ICN-AO-1035, ICN-AO-1036, ICN-AO-1037, ICN-AO-1038, ICN-AO-1039, ICN-AO-1040). Intraspecific variation of the pattern of spots in dorsal scutum. Scale bar: 1mm.

Variation. The color pattern of dorsal scutum varies especially with respect to the completeness of medial line of the dorsal scutum (Fig. 6).

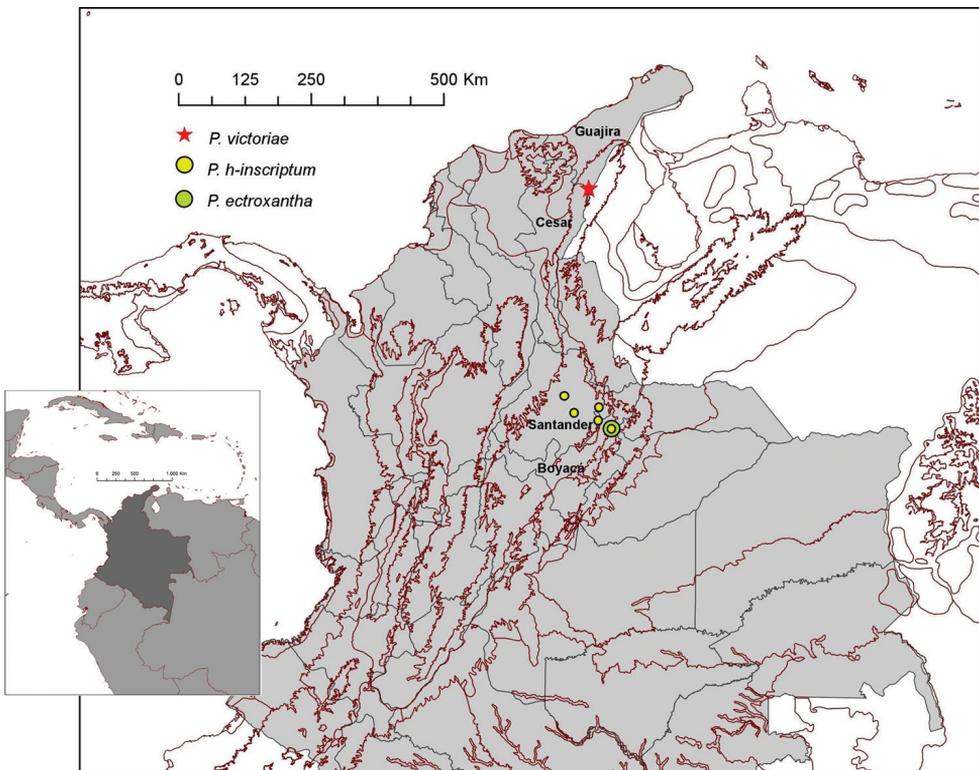
Color in ethanol. Body is “Cinnamon-Brown” (XV-15’*k*), legs are “Buckthorn-Brown” (XV-17’*i*), blots and lines are “Light Orange-Yellow” (III-17 *d*).

Distribution. Only known from the type locality (Fig. 5).

Ecology. In the Páramo de Sabana Rubia, the temperature may drop to 0 °C, the specimens were collected in the necromass of frailejones (*Asteraceae*).

Table 3. Range of measurements of body and appendage in *Platymessa victoriae* sp. n.

	Males n=5			Females n=5		
	Max	Min	Mean	Max	Min	Mean
DSL	5,05	4,19	4,49	4,57	4,12	4,31
DSW	4,80	3,96	4,14	4,06	3,83	3,95
TBL	5,66	4,60	5,01	5,45	4,85	5,11
Fe I	2,02	1,73	1,83	1,76	1,49	1,64
Ti I	1,46	0,82	1,14	1,25	0,95	1,10
Fe II	4,05	3,50	3,72	3,36	3,13	3,27
Ti II	3,23	1,47	2,59	2,64	2,39	2,53
Fe III	3,03	2,68	2,82	2,63	2,34	2,52
Ti III	1,99	1,44	1,65	1,7	1,45	1,59
Fe IV	3,80	3,33	3,55	3,37	3,04	3,22
Ti IV	2,43	2,12	2,33	2,52	1,91	2,28

**Figure 7.** Northwestern region of South America showing the distribution of the three species of *Platymessa* in Colombia. Locations were added using WWF Terrestrial Ecoregions of the World (Olson et al., 2011).

Discussion

The genus *Platymessa* was revised by Medrano and Kury (2016) and the following combination of characters was used to diagnose the genus: 1) outline of the dorsal scutum β form in males and “almost” α form in females; 2) scutal area V with a pair of small paramedian granules; 3) dorsal color pattern of a “ladder mask”; 4) monomorphic chelicerae, weak with marginal rows of acuminate tubercles of variable size on posterior border; 5) groin warts present, larger in the female; 6) femora III and IV with five longitudinal rows of small tubercles; 7) basitarsomeres of leg I larger than distitarsomeres in males; and 8) cheliceral sockets shallow with lateral triangular projections. *Platymessa victoriae* sp. n. exhibits most of these characteristics except with respect to the armature of the dorsal scutum (scutal area III has a pair of triangular tubercles and scutal area V lacks paired paramedian granules) and the absence of a “ladder mask” with respect to the dorsal coloration.

With regards to penis morphology, the shape of the ventral plate, the number and sizes of the marginal setae (MS), and the distribution of microsetae are similar between *P. h-inscriptum* and *P. victoriae* sp. n. However, there is interspecific variation with respect to the size and position of the MS on the ventral plate. In *P. victoriae* sp. n., MS D1 is more cylindrical and considerably shorter than C1 and C2. In addition, MS A1 and A2 are located more basally on the ventral plate and MS E1 and E2 occur between D1 and D2 (in *P. h-inscriptum*, MS A1 and A2 are more medial and are closer to the margin of the ventral plate and MS E1 and E2 are situated between D1 and A1).

Acknowledgments

We thank the Universidad del Atlántico (UA) for financial support, Professor Hermes Cuadros Villalobos for leading us to the type locality, for his comments on the manuscript, and for assistance with the distribution map, and Professor Miguel Gonzalo Andrade (UNAL) for the loan of the camera lucida. We also thank two anonymous referees for constructive comments on an earlier version of our manuscript and Prof. Eduardo Flórez (ICN) for timely assistance with the deposition of type specimens.

References

- Kury AB (2016) A classification of the penial microsetae of Gonyleptoidea (Opiliones: Laniatores). *Zootaxa* 4179: 144–150. <https://doi.org/10.11646/zootaxa.4179.1.13>
- Kury AB, Pinto-da-Rocha R (2007) Cosmetidae Koch, 1839. In: Pinto-da-Rocha R, Machado G, Giribet G (Eds) *Harvestmen: The Biology of the Opiliones*. Harvard University Press, Cambridge and London, 182–185.

- Kury AB, Villarreal O, Sampaio C (2007) Redescription of the type species of *Cynorta* (Arachnida, Opiliones, Cosmetidae). *Journal of Arachnology* 35: 325–333. <https://doi.org/10.1636/H06-35.1>
- Kury AB, Villarreal O (2015) The prickly blade mapped: Establishing homologies and a chaetotaxy for macrosetae of penis ventral plate in Gonyleptoidea (Arachnida, Opiliones, Laniatores). *Zoological Journal of the Linnean Society* 174: 1–46. <https://doi.org/10.1111/zoj.12225>
- Medrano M, Kury AB (2016) Characterization of *Platymessa* with redescription of the type species and a new generic synonymy (Arachnida, Opiliones, Cosmetidae). *Zootaxa* 4085: 52–62. <http://doi.org/10.11646/zootaxa.4085.1.2>
- Mello-Leitão CF de (1941) Alguns opiliões novos da Colombia. *Anais da Academia Brasileira de Ciências* 13: 165–171.
- Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel W, Hedao P, Kassem, KR (2001) Terrestrial Ecoregions of the World: A New Map of Life on Earth. *BioScience* 51: 933–938. [http://dx.doi.org/10.1641/0006-3568\(2001\)051\[0933:TEOTWA\]2.0.CO;2](http://dx.doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2)
- Pinto-da-Rocha R, Hara MR (2011) Redescription of *Platygyndes* Roewer 1943, a false Gonyleptidae, (Arachnida, Opiliones, Cosmetidae). *ZooKeys* 143: 1–12. <https://doi.org/10.3897/zookeys.143.1916>
- Ridgway R (1912) *Colors standards and color nomenclature*. A. Hoen & Company, Washington, DC, 44 pp.
- Roewer CF (1963) Opiliones aus Peru und Colombien. [Arachnida Arthrogastra aus Peru V]. *Senckenbergiana Biologica* 44: 5–72.

Disjunctitermes insularis, a new soldierless termite genus and species (Isoptera, Termitidae, Apicotermatinae) from Guadeloupe and Peru

Rudolf H. Scheffrahn¹, Tiago F. Carrijo², Anthony C. Postle³, Francesco Tonini⁴

1 Fort Lauderdale Research and Education Center, Institute for Food and Agricultural Sciences, 3205 College Avenue, Davie, Florida 33314, USA **2** Centro de Ciências Naturais e Humanas, Universidade Federal do ABC, Rua Arcturus 03, Jardim Antares, 09606-070, São Bernardo do Campo, SP, Brazil **3** P.O. Box 5473 Cairns Queensland 4870, Australia **4** Center for Systems Integration and Sustainability, Michigan State University, 115 Manly Miles Building, 1405 S. Harrison Rd., East Lansing, MI 48823, USA

Corresponding author: *Rudolf H. Scheffrahn* (rhsc@ufl.edu)

Academic editor: *E. Cancellato* | Received 22 December 2016 | Accepted 16 March 2017 | Published 4 April 2017

<http://zoobank.org/89220C7C-D27C-4516-A3D4-2525BA39FB27>

Citation: Scheffrahn RH, Carrijo TF, Postle AC, Tonini F (2017) *Disjunctitermes insularis*, a new soldierless termite genus and species (Isoptera, Termitidae, Apicotermatinae) from Guadeloupe and Peru. ZooKeys 665: 71–84. <https://doi.org/10.3897/zookeys.665.11599>

Abstract

Disjunctitermes insularis **gen. n. & sp. n.** is described from workers collected on Guadeloupe and in Peru and is the first soldierless termite found on a deep-water island. As with many soldierless and soil-feeding termite species, the enteric valve morphology is an essential diagnostic character of *D. insularis*. The *D. insularis* sequence cluster, derived from a barcode analysis with twelve other described genera of New World Apicotermatinae, is well resolved. Results of a stochastic dynamic spread model suggest that the occurrence of *D. insularis* on Guadeloupe may be the result of a pre-Colombian overwater dispersal event from mainland South America.

Keywords

Soil-feeder, taxonomy, barcode sequence, stochastic spread, overwater dispersal

Introduction

All New World species of the soil-feeding termite subfamily Apicotermitinae lack soldiers. The absence of the soldier caste has historically hindered the classification of this diverse group until the gradual adoption of worker digestive tract characters, especially the enteric valve (EV) morphology allowing for genus and species level discrimination (Bourguignon et al. 2016a, b). Recently, seven new genera, numerous new species, reassignments, and synonyms of Neotropical apicotermitines have been reported (Bourguignon et al. 2010, 2016a, Carrijo et al. 2015, Scheffrahn 2013, Scheffrahn et al. 2006).

Darlington (1992) listed 12 termite species, all wood feeders, on the island of Guadeloupe. In 1999, as part of our ongoing diversity study of the West Indies (Puerto Rico and the U.S. Virgin Is.: Scheffrahn et al. 2003a, Trinidad: Scheffrahn et al. 2003b, and the Bahamas: Scheffrahn et al. 2006) we also surveyed Guadeloupe and were astonished to collect numerous samples of a small soldierless termite species. In 2014, we collected a single sample of this same species in the Peruvian Amazon. We herein describe a new genus, *Disjunctitermes*, a single new species, *D. insularis*, discuss its remarkable distribution, and estimate its dispersal rate on Guadeloupe.

Materials and methods

Workers were collected and preserved in 85% ethanol. External and internal dissections were suspended in Purell® Instant Hand Sanitizer in a plastic Petri dish and photographed using a Leica M205C stereomicroscope controlled by Leica Application Suite version 3.0 montage software. The EV was prepared by removing the entire worker P2 section in ethanol. Food particles were expelled from the P2 tube by pressure manipulation. The tube was quickly submerged in a droplet of PVA medium (BioQuip Products Inc.) which, by further manipulation, eased muscle detachment. The remaining EV cuticle was left intact or longitudinally cut, splayed open, and mounted on a microscope slide using the PVA medium. The EV was photographed with a Leica CTR 5500 compound microscope with phase-contrast optics using the same montage software. Terminology of the worker gut follows that of Sands (1998) and Noirot (2001).

Sequences of three specimens of *D. insularis* and twelve other samples of Neotropical Apicotermitinae (eight species in six genera, Table 1) were obtained by DNA extraction and PCR performed by the Canadian Centre for DNA Barcoding following standard high-throughput protocols (deWaard et al. 2008). The PCR employed the primers LepF1 and LepR1 (Hebert et al. 2003) which generated 622 to 652bp of the barcode region of the mitochondrial gene cytochrome c oxidase subunit 1 (COI). In addition, GenBank sequences from 20 neotropical Apicotermitinae (13 species in 10 genera), five non-apicotermitine Termitidae, and one Rhinotermitidae to root the tree (Table 1) were included in our analysis.

Table I. Species used in the phylogeny, GenBank accession number, and UF collection code for those used in this study.

Species	GenBank	UF Code
<i>Amplucruterme inflatus</i>	KT215783	
<i>Anoplotermes parvus</i>	HQ398187	
<i>Anoplotermes parvus</i>	HQ398189	
<i>Anoplotermes janus</i>	HQ398188	
<i>Anoplotermes janus</i>	KY683193	UF.FG208
<i>Anoplotermes janus</i>	KY683187	UF.PU827
<i>Anoplotermes banksi</i>	HQ398185	
<i>Anoplotermes banksi</i>	KT215785	
<i>Aparatermes spA</i>	KT215784	
<i>Aparatermes sivestrii</i>	KY683197	UF.TT2018
<i>Aparatermes silvestrii</i>	KY683190	UF.PA453
<i>Aparatermes cingulatus</i>	KY683194	UF.SA252
<i>Aparatermes cingulatus</i>	KY683192	UF.PA591
<i>Compositermes bani</i>	KM538651	
<i>Compositermes vindai</i>	KM538649	
<i>Compositermes vindae</i>	KM538652	
<i>Disjunctitermes insularis</i>	KY683195	UF.PU505
<i>Disjunctitermes insularis</i>	KY683188	UF.GU753
<i>Disjunctitermes insularis</i>	KY683199	UF.GU788
<i>Grigiotermes hageni</i>	KY683196	UF.PA532
<i>Grigiotermes hageni</i>	KT215781	
<i>Grigiotermes hageni</i>	KY683200	BO241
<i>Heterotermes crinitus</i>	KF430191	
<i>Humutermes krishnai</i>	KT215787	
<i>Hydrecotermes kawaii</i>	KT215788	
<i>Longustitermes manni</i>	KF430187	
<i>Longustitermes manni</i>	HQ398186	
<i>Longustitermes manni</i>	KF430083	
<i>Macrotermes bellicosus</i>	AY127702	
<i>Nasutitermes octopilis</i>	KF430192	
<i>Patawatermes turricola</i>	KY683191	UF.PU597
<i>Patawatermes turricola</i>	KY683189	UF.PA1086
<i>Patawatermes nigripunctatus</i>	KY683186	UF.EC437
<i>Patawatermes nigripunctatus</i>	KT215786	
<i>Rubeotermes jberingi</i>	KF430151	
<i>Rubeotermes jberingi</i>	KT215778	
<i>Ruptitermes reconditus</i>	KM538647	
<i>Silvestritermes minutus</i>	KT215789	
<i>Syntermes grandis</i>	EU253863	
<i>Termes hispaniolae</i>	FJ802753	
<i>Tetimatermes sp.</i>	KY683198	UF.SA448

All sequences were aligned using the MUSCLE algorithm in Geneious v6.1.6 (Biomatters Ltd., Auckland, New Zealand). A phylogenetic analysis was conducted under Bayesian inference (BI) with *Heterotermes crinitus* as the outgroup. The substitution model (GTR+I+G) was selected through the Akaike Information Criterion (AIC) with the jModelTest2 (Darriba et al. 2012). The XML input file was generated with BEAUti 1.8.0, and the BI was performed with BEAST 1.8.0 (Drummond et al. 2012). A Yule speciation process with a random starting tree and relaxed molecular clock was used as tree priors. Final Markov chain Monte Carlo (MCMC) searches were conducted for 15,000,000 generations. Convergence and stationarity were assessed with Tracer 1.5 (Rambaut et al. 2014) and the first 150 trees were discarded as burn-in with TreeAnnotator 1.8.0 and visualized using FigTree 1.3.1.

The spatiotemporal spread of *D. insularis* was simulated using methods and biological parameters as described in Tonini et al. 2014. The mean flight distance was defined as 100 meters for this small forest species.

Taxonomy

Disjunctitermes Scheffrahn, gen. n.

<http://zoobank.org/86068307-7A76-4DBF-A369-0B3AC46DD82E>

Figs 1–3, Table 2

Type species. *Disjunctitermes insularis* sp. n.

Diagnosis. *Disjunctitermes* is one of the described Neotropical apicotermittines that, along with *Anoplotermes banksi*, *A. pacificus*, and *Hydrecoptermes* spp., possess strongly inflated fore tibia and lack spiny sclerotized enteric valves. *Disjunctitermes* is closest to *A. banksi*, but can be distinguished from the latter by the subsidiary tooth on the left mandible, the larger EV seating and the more truncate terminus of P2 (Fig. 3C, D). *Hydrecoptermes* lacks a spheroidal mesenteric tongue.

Imago. Unknown.

Worker (Figs 1–3, Table 2). Monomorphic, small. Head capsule yellowish, covered with about 100 setae of varying length. Postclypeus moderately inflated, fontanelle barely discernible. Antennae with 14 articles. Left mandible with apical and first marginal teeth well separated, long, and projecting well beyond line formed by third marginal tooth and molar prominence. A subsidiary (fourth) marginal tooth visible above molar prominence in both dorsal (Fig. 1C, bottom) and ventral (Fig. 1D, bottom) views. Right mandible with apical tooth much longer than first marginal; third marginal nearly symmetrical. Fore-tibia strongly inflated; about three times longer than at its widest (median) point. Mesenteric tongue spheroidal (Fig. 2C). P2 entering through large, robustly trilobed EV seating (two lobes prominently visible through integument, Figs 1F, 2C). Enteric valve morphology consists of six elongate, inflated pads (Fig. 3A, B) that face the valve lumen (Fig. 3D). The posterior

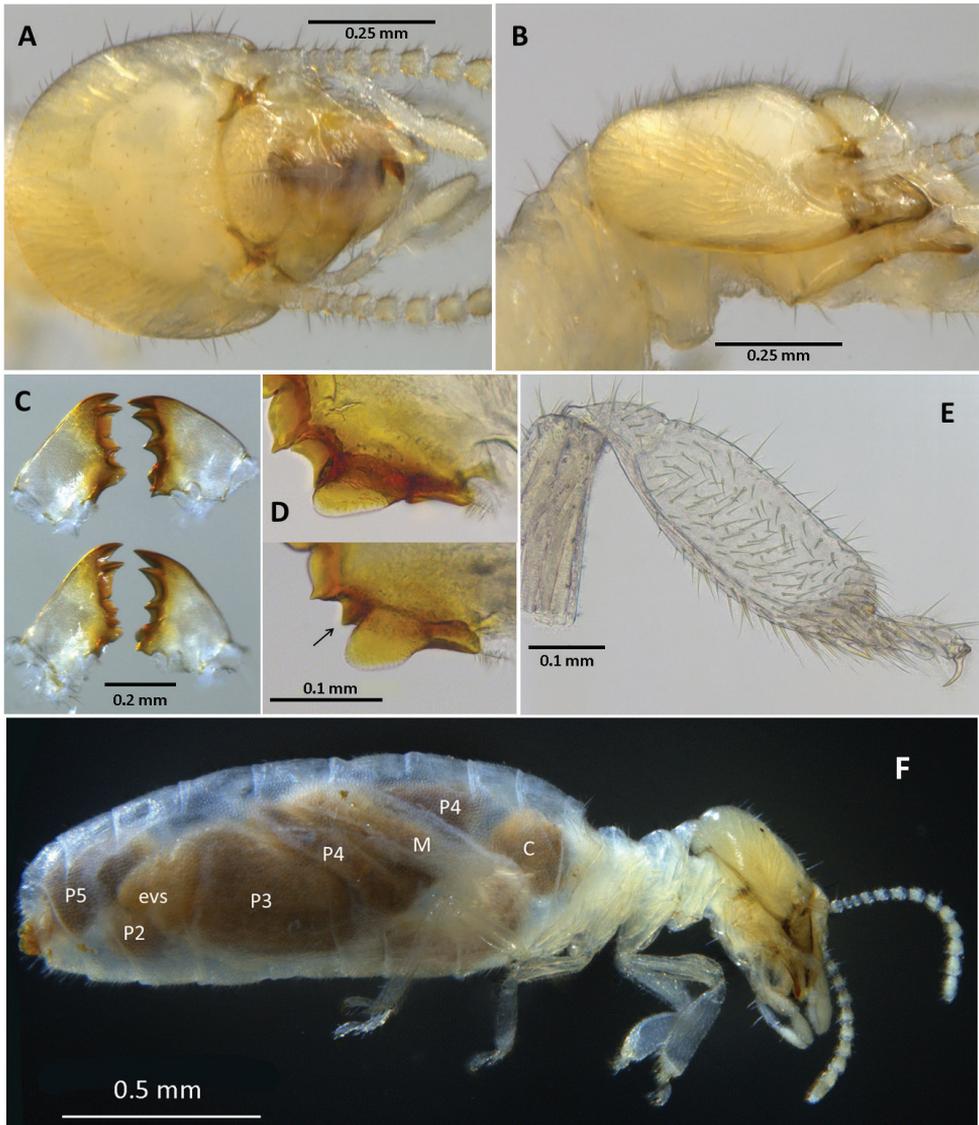


Figure 1. Dorsal (**A**) and lateral (**B**) views of the *Disjunctitermes insularis* worker head capsule **C** Dorsal views of newly molted worker mandibles of *Anoplotermes banksi* Emerson (top) and *D. insularis* (bottom) **D** Ventral views of the molar portion of the left mandibles of newly molted workers of *A. banksi* (top) and *D. insularis* (bottom) **E** Right fore-tibia, and **F** right lateral view of *D. insularis* worker.

end of the P2, containing the EV, with truncate terminus projecting about half way into EV seating.

Etymology. The genus name is derived from its current, widely disjunct distribution on Guadeloupe and Peru (Fig. 4, inset)

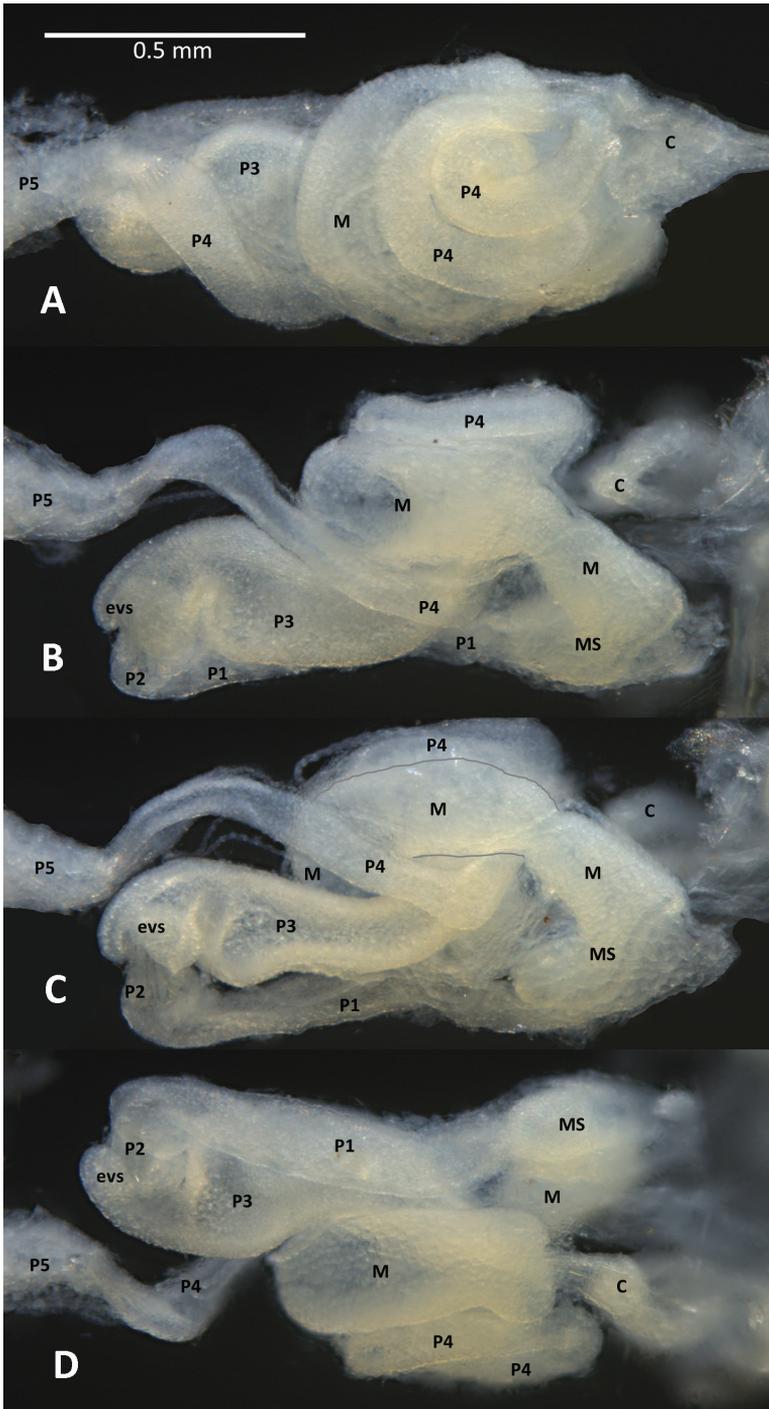


Figure 2. Dorsal (A), right (B), ventral (C), and left (D) views of a newly molted, unfed *Disjunctitermes insularis* worker. Abbreviations: C, crop; evs, enteric valve seating; M, mesenteron; MS, mixed segment; P1, P2, P3, P4 and P5 proctodeal segments 1-5, respectively.

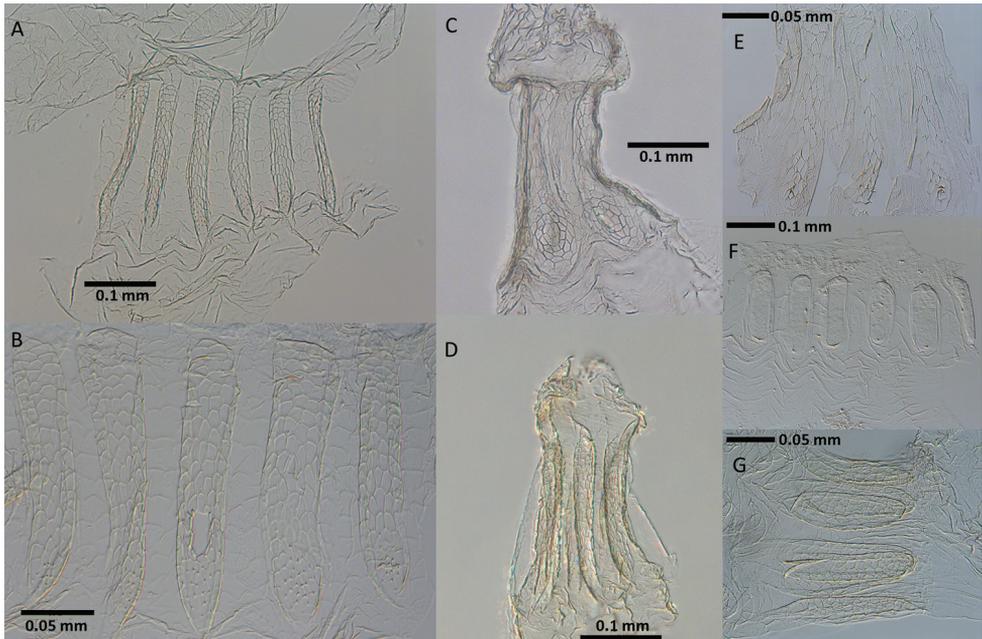


Figure 3. Enteric valve morphology of *Disjunctitermes insularis* worker not fully stretched laterally (**A**) and fully stretched laterally showing five of six pads (**B** center pad with small tear). Whole EV mounts of *A. banksi* (**C**) and *D. insularis* (**D**) with posterior ends at top. Enteric valves of *A. pacificus* (**E**, 3 pads shown), *Hydrecotermes arienesho* (**F**), and *H. kawaii*, whole mount (**G**).

***Disjunctitermes insularis* Scheffrahn, sp. n.**

<http://zoobank.org/975729E6-5A94-4DFC-9E00-162E50082D5E>

Material examined. Holotype: labelled “(UF code GU 105) GUADELOUPE Basse-Terre, Trail Mamelles de Petite Bourg, Parc Nat., undisturbed forest, 16.1778; -61.7321, 23MAY99, col. Chase, Krececk, Maharajh, Mangold, and Scheffrahn. Paratype colonies (the holotype is kept in the same vial as the paratypes): GUADELOUPE, Basse-Terre 16.1778; -61.7321, 23MAY1999 (GU106), 12 workers; 16.1814; -61.7361, 29MAY1999 (GU753), 12 workers; 16.1814; -73.61, 29MAY1999 (GU754), 11 workers; 16.1674; -61.6644, 29MAY1999 (GU783), 12 workers; 16.1674; -61.6644, 29MAY1999 (GU784), 12 workers; 16.1674; -61.6644, 29MAY1999 (GU785), 12 workers; 16.1674; -61.6644, 29MAY1999, (GU786), 12 workers; 16.1674; -61.6644, 29MAY1999, (GU787), 12 workers; 16.1674; -61.6644, 29MAY1999, (GU788), 12 workers. PERU, 6 km S von Humboldt, disturbed forest, -8.8769; -75.0465, 28MAY2014 (PU505), 12 workers, col. Carrijo, Chase, Constantino, Mangold, Mullins, Křeček, Kuswanto, Nishimura, and Scheffrahn. All material housed at the University of Florida Termite Collection in Davie, Florida. Collection sites are mapped in Fig. 4.

Diagnosis. See also comparison for *Disjunctitermes* above. The EV pads of *D. insularis* differ from those of the four other described species with unarmed EV as follows



Figure 4. Type localities (red dots) for *D. insularis* on Basse-Terre, Guadeloupe. Inset shows the Guadeloupe and Peru localities (red dots) and all other termite collecting localities in the UF database (green dots) where *D. insularis* was not found.

Table 2. Measurements (mm) of 12 workers from each of 11 colonies of *D. insularis*.

Colony	Head length to end of postclypeus	Postclypeal length	Max. head width	Pronotal width	Hind tibia length	Fore-tibia width: length ratio
Holotype	0.61	0.14	0.64	0.39	0.49	0.29
GU105	0.59–0.66	0.13–0.16	0.64–0.69	0.36–0.41	0.48–0.52	0.26–0.31
GU106	0.64–0.69	0.14–0.18	0.66–0.69	0.39–0.42	0.48–0.52	0.26–0.33
GU753	0.63–0.66	0.14–0.18	0.65–0.69	0.37–0.42	0.48–0.56	0.30–0.36
GU754	0.59–0.67	0.13–0.16	0.65–0.69	0.37–0.43	0.46–0.52	0.27–0.35
GU783	0.60–0.66	0.14–0.16	0.64–0.66	0.36–0.42	0.48–0.54	0.26–0.35
GU784	0.61–0.64	0.13–0.14	0.64–0.67	0.38–0.40	0.49–0.52	0.28–0.33
GU785	0.61–0.64	0.13–0.15	0.64–0.67	0.39–0.42	0.46–0.52	0.28–0.34
GU786	0.62–0.66	0.14–0.17	0.64–0.70	0.38–0.41	0.49–0.52	0.28–0.34
GU787	0.60–0.64	0.14–0.17	0.65–0.68	0.38–0.40	0.49–0.51	0.28–0.35
GU788	0.59–0.63	0.13–0.18	0.63–0.65	0.38–0.42	0.46–0.50	0.28–0.31
PU505	0.58–0.64	0.15–0.18	0.64–0.67	0.38–0.42	0.48–0.52	0.28–0.36
Range (n=132)	0.58–0.67	0.13–0.18	0.63–0.70	0.36–0.43	0.46–0.56	0.26–0.36

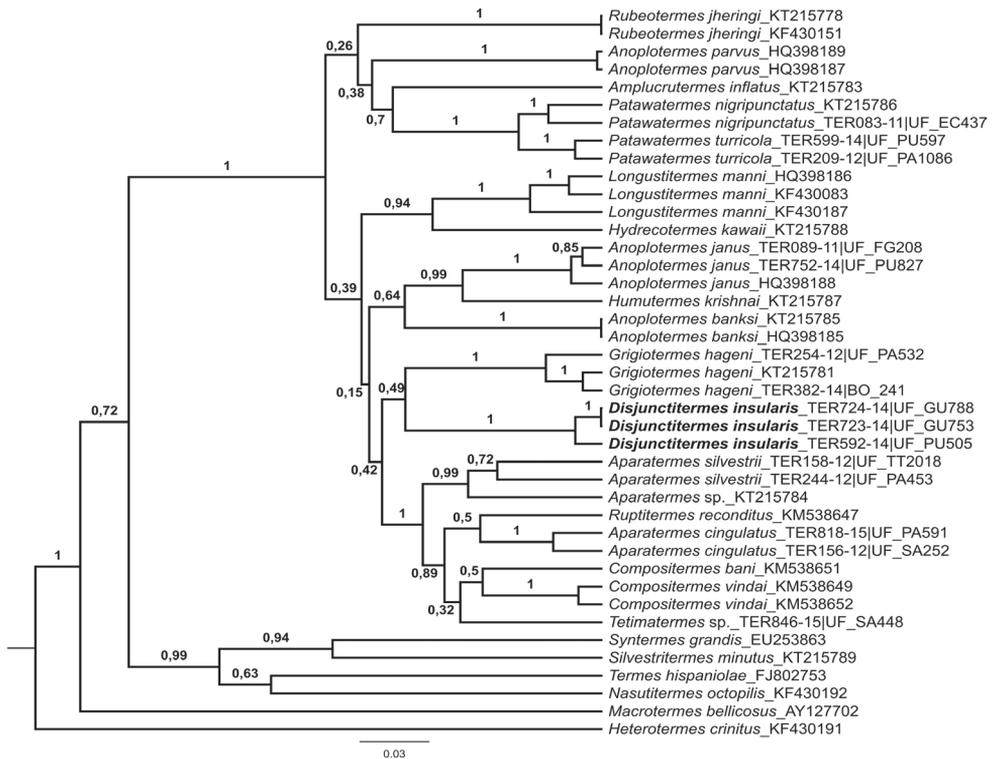


Figure 5. Bayesian phylogeny of all described soldierless New World genera using the mitochondrial CO1 barcode gene showing posterior probabilities. Tree rooted on terminal *Heterotermes crinitus*.

(Fig. 3): each pad of *A. banksi* is vase-shaped, with a narrow posterior end that widens into an oval base reminiscent of an orb-weaving spider web (Fig. 3C); the *A. pacificus* pads are shaped similarly to those of *A. banksi* but are less concentric and are adorned with a few unsclerotized spines (Fig. 3E); while the pads of *H. arienesho* and *H. kawaii* are ovoid in shape (Figs 3F and 3G, respectively).

Imago. Unknown.

Worker (Figs 1–3, Table 2). See *Disjunctitermes* gen. n. description above. EV devoid of sclerotized spiny armature. Pads about six times longer than wide; slight difference in length when stretched horizontally. Anterior fourth of each pad composed of about 10–20 ovoid scales each with one point facing posteriorly. Posterior portion of pads truncate with about 30–50 polygonal scales adorned with fringes on their posterior margins. Cuticle between pads with about 15–20 faint arching ridges; ridges fringed posteriorly.

Etymology. The species name is derived from its unexpected island locality.

Habitat and biology. Workers were collected in foraging groups under rocks and stones in rainforest habitats. Like many New World Apicotermatinae, *D. insularis* does not build any above-ground structures. Mature worker gut contents confirm that they feed on the organic fraction of soil.

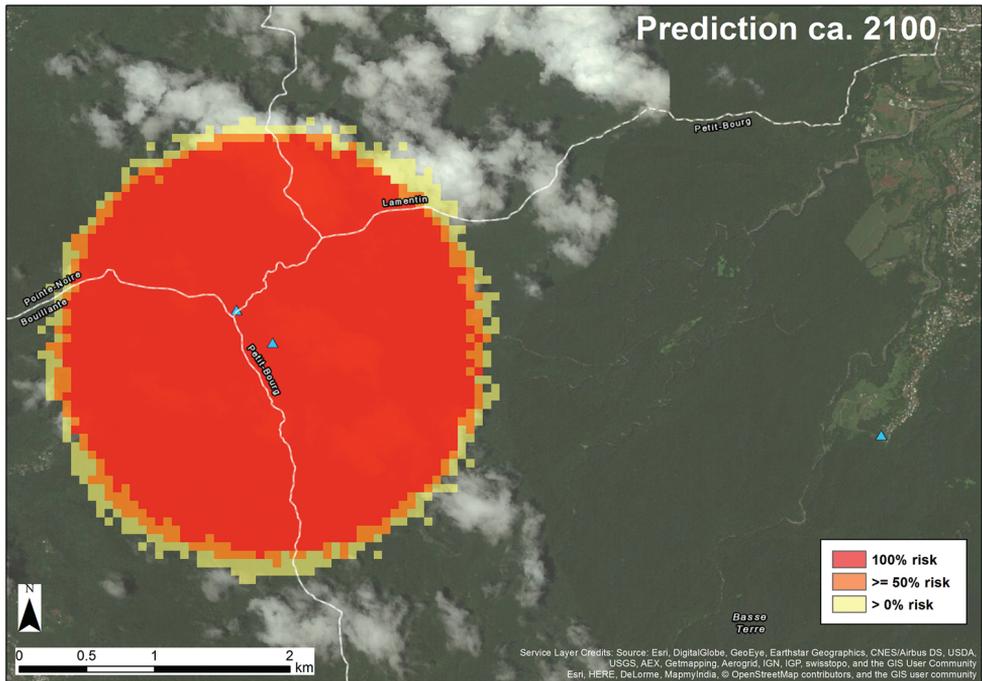


Figure 6. An 85-year stochastic lattice-based model simulation of *Disjunctitermes insularis* spread from a single founder point locality on Basse-Terre, Guadeloupe.

Molecular phylogeny. The molecular phylogeny performed with the mitochondrial gene COI clearly clustered *D. insularis* specimens from Guadeloupe and Peru, as well as specimens belonging to the same species of other genera (Fig. 5). However, the phylogeny showed low resolution in the relationships between the Apicotermitinae genera.

Dispersal rate on land. Starting from a single founder location, the stochastic spread models predicts a 2,778-meter spread over 85 years (Fig. 6) or about 265 years to reach the ca. 8 km expanse between the easternmost and westernmost collection localities (Fig. 4). This suggests a very remote possibility that a single human transport event delivered *D. insularis* to Guadeloupe which would have taken place at a time when French colonization of Basse-Terre was limited to the coast (Hoy 1961). It is far more likely, however, that *D. insularis* reached Guadeloupe via a natural overwater dispersal event (De Queiroz 2005) during pre-Colombian times.

Taxonomic correction. Darlington (1992) reported a *Neotermes* sp. between 600–1000 m on Basse-Terre which we found to be *Comatermes perfectus* (Hagen).

Discussion

Before 1960, all New World soldierless termites were described from the imago caste and placed in the genus *Anoplotermes* (Krishna 2013). Using Sands (1972) descriptive

methods for Old World taxa, Mathews (1977) was the first to adopt internal worker characters, including the EV (Grassé and Noirot 1954), for New World soldierless termites (*Anoplotermes*, *Grigiatermes*, and *Ruptitermes*). As imagos are sometimes difficult to collect, Fontes (1986) was the first to describe a neotropical soldierless taxon based only on diagnostic characters of the worker caste (*Tetimatermes*, fore tibia), followed by Scheffrahn 2013 (*Compositermes*, EV), and Bourguignon et al. 2016a (*Amplucrutermes*; fore tibia, EV, and gene sequence). Given the robust morphology of the EV of soldierless and other soil-feeding termites, and guidance from sequence reconstructions (Bourguignon et al. 2013, Bourguignon et al. 2016a, Carrijo et al. 2015), *Disjunctitermes insularis* is the newest worker-based soldierless taxon. The senior author has participated in over 75 termite diversity expeditions from 1990-2014 and recognizes about 40 undescribed soldierless genera from the Neotropics based, in large part, on EV morphology and CO1 sequences. All specimens are housed in the UF collection.

Short overwater or vicariant dispersal transported the Apicotermitinae to continental shelf islands such as Cuba and the Bahamas (Scheffrahn et al. 2006) or Trinidad and Tobago (Scheffrahn, unpublished) during low sea level stands of the Late Pleistocene. As with all the Termitidae, the Apicotermitinae diversified some 40 mya (Engel et al. 2009) after the continents were separated by vast oceans (Scotese 2004). Therefore, the more basal Old World Apicotermitinae probably arrived in the New World via a single transoceanic dispersal event (Bourguignon et al. 2017).

To our knowledge, *D. insularis* is the only soldierless or soil-feeding termite inhabiting a deep-water (>950 m for Guadeloupe) island. Snyder (1949) listed *Termes morio* Latreille from Martinique as a synonym of *Anoplotermes meridianus* Emerson, however, Emerson (1925) found that *T. morio*, as described by Latreille, is actually *Nasutitermes costalis* (=corniger). Basse-Terre Guadeloupe, part of the Antillean volcanic arc, was formed 2.8 mya (Samper et al. 2007). Our discovery of *D. insularis* on Basse-Terre is also the first record of a non-wood-feeding termite on a deep-water island (cf. Krishna et al. 2013 volumes 4–6). There is no record of anthropogenic transport of any non-wood-feeding termite (Evans 2011) and the localities of *D. insularis* (Fig. 4) are mountainous with rocky soil that is ill-suited for agriculture and development (Hoy 1961). Even today there are no villages or towns in the climax forests between Mahaut and Vernou (Fig. 4).

We surmise that the establishment of *D. insularis* was the result of a natural overwater dispersal event from the mainland Neotropics followed by natural spread presumably across the entire forested interior of Guadeloupe which we incompletely surveyed (Fig. 4). Although known only from a single Amazonian locality in Peru, *D. insularis* is probably widespread in the Neotropics as has been the case for many other soldierless species (Bourguignon et al. 2010, 2016a; Scheffrahn 2013).

Acknowledgments

We thank James A. Chase, Reginaldo Constantino, Jan Křeček, Eko Kuswanto, Boudanath Maharajh, John R. Mangold, Aaron Mullins, and Thomas Nishimura for

their expert field collecting. We also thank the General Director of Forestry and Wildlife, Peru for their 11 April 2014 permission to collect and export specimens, in conformity with Ministry of Agriculture Resolution Number 212-2011-AG. We also thank the Regional Government of Huánuco, Peru for their 7 October 2010 permission to collect and export specimens, Regional Decree Number 098-2010-CR/GRH and the Regional Government of Ucayali, Regional Decree Number 016-2008-GRU/CR.

References

- Bourguignon T, Lo N, Šobotník J, Simon YWH, Iqbal N, Coissac E, Lee M, Jendryka MM, Sillam-Dussès D, Křížková B, Roisin Y, Evans TA (2017) Mitochondrial phylogenomics resolves the global spread of higher termites, ecosystem engineers of the tropics. *Molecular Biology and Evolution*. <https://doi.org/10.1093/molbev/msw253>
- Bourguignon T, Scheffrahn RH, Křeček J, Nagy ZT, Sonet G, Roisin Y (2010) Towards a revision of the neotropical soldierless termites (Isoptera: Termitidae): redescription of the genus *Anoplotermes* and description of *Longustitermes* gen. nov. *Invertebrate Systematics* 24: 357–370. <https://doi.org/10.1071/IS10012>
- Bourguignon T, Scheffrahn RH, Nagy ZT, Sonet G, Host B, Roisin Y (2016a) Towards a revision of the Neotropical soldierless termites (Isoptera: Termitidae): redescription of the genus *Grigiotermes* Mathews and description of five new genera. *Zoological Journal of the Linnean Society* 176: 15–35. <https://doi.org/10.1111/zoj.12305>
- Bourguignon T, Šobotník J, Dahlsjö CAL, Roisin Y (2016b) The soldierless Apicotermitinae: insights into a poorly known and ecologically dominant tropical taxon. *Insectes Sociaux* 63: 39–50. <https://doi.org/10.1007/s00040-015-0446-y>
- Bourguignon T, Šobotník J, Hanus R, Krasulová J, Vrkoslav V, Cvačka J, Roisin Y (2013) Delineating species boundaries using an iterative taxonomic approach: The case of soldierless termites (Isoptera, Termitidae, Apicotermitinae). *Molecular Phylogenetics and Evolution* 69: 694–703. <https://doi.org/10.1007/s00040-015-0446-y>
- Carrizo TF, Scheffrahn RH, Křeček J (2015) *Compositermes bani* sp. n. (Isoptera, Termitidae, Apicotermitinae), a new species of soldierless termite from Bolivia. *Zootaxa* 3941: 294–298. <https://doi.org/10.11646/zootaxa.3941.2.10>
- Darlington JPEC (1992) Survey of termites in Guadeloupe, Lesser Antilles (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae). *Florida Entomologist* 75: 104–109. <https://doi.org/10.2307/3495487>
- Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9: 772–772. <https://doi.org/10.1038/nmeth.2109>
- De Queiroz A (2005) The resurrection of oceanic dispersal in historical biogeography. *Trends in Ecology and Evolution* 20: 68–73. <https://doi.org/10.1016/j.tree.2004.11.006>
- deWaard JR, Ivanova NV, Hajibabaei M, Hebert PDN (2008) Assembling DNA Barcodes: analytical Protocols. In: Martin C (Ed.) *Methods in Molecular Biology: Environmental Genetics*, Humana Press Inc., Totowa USA, 275–293. https://doi.org/10.1007/978-1-59745-548-0_15

- Drummond AJ, Suchard MA, Xie D, Rambaut A (2012) Bayesian Phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* 29: 1969–1973. <https://doi.org/10.1093/molbev/mss075>
- Emerson AE (1925) The termites of Kartabo, Bartica District, British Guiana. *Zoologica*, New York, 6: 291–459.
- Engel MS, Grimaldi DA, Krishna K (2009) Termites (Isoptera): their phylogeny, classification, and rise to ecological dominance. *American Museum Novitates* 3650: 1–27. <https://doi.org/10.1206/651.1>
- Evans TA (2011) Invasive termites. In: Bignell D, Roisin Y, Lo N (Eds) *Biology of termites: A modern synthesis*. Springer Netherlands, Dordrecht, 519–562. https://doi.org/10.1007/978-90-481-3977-4_19
- Fontes LR (1986) Two new genera of soldierless Apicotermitinae from the Neotropical region (Isoptera, Termitidae). *Sociobiology* 12: 285–297.
- Grassé P-P, Noirot C (1954) *Apicotermes arquieri* (Isoptere): ses constructions, sa biologie. Considerations generales sur la sousfamille des Apicotermitinae nov. *Annales des Sciences Naturelles, Zoologie* (11) 16(3-4): 345–388.
- Hebert PDN, Cywinska A, Ball S, deWaard J (2003) Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London series B - Biological Sciences* 270: 313–321. <https://doi.org/10.1098/rspb.2002.2218>
- Hoy DR (1961) Agricultural land use of Guadeloupe. No. 12 National Academies. <https://doi.org/10.1111/j.1467-8306.1962.tb00424.x>
- Krishna K, Grimaldi DA, Krishna V, Engel MS (2013a) Treatise on the Isoptera of the world. Vols. 1–6. *Bulletin of the American Museum of Natural History* 377. <https://doi.org/10.1206/377.6>
- Mathews AGA (1977) *Studies on Termites from the Mato Grosso State, Brazil*. Rio de Janeiro: Academia Brasileira de Ciências, 267 pp.
- Noirot C (2001) The gut of termites (Isoptera). *Comparative anatomy, systematics, phylogeny. II. Higher termites*. *Annales de la Société Entomologique de France (N. S.)* 37: 431–471. <https://doi.org/10.1080/00379271.2009.10697634>
- Rambaut A, Suchard MA, Xie D, Drummond A J (2014) Tracer v1.6. <http://beast.bio.ed.ac.uk/Tracer> [15/12/2016]
- Samper A, Quidelleur X, Lahitte P, Mollex D (2007) Timing of effusive volcanism and collapse events within an oceanic arc island: Basse-Terre, Guadeloupe archipelago (Lesser Antilles Arc). *Earth and Planetary Science Letters* 258: 175–191. <https://doi.org/10.1016/j.epsl.2007.03.030>
- Sands WA (1972) The Soldierless Termites of Africa: (Isoptera: Termitidae). *Bulletin of the British Museum of Natural History* 18. Trustees of the British Museum, 9 Pl., 661 Text-fig., 244 pp.
- Scheffrahn RH (2013) *Compositermes vindai* (Isoptera: Termitidae: Apicotermitinae), a new genus and species of soldierless termite from the Neotropics. *Zootaxa* 3652: 381–391. <https://doi.org/10.11646/zootaxa.3652.3.6>
- Scheffrahn RH, Křeček J (2001) New World revision of the termite genus *Procryptotermes* (Isoptera: Kalotermitidae). *Annals of the Entomological Society of America* 94: 530–539. [https://doi.org/10.1603/0013-8746\(2001\)094\[0530:nwrott\]2.0.co;2](https://doi.org/10.1603/0013-8746(2001)094[0530:nwrott]2.0.co;2)

- Scheffrahn RH, Jones SC, Křeček J, Chase JA, Mangold JR, Su N-Y (2003a) Taxonomy, distribution, and notes on the termites (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae) of Puerto Rico and the US Virgin Islands. *Annals of the Entomological Society of America* 96: 181–201. [https://doi.org/10.1603/0013-8746\(2003\)096\[0181:tdanot\]2.0.co;2](https://doi.org/10.1603/0013-8746(2003)096[0181:tdanot]2.0.co;2)
- Scheffrahn RH, Křeček J, Maharajh B, Chase JA, Mangold JR, Starr CK (2003b) Termite fauna (Isoptera) of Trinidad & Tobago, West Indies. *Occasional Papers of the Department of Life Sciences, University of the West Indies* 12: 33–38.
- Scheffrahn RH, Křeček J, Chase JA, Maharajh B, Mangold JR (2006) Taxonomy, biogeography, and notes on termites (Isoptera: Kalotermitidae, Rhinotermitidae, Termitidae) of the Bahamas and Turks and Caicos Islands. *Annals of the Entomological Society of America* 99: 463–486. [https://doi.org/10.1603/0013-8746\(2006\)99\[463:tbanot\]2.0.co;2](https://doi.org/10.1603/0013-8746(2006)99[463:tbanot]2.0.co;2)
- Scotese CR (2004) A continental drift flipbook. *The Journal of Geology* 112: 729–741. <https://doi.org/10.1086/424867>
- Snyder TE (1949) Catalog of termites (Isoptera) of the world. *Smithsonian Miscellaneous Collections* 112 (3953): 1–490.
- Tonini F, Hochmair HH, Scheffrahn RH, DeAngelis DL (2014) Stochastic spread models: A comparison between an individual-based and a lattice-based model for assessing the expansion of invasive termites over a landscape. *Ecological Informatics* 24: 222–230. <https://doi.org/10.1016/j.ecoinf.2014.09.011>

Isolated populations of the bush-cricket *Pholidoptera frivaldszkyi* (Orthoptera, Tettigoniidae) in Russia suggest a disjunct area of the species distribution

Peter Kaňuch¹, Martina Dorková¹, Andrey P. Mikhailenko²,
Oleg A. Polumordvinov³, Benjamín Jarčuška¹, Anton Krištín¹

1 Institute of Forest Ecology, Slovak Academy of Sciences, L. Štúra 2, 960 53 Zvolen, Slovakia **2** Moscow State University, Department of Biology, Botanical Garden, Leninskie Gory 1, Moscow 119991, Russia **3** Penza State University, Department of Zoology and Ecology, Lermontova 37, Penza 440602, Russia

Corresponding author: Peter Kaňuch (kanuch@netopiere.sk)

Academic editor: F. Montealegre-Z | Received 20 February 2017 | Accepted 14 March 2017 | Published 4 April 2017

<http://zoobank.org/EE2C7B17-006A-4836-991E-04B8038229B4>

Citation: Kaňuch P, Dorková M, Mikhailenko AP, Polumordvinov OA, Jarčuška B, Krištín A (2017) Isolated populations of the bush-cricket *Pholidoptera frivaldszkyi* (Orthoptera, Tettigoniidae) in Russia suggest a disjunct area of the species distribution. ZooKeys 665: 85–92. <https://doi.org/10.3897/zookeys.665.12339>

Abstract

Phylogenetic analysis and assessment of the species status of mostly isolated populations of *Pholidoptera frivaldszkyi* in south-western Russia occurring far beyond the accepted area of the species distribution in the Carpathian-Balkan region were performed. Using the mitochondrial DNA cytochrome *c* oxidase subunit I gene fragment, we found a very low level of genetic diversity in these populations. Phylogeographic reconstruction did not support recent introduction events but rather historical range fragmentation. The grouping of the Russian and Romanian haplotypes in a distinct phylogenetic clade suggests that the pre-glacial range of *P. frivaldszkyi* had extended towards the Ponto-Caspian region, with considerable gene flow between different refugia. However, post-glacial northward expansion of the species from supposed Caucasus refugia contributed most likely to the current disjunct distribution of this relict-like bush-cricket.

Keywords

Declining species, Insecta, mountain habitats, mtDNA, phylogeography, range fragmentation

Introduction

The Green dark bush-cricket, *Pholidoptera frivaldszkyi* (Herman, 1871), is a regionally rare and endangered grassland-dwelling Orthoptera (Tettigoniidae) species with a decreasing population trend (Krištín and Iorgu 2014; Hochkirch et al. 2016). Genetic structure (mitochondrial DNA) and variation of morphological traits as individually specific pattern of black spots on the light green shield and head in fragmented and isolated populations of this flightless sedentary insect occurring in central and south-eastern Europe confirm the species' relict-like character (Fabriciusová et al. 2008; Kaňuch et al. 2014). Scarce records have determined its main distribution area in the Carpathian Mountains and mountains on the Balkan Peninsula, with an emphasis on the former (e.g. Harz 1969; Nagy 2005; Warchałowska-Śliwa et al. 2005; Fabriciusová et al. 2008; Iorgu et al. 2008; Chobanov and Mihajlova 2010; Krištín et al. 2013; Hochkirch et al. 2016). Findings further to the north-east, beyond the Carpathian massif, reported from Ukraine and Russia were relatively old, unlocalised or incomplete (e.g. Medvedev 1954; Bey-Bienko 1964, 1970; Yakushenko et al. 1984; Heller et al. 1998). Such unreliable character of occurrence data together with questioning of the species status due to song differences in Russian populations (Heller 1988) gave rise to doubts and therefore the only distribution area of *P. frivaldszkyi* was validated for Carpathian-Balkan region also in the recent check-list of European Orthoptera fauna (cf. Hochkirch et al. 2016). However, several isolated populations have recently been found or rediscovered in Russia (Mikhailenko and Polumordvinov 2015) thus confirming the species presence in that area. Thanks to collected tissues of specimens we could perform phylogenetic analysis and assessment of the populations origin there as either a range fragmentation or the result of some introduction events. In this article we report the phylogeographic pattern of *P. frivaldszkyi* populations in Russia at the maternally-inherited mtDNA level and discuss our results with recent species inference from the Carpathian-Balkan region (Kaňuch et al. 2014).

Materials and methods

A total of 26 adult individuals of *P. frivaldszkyi* (12 males and 14 females) were collected at seven sites (3–6 ind. per site) from the Kursk (sites Petropavlovka, Bogatyrevo, Panino), Tambov (Novospasskoe, Khabotovo, Ranino) and Penza (Krutec) regions in Russia (51.5367°–53.0925°N, 36.0906°–44.5840°E, 140–230 m a.s.l., Fig. 1; for a detailed description of the sites, see in Mikhailenko and Polumordvinov 2015), between June 30th and August 3rd 2016. Extraction of genomic DNA from muscle tissue and amplification of a fragment of the mitochondrial cytochrome *c* oxidase subunit I (*COI*) gene from each sampled individual followed the protocol described in Kaňuch et al. (2014). In the phylogenetic analyses, we employed the HKY+I model

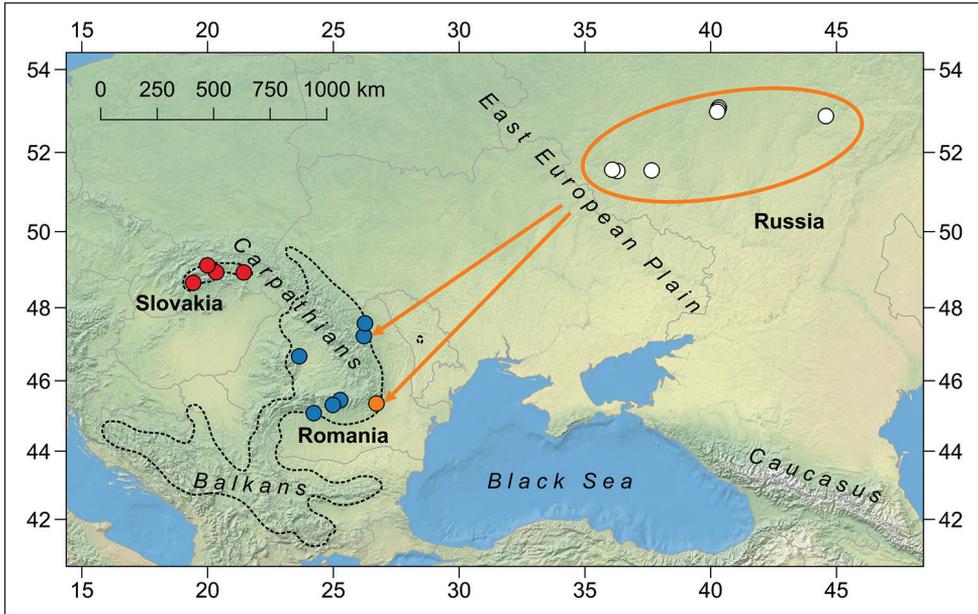


Figure 1. Sampled sites of *Pholidoptera frivaldszkyi* populations in Central and Eastern Europe. Three geographically homogeneous genetic clusters in the Carpathian Mountains defined by spatial analysis of molecular variance are colour coded according to Kaňuch et al. (2014). Arrows denote sites in eastern Romania where individuals that share the most similar haplotypes to populations found in Russia (ellipse) have occurred (see Fig. 2). The species range validated by the IUCN Red List (Hochkirch et al. 2016) is outlined by the dotted line.

that was previously determined as the best-fit substitution site evolutionary model for the organism studied (Kaňuch et al. 2014). We reconstructed phylogenetic relationships among haplotypes using maximum-likelihood (ML) analysis and Bayesian inference. For construction of an ML tree we used the MEGA5.2 software (Tamura et al. 2011), for which an initial tree was built using the neighbour-joining method, and variants of the topology were created using the nearest neighbour interchange method. A bootstrap analysis with 1000 replicates was performed to determine the support values for each node. Bayesian inference was performed with MrBayes 3.2 software (Ronquist et al. 2012). Markov chain Monte Carlo sampling was performed with four chains that were run twice, producing one million replicates, and sampled every 100 generations, from which the first 250,000 generations were discarded as burn-in (subsequent combination of the runs was done in a default manner). The remaining trees were used to calculate the posterior probabilities of branches in a 50% majority-rule consensus topology. Sequences of four related *Pholidoptera* species and *Eupholidoptera danconai* were also amplified or downloaded from GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>), respectively, in order to use them as outgroup species in rooted trees.

Results and discussion

A very low level of genetic diversity was found within seven mostly isolated populations of *P. frivaldszkyi* in Russia. Analysis of the 778 bp long sequences of mtDNA *COI* gene in 26 individuals revealed only two (0.3%) variable sites with three unique haplotypes (GenBank accession numbers KY554960–KY554962), which may indicate a strong demographic decline (cf. Kaňuch et al. 2014). All but three individuals shared the haplotype pf14 (haplotype pf15, 2 ind., Bogatyrevo; pf16, 1 ind., Panino). The Russian and two other haplotypes from eastern Romania (pf7, pf10) grouped together in a distinct clade having significant statistical support in both phylogenetic reconstructions (Fig. 2). Furthermore, the high level of genetic differentiation in eastern Romania previously found by spatial analysis of molecular variance (Kaňuch et al. 2014) suggests a possible phylogeographic connection between the Russian and Carpathian populations (Fig. 1). The ratio of the black spotted area on the males' shields, a quantitative trait that retains useful information on population genetic structure (Kaňuch et al. 2014), has also supported such a scenario. In Russian specimens, the light or intermediate phenotype prevailed (data not presented), similarly to the Romanian specimens (Kaňuch et al. 2014).

The well preserved mountain meadows in the Carpathian-Balkan region (average altitude 650 m a.s.l.) are considered as typical habitat for *P. frivaldszkyi* (e.g. Nagy 2005; Fabriciusová et al. 2008; Iorgu et al. 2008; Krištín et al. 2013); thus, one could have expected that lowland populations in the remote (1300–2400 km) East European Plain should be founded by unintentional vector-born or human-mediated introductions. Similar events have already been confirmed in some Orthoptera species (Wagner 2004; Kaňuch et al. 2013). However, the almost uniform genetic diversity of the mostly isolated Russian populations spread over a relatively large area (similar in size to the populations in the Carpathians; Fig. 1) rejects this hypothesis. A reverse option that some individual lineages in eastern Romania were introduced recently from Russia is more likely. However, differentiation among and within all the Romanian populations is less pronounced compared to adjacent (~500 km) and genetically and morphologically well differentiated cluster of populations in Slovakia (cf. Kaňuch et al. 2014).

The most plausible evolutionary explanation of the observed phylogeographic pattern is range contraction during the last glacial period and subsequent post-glacial species expansion. Traces of a genetic connection between the eastern Romanian and Russian populations suggest that the pre-glacial range of *P. frivaldszkyi* also extended towards the Ponto-Caspian region, similarly to the ranges of many other recent Orthoptera species (e.g. Heller et al. 1998). After the retreating of ice (<18 ka before the present), re-colonisation of Eastern Europe and Russia would then have been from the southern Carpathians or Balkans and from the Caucasus refugia (Hewitt 1999). Such post-glacial expansions of some eastern lineages from the Caucasus towards the north have been also inferred in similar relict (Todisco et al. 2010) and related insect species (Cooper et al. 1995). On the other hand, the little genetic differentiation found between these lineages (Fig. 2) is probably due to considerable gene flow between the

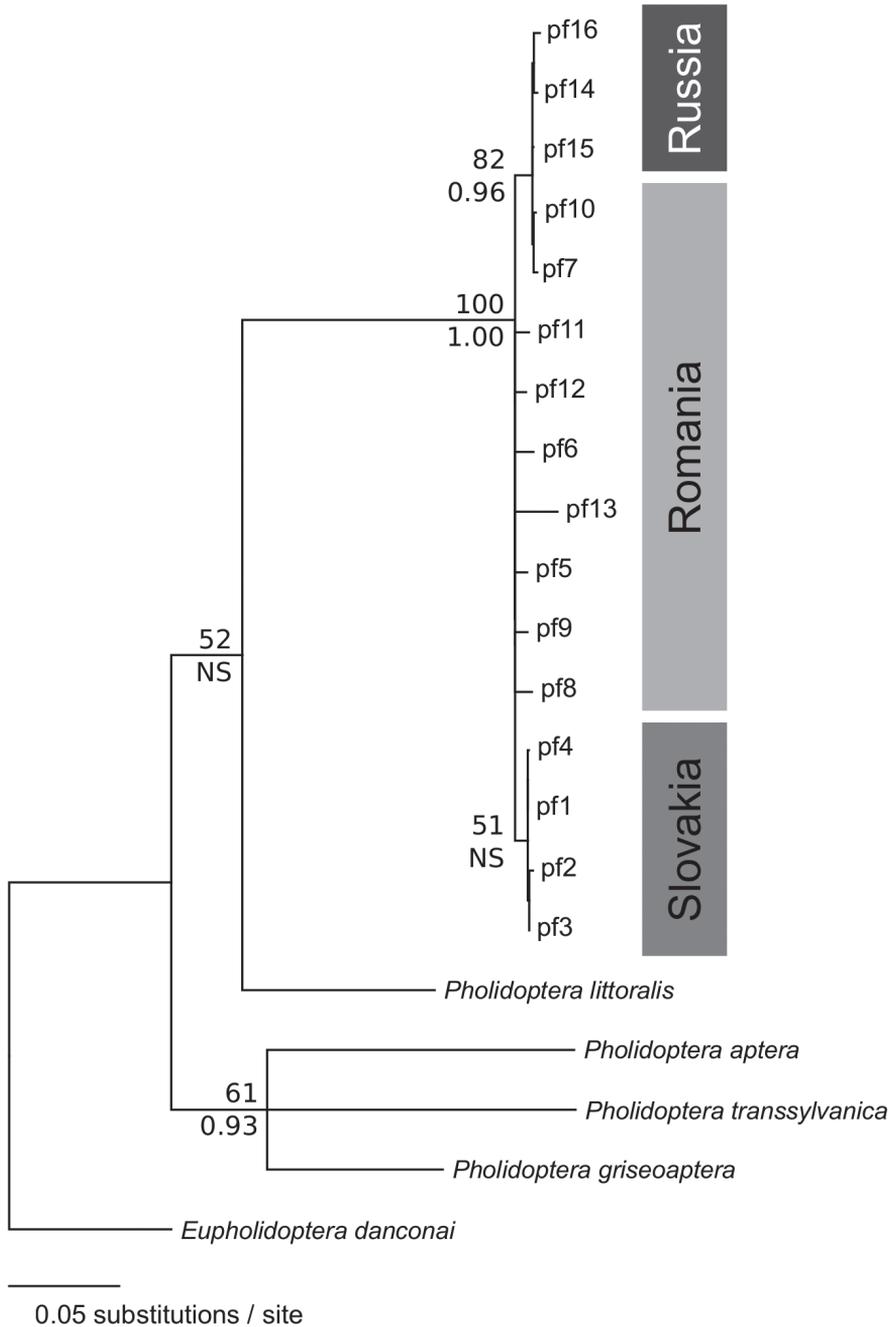


Figure 2. Maximum-likelihood (ML) phylogenetic tree for 16 haplotypes of *Pholidoptera frivaldszkyi* (pf1–pf16; GenBank accession numbers KF706416–KF706428, KY554960–KY554962) with outgroup species (KC852400, KY554963–KY554966) based on a 778 bp fragment of the mtDNA *COI* gene. Tree topology and branch lengths of Bayesian inference were congruent with ML analysis. Nodes with significant support values are indicated (upper, ML bootstrap > 50%; lower, Bayesian posterior probability > 0.90).

Mediterranean and Pontic refugia during the last ice-age (Schmitt 2007). Although some very isolated populations in the East European Plain (see Bey-Bienko 1964; Pushkar 2009) as former stepping stones between the Carpathian-Balkan and Russian lineages may still exist (cf. Chobanov and Mihajlova 2010), the gene flow would be very restricted nowadays (Habel et al. 2010). Thus, strong historical range fragmentation most likely produced the current disjunct distribution of *P. frivaldszkyi*. This situation could therefore attract even more attention on the evolution and ecology (e.g. relict habitats, Kaňuch et al. 2014, Mikhailenko and Polumordvinov 2015; song differences, Heller 1988) of this bush-cricket.

Acknowledgements

We are grateful to Sandra Vigiášová for her lab assistance and to Sigfrid Ingrisch and Klaus-Gerhard Heller for their comments on the manuscript. This study was supported by the Slovak Scientific Grant Agency VEGA (grants no. 2/0061/15, 2/0097/16).

References

- Bey-Bienko GY (1970) Orthopterans (Orthopteroidea) of protected areas near Kursk as indicators of the local landscape. *Zhurnal obshchey biologii* 21(1): 30–46. [In Russian]
- Bey-Bienko GY (1964) Orthoptera. In: Bey-Bienko GY (Ed.) Key to identification of insects in Soviet Union (USSR) I. Nauka, Moskva, Saint Petersburg, 205–284. [In Russian]
- Chobanov D, Mihajlova B (2010) Orthoptera and Mantodea in the collection of the Macedonian Museum of Natural History (Skopje) with an annotated check-list of the groups in Macedonia. *Articulata* 25: 73–107.
- Cooper SJB, Ibrahim KM, Hewitt GM (1995) Postglacial expansion and genome subdivision in the European grasshopper *Chorthippus parallelus*. *Molecular Ecology* 4: 49–60. <https://doi.org/10.1111/j.1365-294X.1995.tb00191.x>
- Fabriciusová V, Kaňuch P, Krištín A (2008) Body size patterns of *Pholidoptera frivaldszkyi* (Orthoptera) in very isolated populations. *Journal of Orthoptera Research* 17: 171–176. <https://doi.org/10.1665/1082-6467-17.2.171>
- Habel JC, Augenstein B, Meyer M, Nève G, Rödder D, Assmann T (2010) Population genetics and ecological niche modelling reveal high fragmentation and potential future extinction of the endangered relict butterfly *Lycaena helle*. In: Habel JC, Thorsten A (Eds) *Relict species*. Springer, Berlin, 417–439. https://doi.org/10.1007/978-3-540-92160-8_25
- Harz K (1969) Die Orthopteren Europas I. *Series Entomologica* 5. Dr. W. Junk BV, Hague, 749 pp.
- Heller K-G (1988) Bioakustik der europäischen Laubheuschrecken. *Ökologie in Forschung und Anwendung* 1: 1–358.
- Heller K-G, Korsunovskaya O, Ragge DR, Vedenina V, Willemsse F, Zhantiev RD, Frantsevich L (1998) Check-List of European Orthoptera. *Articulata* 7: 1–61.

- Hewitt GM (1999) Post-glacial re-colonization of European biota. *Biological Journal of the Linnean Society* 68: 87–112. <https://doi.org/10.1111/j.1095-8312.1999.tb01160.x>
- Hochkirch A, Iorgu IȘ, Lemonnier-Darcemont M, Szövényi G, Krištín A, Ivković S, Chobanov DP, Willemsse LPM, Skejo J, Pushkar T, Puskas G, Sirin D, Vedenina V (2016) *Pholidoptera frivaldszkyi*. The IUCN Red List of Threatened Species 2016, e.T62148031A74621932. [Accessed 30 January 2017] <https://doi.org/10.2305/IUCN.UK.2016-3.RLTS.T62148031A74621932.en>
- Iorgu IȘ, Pisičă E, Păiș L, Lupu G, Iușan C (2008) Checklist of Romanian Orthoptera (Insecta: Orthoptera) and their distribution by ecoregions. *Travaux du Muséum d'Histoire Naturelle "Grigore Antipa"* 51: 119–135.
- Kaňuch P, Berggren Å, Cassel-Lundhagen A (2013) Colonization history of *Metrioptera roeselii* in northern Europe indicates human-mediated dispersal. *Journal of Biogeography* 40: 977–987. <https://doi.org/10.1111/jbi.12048>
- Kaňuch P, Jarčuška B, Iorgu EI, Iorgu IȘ, Krištín A (2014) Geographic variation in relict populations: Genetics and phenotype of bush-cricket *Pholidoptera frivaldszkyi* (Orthoptera) in Carpathians. *Journal of Insect Conservation* 18: 257–266. <https://doi.org/10.1007/s10841-014-9636-6>
- Krištín A, Iorgu IȘ (2014) Red List of Grasshoppers, Bush-crickets and Crickets (Orthoptera) of the Carpathian Mountains. In: Kadlečík J (Ed.) *Carpathian Red List of Forest Habitats and Species*. The State Nature Conservancy of the Slovak republic, Banská Bystrica, 186–199.
- Krištín A, Jarčuška B, Kaňuch P, Iorgu IȘ, Iorgu EI (2013) Notes on Orthoptera (Insecta) and their assemblages in the Romanian Carpathians. *Travaux du Muséum d'Histoire Naturelle "Grigore Antipa"* 56: 19–32. <https://doi.org/10.2478/travmu-2013-0002>
- Medvedev SI (1954) Features of distribution of some ecological forms of insects in different landscape-geographical zones of Ukraine. *Zoologicheskii zhurnal* 33: 1245–1263. [In Russian]
- Mikhailenko AP, Polumordvinov OA (2015) Distribution and ecology of the bush-cricket *Pholidoptera frivaldszkyi* (Herman, 1871) (Orthoptera: Tettigoniidae) in European Russia. *Caucasian Entomological Bulletin* 11(2): 271–278. [In Russian with English abstract]
- Nagy B (2005) Orthoptera fauna of the Carpathian basin – recent status of knowledge and revised checklist. *Entomofauna Carpathica* 17: 14–22.
- Pushkar TI (2009) To the Study of Orthopterous Insects (Orthoptera) of the Ukrainian Steppe Natural Reserve “Mykhajlivska Tcilyna” (North-East Ukraine). *Vestnik Zoologii* 22(Supplement): 67–76. [In Ukrainian with English abstract]
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Schmitt T (2007) Molecular biogeography of Europe: Pleistocene cycles and postglacial trends. *Frontiers in Zoology* 4: 11. <https://doi.org/10.1186/1742-9994-4-11>
- Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S (2011) MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution* 28: 2731–2739. <https://doi.org/10.1093/molbev/msr121>

- Todisco V, Gratton P, Cesaroni D, Sbordoni V (2010) Phylogeography of *Parnassius apollo*: hints on taxonomy and conservation of a vulnerable glacial butterfly invader. *Biological Journal of the Linnean Society* 101: 169–183. <https://doi.org/10.1111/j.1095-8312.2010.01476.x>
- Wagner C (2004) Passive dispersal of *Metrioptera bicolor* (Phillipi 1830) (Orthopteroidea: Ensifera: Tettigoniidae) by transfer of hay. *Journal of Insect Conservation* 8: 287–296. <https://doi.org/10.1007/s10841-004-0404-x>
- Warchałowska-Śliwa E, Heller K-G, Maryańska-Nadachowska A (2005) Cytogenetic variability of European Tettigoniinae (Orthoptera, Tettigoniidae): karyotypes, C- and Ag-NOR-banding. *Folia Biologica (Kraków)* 53: 161–171. <https://doi.org/10.3409/173491605775142800>
- Yakushenko BM, Gramma VN, Zakharenko AV, Garazhin VG, Polchaninova NY, Filatov VA, Lezhenina IP (1984) On the fauna and ecology of insects and spiders of “Yamskoy” sector of Tsentralno-Chernozemnyy Reserve. In: *Ecological and faunal studies of central forest-steppe in European part of the USSR, the collection of scientific papers of Central Research Laboratory of hunting and nature reserves of Glavokhota RSFSR*. Moscow, 51–54. [In Russian]

Six new species of the genus *Exocelina* Broun, 1886 from Wano Land, New Guinea (Coleoptera, Dytiscidae, Copelatinae)

Helena Shaverdo¹, Michael Wild², Bob Sumoked³, Michael Balke⁴

1 Naturhistorisches Museum Wien, Burgring 7, 1010 Vienna, Austria **2** PO Box 369, Sentani 99352, Jayapura, Papua, Indonesia **3** Walian 2, Tomohon Selatan, N Sulawesi 95439, Indonesia **4** SNSB-Zoologische Staatssammlung München, Münchhausenstraße 21, D-81247 Munich, Germany and GeoBioCenter, Ludwig-Maximilians-University, Munich, Germany

Corresponding author: *Helena Shaverdo* (shaverdo@mail.ru; helena.shaverdo@nhm-wien.ac.at)

Academic editor: *M. Michat* | Received 13 January 2017 | Accepted 28 February 2017 | Published 4 April 2017

<http://zoobank.org/4D5230AC-67CB-47AD-AF2F-051CA10D9724>

Citation: Shaverdo H, Wild M, Sumoked B, Balke M (2017) Six new species of the genus *Exocelina* Broun, 1886 from Wano Land, New Guinea (Coleoptera, Dytiscidae, Copelatinae). ZooKeys 665: 93–120. <https://doi.org/10.3897/zookeys.665.11792>

Abstract

Six new species of New Guinea *Exocelina* Broun, 1886 are described in this paper: *E. iratoi* sp. n., *E. likui* sp. n., *E. pui* sp. n., *E. pulukensis* sp. n., *E. tomhansi* sp. n., and *E. wigodukensis* sp. n. Although different morphologically, together with *Exocelina ascendens* (Balke, 1998), *E. bagus* (Balke & Hendrich, 2001), and *E. ransikiensis* Shaverdo, Panjaitan & Balke, 2016, they are found to form a monophyletic clade and be closely related to representatives of the *E. ekari*-group, based on preliminary analysis of sequence data. An identification key to the species is provided, and important diagnostic characters are illustrated. The present data on the species' distribution show that most of them are local endemics.

Keywords

Copelatinae, Dytiscidae, *Exocelina*, New Guinea, new species, key

Introduction

This paper is in continuity with our previous taxonomic studies on the New Guinea species of the diving beetle genus *Exocelina* Broun, 1886 (Balke 1998, 1999, Shaverdo and Balke 2014, Shaverdo et al. 2005, 2012, 2013, 2014, 2016a, b, c, d). *Exocelina* species have also been used as a model to reveal lineage diversification trends in New Guinea where the complex geological formation of the island gave rise to intriguing biogeographic patterns (Toussaint et al. 2014). The genus also served as a model taxon to study diversification across major Melanesian islands (Toussaint et al. 2015).

Here, the discovery of six new *Exocelina* species is reported as the result of surveys in the most remote heart of Papua, at the interface of the central highlands and the central Papuan lake plains. The preliminary molecular analysis of these species and old material of *Exocelina ascendens* (Balke, 1998) from the Star Mountains of the eastern Papua, suggests that they form a monophyletic clade which also includes *E. bagus* (Balke & Hendrich, 2001) and the recently described *E. ransikiensis* Shaverdo, Panjaitan & Balke, 2016. As shown on the example of *E. bagus* and *E. ransikiensis* (undescribed sp. MB1269) in the phylogenetic trees (Figs 1–2) by Toussaint et al. (2014), this clade is closely related to the representatives of the *E. ekari*-group and consists of very distinct, morphologically isolated lineages, which we treat as species groups here. An identification key to all included species is provided.

Materials and methods

The present work is based on the material from the following collections:

- CGW** collection of Dr. Günther Wewalka, Vienna, Austria
MZB Museum Zoologicum Bogoriense, Cibinong, Indonesia
NHMW Naturhistorisches Museum Wien, Vienna, Austria
ZSM Zoologische Staatssammlung München, Munich, Germany

All methods follow those described in detail in our previous articles (Shaverdo and Balke 2014, Shaverdo et al. 2012, 2014).

Checklist and distribution of the species

Abbreviations: P – Papua; WP – West Papua.

Exocelina ascendens-group

- | | |
|---|------------------------|
| 1. <i>Exocelina ascendens</i> (Balke, 1998) | P: Pegunungan Bintang |
| 2. <i>Exocelina tombansi</i> sp. n. | P: Puncak Jaya, Puncak |

Exocelina bagus-group

- | | |
|--|-----------|
| 3. <i>Exocelina bagus</i> (Balke & Hendrich, 2001) | P: Nabire |
|--|-----------|

- Exocelina iratoi*-group**
4. *Exocelina iratoi* sp. n. P: Puncak
- Exocelina likui*-group**
5. *Exocelina likui* sp. n. P: Puncak Jaya
- Exocelina pui*-group**
6. *Exocelina pui* sp. n. P: Puncak
- Exocelina ransikiensis*-group**
7. *Exocelina ransikiensis* Shaverdo, Panjaitan & Balke, 2016 WP: Manokwari; P: Nabire
- Exocelina wigodukensis*-group**
8. *Exocelina wigodukensis* sp. n. P: Puncak Jaya
9. *Exocelina pulukensis* sp. n. P: Puncak Jaya

Species descriptions

Exocelina ascendens-group

1. *Exocelina ascendens* (Balke, 1998)

Figs 3, 11

Copelatus (*Papuadytes*) *ascendens* Balke, 1998: 322; Nilsson 2001: 76 (catalogue).

Papuadytes ascendens (Balke, 1998): Nilsson and Fery 2006: 56 (comb. n.).

Exocelina ascendens (Balke, 1998): Nilsson 2007: 33 (comb. n.).

Type locality. Papua: Pegunungan Bintang Regency, trek between Aipomek and Diruemna, 04°25'S; 139°57'E, 2600 m a.s.l.

Type material studied. *Holotype*: male “IRIAN JAYA, 3.9.1992 Aipomek - Diuremna [sic!] 139°57'E 04°25'S 2600m, leg. Balke (35)”, “HOLOTYPUS” [red], “*Copelatus ascendens* Balke des. 1997” [red] (NHMW). *Paratypes*: 4 males, 2 females with the same label as the holotype and additionally with red labels “*Paratypus Copelatus ascendens* Balke des. 1997”, one of the males with an additional label “M. Balke 3282” [green], another male with two additional labels “M. Balke 3283” [green] and “M. Balke 6409” [green text] (NHMW). 1 male, 2 females “IRIAN JAYA, 9.9.1992 Kono - Angguruk 139°47'E 04°19'S 2600m, leg. Balke (44)”, “*Paratypus Copelatus ascendens* Balke des. 1997” [red] (NHMW), note: the original description says “2 males and 1 female”, it is probably a mistake in the sex identification or type error. 4 males, 3 females “IRIAN JAYA, 24.-26.9.1993 Eipomek [sic!] Gebiet Eipomek [sic!] - Diruemna”, “ca. 140°01'E 04°27'S 1800-2600m, leg. M. Balke (21 [crossed out] -22)”, “*Paratypus Copelatus ascendens* Balke des. 1997” [red] (NHMW, CGW).

Diagnosis. Beetle large (TL-H 5.3–5.75 mm), elongate; piceous, with dark brown pronotal sites and head anteriorly; submatt, with fine but evident punctation and rather strongly impressed microreticulation; pronotum with distinct lateral bead; male antennae simple, slender (Fig. 3); male protarsomere 4 with small (slightly larger than more laterally situated large seta), weakly curved anterolateral hook-like seta; male protarsomere 5 ventrally with anterior row of 23 and posterior row of 8 short, strong,

spine-like setae (Fig. 11D); median lobe evenly curved, pointed in lateral view and evenly tapering, with broadly pointed apex in ventral view, on both lateral sides with numerous fine setae situated linearly on anterior half of distal part of median lobe; paramere robust, with notch on dorsal side and very dense, strong setae on subdistal part; proximal setae sparse and fine (Fig. 11A–C). For complete description, see Balke (1998).

Distribution. Papua: Pegunungan Bintang Regency. The species is known only from the type material (Fig. 19).

2. *Exocelina tomhansi* sp. n.

<http://zoobank.org/C135B374-683A-469E-BB57-F4A115245841>

Figs 4, 12

Type locality. Papua: Puncak Jaya Regency, 03°36'42.5"S; 137°31'40.1"E.

Type material. *Holotype*: male “Indonesia: Papua, Wano Land, S of pass to lake plains, 1700m, 2.ix.2014, -3,6117913 137,5277983, Balke & Wild (Pap022)”, “M.Balke 6512” [green text] (MZB). *Paratypes*: 1 female with the same label as the holotype and with an additional label “M.Balke 6513” [green text] (ZSM). 1 female “Indonesia: Papua, Wano Land, creek @ jungle helipad, 870m, 4.ix.2014, -3,584077 137,5042947, Balke & Wild (Pap027)” (ZSM).

Diagnosis. Beetle medium-sized, oblong-oval, piceous, with brown sides of pronotum, dorsal punctation inconspicuous, microreticulation weakly impressed; pronotum without lateral bead; male antennae simple; male protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta; median lobe evenly curved, pointed in lateral view and evenly tapering, with broadly pointed apex in ventral view, on both lateral sides with numerous short, thick setae situated on anterior half of distal part of median lobe; paramere robust, with notch on dorsal side and very dense, strong setae on subdistal part; proximal setae sparse and fine. The new species is very similar to *E. ascendens* in shape of the median lobe and in shape and setation of the paramere but distinctly differs from it having smaller body size, shiny dorsal surface due to much more weakly impressed microreticulation, larger anterolateral hook-like seta on the male protarsomere 4, longer setae of the male protarsomere 5 and, especially in absence of the pronotal bead.

Description. *Size and shape*: Beetle medium-sized (TL-H 4.5–4.75 mm, TL 4.8–5.1 mm, MW 2.35–2.45 mm), with oblong-oval habitus, broadest at elytral middle. *Coloration*: Dorsally piceous, with reddish brown to brown narrow anterior margin of head and sides of pronotum; one female with head paler; head appendages and legs yellowish red to reddish brown, metathoracic legs darker distally (Fig. 4).

Surface sculpture: Head with sparse punctation (spaces between punctures 2–3 times size of punctures), evidently finer and sparser anteriorly; diameter of punctures smaller than to almost equal to diameter of cells of microreticulation. Pronotum with much sparser and finer punctation than head. Elytra with extremely sparse and fine

punctuation, almost invisible. Pronotum and elytra with slightly impressed microreticulation, dorsal surface shiny. Head with microreticulation stronger. Metaventricle and metacoxae distinctly microreticulate, metacoxal plates with longitudinal striae and transverse wrinkles. Abdominal ventrites with distinct microreticulation, striae, and very fine and sparse punctuation.

Structures: Pronotum without lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, smooth and slightly rounded anteriorly. Blade of prosternal process lanceolate, narrow, slightly convex, with distinct lateral bead and few setae; neck and blade of prosternal process evenly jointed. Abdominal ventrite 6 broadly rounded or slightly truncate apically.

Male: Antenna simple (Fig. 4). Pro- and mesotarsomeres 1–3 not dilated. Protarsomere 4 cylindrical, narrow, with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior band of 26 and posterior row of six relatively long, not pointed setae (Fig. 12D). Median lobe evenly curved, pointed in lateral view and evenly tapering, with broadly pointed apex in ventral view, on both lateral sides with numerous short, thick setae situated on anterior half of distal part of median lobe. Paramere robust, with notch on dorsal side; subdistal part large and elongate, with very dense, strong setae; proximal setae sparse and fine (Fig. 12A–C). Abdominal ventrite 6 slightly truncate ventrally, with 18–19 fine lateral striae on each side.

Holotype: TL-H 4.75 mm, TL 5.1 mm, MW 2.45 mm.

Female: Pro- and mesotarsi not modified. Abdominal ventrite 6 without lateral striae.

Distribution. Papua: Puncak Jaya and Puncak Regencies (Fig. 19).

Etymology. The species is named in honour of helicopter pilot Tom Hans who has served the Papuan people for many years. The name is a noun in the genitive case.

Exocelina bagus-group

3. *Exocelina bagus* (Balke & Hendrich, 2001)

Figs 6, 14

Copelatus (Papuadytes) speciosus Balke & Hendrich, 1998: 336; Nilsson 2001: 77 (catalogue).

Copelatus (Papuadytes) bagus Balke & Hendrich, in Balke 2001: 361.

Exocelina bagus (Balke & Hendrich, 2001): Nilsson 2007: 33 (as *E. бага*, comb.n.).

Exocelina bagus MB4915: Toussaint et al. 2014: Supplementary figs 1–4, Tab. 2.

Type locality. Papua: Nabire Regency, 54–55 km of road Nabire to Enarotali, ca. 03°29.80'S; 135°43.89'E. *Note:* the road only goes up to Enarotali, Ilaga is much further in the mountains, therefore, people now refer to the road as Nabire-Enarotali.

Type material studied. *Holotype:* male “IR90-11: W. New Guinea, Trek Nabire-Ilaga, km55, 19.-25.ix.1990, Balke”, “HOLOTYPUS” [red], “*Copelatus specio-*

sus sp.n. Balke des. 1997” [red] (NHMW). *Paratypes*: 9 males, 12 females with the same label as the holotype (NHMW). 6 females “W.-Neuguinea/Paniai Prov. Strasse Nabire-Illaga km 54 700m, 22.–25.9.1990/IR 11 leg: Balke & Hendrich” (NHMW). 7 males, 8 females “IR 20-W. New Guinea, track Nabire-Illaga KM 59, ca.750m, 18.vii.1991, Balke & Hendrich leg.” (NHMW). 1 female “IR 21-W. New Guinea track Nabire-Illaga KM 65, Kali Utowa, 250 M, 18–19.vii.1991 Balke & Hendrich leg.” (NHMW), note: the original description says “one male”, it is probably a mistake in the sex identification or type error. 6 females “IR 23-W. New Guinea, track Nabire-Illaga, KM 62, 250m, 24.vii.1991 Balke & Hendrich leg.” (NHMW). 1 female “IR 24-W. New Guinea, track Nabire-Illaga Km 54, basecamp, 750m, 25.vii.1991 Balke & Hendrich leg.” (NHMW). All paratypes are additionally with red labels “*Paratypus Copelatus speciosus* Balke des. 1997”.

Additional material. 10 males, 15 females “IR #91-7 (IR 24). West New Guinea, Nabire-Illaga km 54, 750m, 25.&27.1991 Balke” (NHMW). 8 males, 8 females “IRIAN JAYA: Paniai Prov. road Nabire-Illaga, km 54 26./27.8.1996, 750-800m leg. M. Balke (96 # 2)” (NHMW). 6 males, 5 females “IRIAN JAYA: Paniai Prov. road Nabire-Illaga, km 54 30.8.1996, 750m leg. M. Balke (96 # 9)” (NHMW). 2 males “IRIAN JAYA: Paniai Prov. road Nabire-Illaga, km 54 10.9.1996, 900m leg. M. Balke (96 # 19)” (NHMW). 7 males, 3 females “IRIAN JAYA: Paniai Prov. road Nabire-Illaga, km 54 10.9.1996, 800m leg. M. Balke (96 # 20)” (NHMW). *Note*: although most of these mentioned above specimens are with the paratype labels, they are not included in the type material of the original description in Balke (1998, p. 336). 1 female “Indonesia: Papua, Road Nabire-Enarotali KM 55, 774m, 22.x.2011, 03 29.796S 135 43.885E, Uncen (PAP09)” (NHMW). 2 males, 1 female “Indonesia: Papua, Road Nabire-Enarotali KM 60, 640m, 22.x.2011, 03 30.474S 135 42.611E, Uncen (PAP10)” (NHMW).

Diagnosis. Beetle medium-sized (TL-H 3.8–4.8 mm), elongate; dark brown, with reddish brown pronotal sites and head anteriorly; submatt, with fine but evident punctation and rather strongly impressed microreticulation; pronotum without lateral bead (Fig. 6; fig. 3 in Balke (1998)); male antennae strongly and modified: antennomeres 2–3 very strongly reduced, 4–6 excessively enlarged and 3 and 7 strongly enlarged (Fig. 6; fig. 16 in Balke (1998)); male protarsomere 4 with large, strongly curved anterolateral hook-like setae; male protarsomere 5 slightly concave ventrally, with anterior band of more than 30 and posterior row of five relatively long, not pointed setae (Fig. 14D); median lobe strongly curved, evenly tapering to apex, apex straight, pointed, with short, thick lateral setae in lateral view, subdistal part of median lobe strongly broadened in ventral view; paramere with distinct dorsal notch and large, elongate subdistal part; subdistal setae very dense, strong, long, proximal setae very sparse, thin, small, weakly visible (Fig. 14A–C; figs 39, 86, 92 in Balke (1998)). For complete description, see Balke (1998).

Distribution. Papua: Nabire Regency. The species is known only from the Mount Gamey area (Fig. 19).

Exocelina iratoi*-group*4. *Exocelina iratoi* sp. n.**

<http://zoobank.org/CAB3EE36-F390-425C-8BBE-7C1BE87B582D>

Figs 5, 13

Type locality. Papua: Puncak Regency, south from Iratoi, 03°54'20.4"S; 137°12'03.2"E.

Type material. *Holotype*: male "Indonesia: Papua Province, S Iratoi, forest, 378m, 22.v.2015, -3,3904028031975, 137,3201, Sumoked & Balke (Pap037)", "M.Balke 6984" [green text] (MZB). *Paratypes*: 1 male with the same label as the holotype (NHMW). 2 females "Indonesia: Papua Province, S Iratoi, forest, 553m, 22.v.2015, -3,391922694, 137,3235278, Sumoked & Balke (Pap038)", one of them with an additional label "M.Balke 6985" [green text] (ZSM).

Diagnosis. Beetle small, oblong-oval, piceous, with dark brown head and pronotum, dorsal punctation inconspicuous, microreticulation weakly impressed; pronotum without lateral bead; male antennae simple; male protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta; apex of median lobe with three small prolongations; paramere without dorsal notch, with long, rather dense, thin setae, situated along dorsal margin, not clearly divided into subdistal and proximal.

In oblong-oval shape of the body, fine dorsal sculpture, and absence of the pronotal bead, the species is similar to many small species of the *E. ekari*-group but distinctly differs from them in shape of the median lobe and paramere.

Description. *Size and shape*: Beetle small (TL-H 3.7–3.9 mm, TL 4–4.25 mm, MW 2–2.1 mm), with oblong-oval habitus, broadest at elytral middle. *Coloration*: Dorsally piceous, with dark brown anterior part of head and sides of pronotum; head appendages and legs yellowish red, metathoracic legs darker distally (Fig. 5).

Surface sculpture: Head with sparse punctation (spaces between punctures 2–3 times size of punctures), evidently finer and sparser anteriorly; diameter of punctures smaller than to almost equal to diameter of cells of microreticulation. Pronotum with much sparser and finer punctation than head. Elytra with extremely sparse and fine punctation, inconspicuous. Pronotum and elytra with slightly impressed microreticulation, dorsal surface shiny. Head with microreticulation stronger. Metaventricle and metacoxae distinctly microreticulate, metacoxal plates with longitudinal striae and transverse wrinkles. Abdominal ventrites with distinct microreticulation, striae, and very fine and sparse punctation.

Structures: Pronotum without lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, smooth and rounded anteriorly. Blade of prosternal process lanceolate, relatively narrow, slightly convex, with distinct lateral bead and few setae; neck and blade of prosternal process evenly jointed. Abdominal ventrite 6 broadly rounded apically.

Male: Antenna simple (Fig. 5). Pro- and mesotarsomeres 1–3 not dilated. Protarsomere 4 cylindrical, narrow, with large, thick, strongly curved anterolateral hook-like

seta. Protarsomere 5 ventrally with anterior row of 20 and posterior row of five relatively long, not pointed setae (Fig. 13D). Median lobe slightly curved, not tapering to apex in lateral view, apex divided into three small prolongations. Paramere without dorsal notch, with long, rather dense, thin setae, situated along dorsal margin, not clearly divided into subdistal and proximal (Fig. 13A–C). Abdominal ventrite 6 broadly rounded apically, without or with 1–3 fine transverse lateral strioles on each side.

Holotype: TL-H 3.7 mm, TL 4 mm, MW 2 mm.

Female: Pro- and mesotarsi not modified. Abdominal ventrite 6 without lateral strioles.

Distribution. Papua: Puncak Regency. The species is known only from the type locality (Fig. 19).

Iratoi is a mixed village of both Edofi and Wano people. It is located just beyond the foot hills coming out of Wano land at the northwestern border of their traditional territory. This area is quite low at an elevation of ca. 200 m, which offers many opportunities to easily access the many small streams and puddles which *Exocelina* inhabits.

Etymology. The name refers to Iratoi, the type locality. The name is a noun in the nominative singular standing in apposition.

Exocelina likui-group

5. *Exocelina likui* sp. n.

<http://zoobank.org/3B1B6701-679A-4646-BCEF-8F09A5ECBF88>

Figs 7, 15

Type locality. Papua: Puncak Jaya Regency, south from Iratoi, 03°23'12.5"S; 137°14'43.5"E.

Type material. *Holotype*: male “Indonesia: Papua Province, S Iratoi, forest, 220m, 21.v.2015, -3,38095162063837, 137,311441982164, Sumoked & Balke (Pap036)”, “M.Balke 6980” [green text] (MZB). *Paratypes*: 1 male, 2 females with the same label as the holotype, one female with an additional label “M.Balke 6981” [green text] (NHMW, ZSM).

Diagnosis. Beetle small, oblong, dark brown to piceous, dorsal punctation dense and coarse, microreticulation distinctly impressed; pronotum without lateral bead; male antennae simple; male protarsomere 4 cylindrical, narrow, with large, thick, strongly curved anterolateral hook-like seta; median lobe slightly curved, with broadly pointed apex in lateral view and abruptly narrowed apically, with apex truncate in ventral view; paramere without dorsal notch, with subdistal setae very dense, strong, long and proximal setae very sparse, thin, small, weakly visible.

In shape of median lobe, the species resembles *E. takime* (Balke, 1998) but distinctly differs from it in absence of the pronotal bead and strong dorsal sculpture. From *E. pui* sp. n., it differs in dense and coarse dorsal punctation and in having medial lobe apically more pointed in lateral view, without lateral setae.

Description. *Size and shape:* Beetle small (TL-H 3.2–3.6 mm, TL 3.8–4.0 mm, MW 1.85–1.95 mm), with oblong habitus, broadest at elytral middle. *Coloration:* Dorsally dark brown to piceous, with head and pronotum paler; head appendages and legs reddish brown distally (Fig. 7).

Surface sculpture: Head with dense, coarse punctation (spaces between punctures 1–2 times size of punctures), finer anteriorly and posteriorly; diameter of punctures equal to diameter of cells of microreticulation. Pronotum with slightly sparser punctation than head. Elytra with dense, coarse punctation, coarser than on pronotum. Pronotum and elytra with distinctly impressed microreticulation, dorsal surface submatt. Head with microreticulation stronger. Metaventricle and metacoxae distinctly microreticulate, with sparse but distinct punctation, metacoxal plates with longitudinal striae and transverse wrinkles. Abdominal ventrites with distinct microreticulation, striae, and sparse, coarse punctation, especially on four last abdominal ventrites.

Structures: Pronotum without lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, smooth, broadly rounded anteriorly. Blade of prosternal process lanceolate, relatively narrow, very slightly convex, with distinct lateral bead and few setae; neck and blade of prosternal process evenly jointed. Abdominal ventrite 6 broadly rounded apically.

Male: Antenna simple (Fig. 7). Pro- and mesotarsomeres 1–3 not dilated. Protarsomere 4 cylindrical, narrow, with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 ventrally with anterior band of more than 40 and posterior row of 14 relatively long, not pointed setae (Fig. 15D). Median lobe slightly curved, with broadly pointed apex in lateral view, and abruptly narrowed apically, with apex slightly truncate in ventral view. Paramere without dorsal notch, with subdistal setae very dense, strong, long and proximal setae very sparse, thin, small, weakly visible. (Fig. 15A–C). Abdominal ventrite 6 broadly rounded apically, 5–6 lateral striae on each side.

Holotype: TL-H 3.5 mm, TL 3.9 mm, MW 1.9 mm.

Female: Pro- and mesotarsi not modified. Abdominal ventrite 6 without lateral striae.

Distribution. Papua: Puncak Jaya Regency. The species is known only from the type locality (Fig. 19).

Etymology. The species is named after Michael Wild's best Wano friend Liku who grew up at Iratoi and hunted many times in the area where the species was collected. The name is a noun in the genitive case.

Exocelina pui-group

6. *Exocelina pui* sp. n.

<http://zoobank.org/19F321EA-88F3-4766-ACF9-9DF953EA40AD>

Figs 8, 16

Type locality. Papua: Puncak Regency, Puluk area, 03°35'56.1"S; 137°27'53.7"E.

Type material. *Holotype*: male “Indonesia: Papua, Wano Land, red clay creek nr cave, 1100m, 3.ix.2014, nr -3.587955 137.5114945, Balke & Wild (Pap024)”, “M.Balke 6518” [green text] (MZB). *Paratypes*: 5 males with the same label as the holotype, one of them with an additional label “M.Balke 6519” [green text] (ZSM).

Diagnosis. Beetle small, dark brown to piceous, with paler anterior part of head and sides of pronotum, dorsal punctation fine, microreticulation distinctly impressed; pronotum without lateral bead; male antennae simple; male protarsomere 4 cylindrical, narrow, with large, thick, strongly curved anterolateral hook-like seta; median lobe slightly curved, with truncate apex in lateral view and abruptly narrowed apically, with apex concave in ventral view, having short, thick subdistal setae laterally; paramere without dorsal notch, with subdistal setae dense, strong, long and proximal setae very sparse, thin, small, weakly visible.

In habitus shape, coloration, and absence of the pronotal bead, *E. pui* sp. n. strongly resembles the small species from the *E. ekari*-group (one of them is its co-occurring species) but it distinctly differs from them in having different shape of the median lobe and paramere. The shape of the median lobe is very similar to that of *E. rivulus* (Balke, 1998), also a co-occurring species, from which *E. pui* sp. n. can be easily distinguished in its smaller size and absence of the pronotal bead. From *E. likui* sp. n., it differs in distinctly finer dorsal punctation and in having median lobe truncate in lateral view, with lateral setae.

Description. *Size and shape*: Beetle small (TL-H 3.35–3.6 mm, TL 3.95–4.0 mm, MW 1.95–2.0 mm), with oblong habitus, broadest at elytral middle. *Coloration*: Head dark brown, almost piceous posteriorly and reddish brown anteriorly. Pronotum and elytra dark brown to piceous, pronotal sides reddish brown; head appendages and legs reddish brown (Fig. 8).

Surface sculpture: Head with fine and relatively dense punctation (spaces between punctures 1–3 times size of punctures), finer and sparser anteriorly; diameter of punctures almost equal to diameter of cells of microreticulation. Pronotum with sparser and finer punctation than head. Elytra with very sparse and fine punctation, often inconspicuous. Pronotum and elytra with distinctly impressed microreticulation, dorsal surface less shiny. Head with microreticulation stronger. Metaventricle and metacoxae distinctly microreticulate, metacoxal plates with longitudinal striae and transverse wrinkles. Abdominal ventrites with distinct microreticulation, striae, and very fine and sparse punctation.

Structures: Pronotum without lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, smooth, broadly rounded anteriorly. Blade of prosternal process lanceolate, relatively narrow, very slightly convex, with distinct lateral bead and few setae; neck and blade of prosternal process evenly jointed. Abdominal ventrite 6 broadly rounded apically.

Male: Antenna simple (Fig. 8). Pro- and mesotarsomeres 1–3 not dilated. Protarsomere 4 cylindrical, narrow, with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 slightly concave ventrally, with anterior band of more than 40 and posterior row of 15 relatively long, not pointed setae (Fig. 16D). Median lobe slightly

curved, with truncate apex in lateral view and abruptly narrowed apically, with apex concave in ventral view, having short, thick subdistal setae laterally. Paramere without dorsal notch, with subdistal setae dense, strong, long and proximal setae very sparse, thin, small, weakly visible (Fig. 16A–C). Abdominal ventrite 6 broadly rounded apically, with 6–8 fine transverse lateral strioles on each side.

Holotype: TL-H 3.6 mm, TL 4.0 mm, MW 2.0 mm.

Female: Pro- and mesotarsi not modified. Abdominal ventrite 6 without lateral strioles.

Distribution. Papua: Puncak Regency. The species is known only from the type locality (Fig. 19).

Etymology. The species is named after a young Wano man Pu, who grew up in Puluk and accompanied his father (now deceased) on many hunting trips in the area where this species was collected. The name is a noun in the genitive case.

Exocelina ransikiensis-group

7. *Exocelina ransikiensis* Shaverdo, Panjaitan & Balke, 2016

Exocelina undescribed sp. MB1269: Toussaint et al. 2014: Supplementary figs 1–4, Tab. 2.

Exocelina ransikiensis Shaverdo, Panjaitan & Balke, 2016d: 104, figs 1–6.

Type locality. West Papua: Manokwari Regency, approximately 10 km NW from Ransiki, Kali Way, 01°25'03"S; 134°01'49"E.

Type material studied. *Holotype*: male “West Papua, ca. 10 km NW Ransiki, Kali Way, 1300 m, 01°25'03"S, 134°01'49"E, 03.III.2007”, “HOLOTYPUS *Exocelina ransikiensis* sp. n. des. H. Shaverdo, R. Panjaitan & M. Balke, 2016” [red] (MZB). *Paratypes*: 6 males, 2 females with the same label as the holotype and additionally with red labels “PARATYPUS *Exocelina ransikiensis* sp. n. des. H. Shaverdo, R. Panjaitan & M. Balke, 2016” (CASK, NHMW, ZSM). 1 male “West Papua, old road Ransiki to Anggi, 1160 m, 01°25'53.6"S, 134.02'45.6"E, Balke (BH 03)”, “M.Balke 1269” [green] (ZSM).

Additional material. West Papua: 3 males “Indonesia: Papua Barat, Manokwari to Kebar, forest stream, 302m, 3.xi.2013, -0.80058566 133.33216397, Balke (BH023)”, one male with an additional label “M.Balke 6185” [green text] (NHMW, ZSM). 4 males, 2 females “Indonesia: Papua Barat, Kebar to Aibogar, forest stream, 644m, 4.xi.2013, -0.85339769 132.87133633, Balke (BH024)”, one male with an additional label “M.Balke 6188” [green text] (NHMW, ZSM). 1 male “Indonesia: Papua Barat, Fumato, forest stream, 820m, 5.xi.2013, -0.90427148 132.71981431, Balke (BH027)” (ZSM). 1 male “Indonesia: Papua Barat, Tamrau Mts N of Kebar, forest stream, 750m, 7.xi.2013, -0.783199 133.072143, Balke (BH033)” (ZSM). 4 males “Indonesia: Papua Barat, Tamrau Mts N of Kebar, forest stream, puddles,

1050m, 7.xi.2013, -0.774519 133.069929, Balke (BH034)” (NHMW, ZSM). **Papua:** 1 female “Indonesia: Papua, Road Nabire–Enarotali KM 108, 140m, 23.x.2011, 03 30.258S 135 54.840E, Balke (PAP16)”, “M.Balke 7235” [green text] (ZSM). 1 female “Irian Jaya: Nabire distr., road Nabire–Ilaga, km 54, 03°29'517"S 135°43'913"E, 750m, iv.1998 M. Balke leg.” (NHMW).

Diagnosis. Small, with oblong with subparallel sides to broadly oval habitus; coloration red to dark brown; dorsal surface with strong punctation and microreticulation, matt; pronotum with distinct lateral bead; male antennomeres simple; male protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta; median lobe slightly tapering in ventral view and with curved apex in lateral view; paramere without notch on dorsal side, with thin, sparse, inconspicuous setae. For the complete description, please see Shaverdo et al. (2016d).

Notes on morphological variability. Recently discovered beetles from the western part of Manokwari Regency show distinct differences in the size, body shape, and coloration from those of the type series. They are larger: TL–H 3.25–3.7 mm (representatives of the type series: TL–H 2.85–3.2 mm) and have darker coloration: dark brown, with paler anterior margin of the head and sides of the pronotum. Very interesting is the variability of the body shape: the beetles from Ransiki and Nabire are oblong, with subparallel sides, the beetles from the Tamrau Mountains (localities BH023, BH033, and BH034) also have this body shape but they are distinctly larger, whereas the beetles from Kebar–Aibogar have a more rounded habitus, which is distinctly broadly oval in the specimen from Fumato. That represents almost gradual change of the body shape from oblong, parallel-sided in the east to broadly oval in the west. No variability has been found in the shape of the median lobe and paramere, or in the surface sculpture. Therefore, at present, we treat all new material as *E. ransikiensis* bearing in mind that more material is needed for a final conclusion.

Distribution. West Papua: Manokwari Regency and Papua: Nabire Regency (Fig. 19).

Exocelina wigodukensis-group

This group includes two species, which have one unique character: few (usually three) last subdistal setae of the paramere, standing isolated, are modified having indistinct or very evident basal prolongation (Figs 17C, 18C). Such a modification is also characteristic for some subdistal setae, which are in the “brash” (see in the description below), but it is less evident.

8. *Exocelina wigodukensis* sp. n.

<http://zoobank.org/8D1B2AFF-4961-480C-BEC2-80E886CB7C78>

Figs 9, 17

Type locality. Papua: Puncak Jaya Regency, Wigoduk, 03°38'14.52"S; 137°46'57.78"E.

Type material. *Holotype*: male “Indonesia: Papua, Wigoduk, 1800m, 29.xi.2014, S3°38'14.52", E137°46'57.78", M. Wild (W19)” (MZB). *Paratypes*: 6 males, 3 females with the same label as the holotype, two males with the additional labels “M.Balke 6528” [green text] and “M.Balke 6529” [green text] (NHMW, ZSM). 4 males “Indonesia: Papua, Mokndoma, 2150m, 5.ix.2014, S3°38'38.94", E137°46'30", M. Wild” (NHMW, ZSM).

Additional material. 3 males, 10 females “Indonesia: Papua, Mokndoma, 2150m, 5.ix.2014, S3° 38' 38.94" E137° 46' 30", M. Wild”, one female additionally with label “M.Balke 6530” [green text] (ZSM).

Diagnosis. Beetle medium-sized, piceous, with pronotum paler anteriorly and laterally, dorsal punctation dense and coarse, microreticulation strongly impressed; pronotum without lateral bead; male antennae evidently modified: antennomeres 3–4 and 9–10 stout, antennomeres 5–8 distinctly enlarged, larger than other antennomeres; protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta; protarsomere 5 slightly concave ventrally; median lobe slightly curved, narrow, with apex slightly curved downwards as very small “beak” in lateral view; with slightly concave apex and subparallel sides in ventral view; paramere without dorsal notch, subdistal setae numerous, long, dense, strong, proximal setae thin and sparse, inconspicuous.

The species is similar to *E. pulukensis* sp. n. but distinctly differs from it in having more strongly modified male antennae, thinner and stronger curved apex of the median lobe in lateral view, and three isolated setae of the paramere with very small basal prolongations. Also see under *E. pulukensis* sp. n.

Description. *Size and shape*: Beetle medium-sized (TL-H 3.7–4.35 mm, TL 4.05–4.7 mm, MW 1.95–2.3 mm), with oblong-oval habitus, broadest at elytral middle. *Coloration*: Head piceous, with narrow reddish brown anterior margin. Pronotum piceous on disc and posterior part and reddish brown anteriorly and laterally. Elytra uniformly piceous. Head appendages reddish brown to dark brown. Legs yellowish red proximally and reddish brown distally (Fig. 9). Ventrums piceous, paler on abdominal ventrites; prosternum, epipleurae, abdominal ventrite 1, and apical part of abdominal ventrite 6 reddish brown. Coloration of teneral specimens paler.

Surface sculpture: Head with dense punctation (spaces between punctures 1–2 times size of punctures), evidently finer and sparser anteriorly; diameter of punctures almost equal to diameter of cells of microreticulation. Pronotum with sparser and finer punctation than head. Elytra with coarse and dense punctation, coarser than on pronotum. Pronotum and elytra with strongly impressed microreticulation, dorsal surface matt. Head with microreticulation stronger. Metaventrite and metacoxae distinctly microreticulate and punctate, metacoxal plates with longitudinal striae and transverse wrinkles. Abdominal ventrites with distinct microreticulation, striae, and distinct sparse punctation.

Structures: Pronotum without lateral bead. Base of prosternum and neck of prosternal process with distinct ridge, slightly rounded anteriorly, with small transverse wrinkles. Blade of prosternal process lanceolate, relatively broad, with distinct lateral bead, with small transverse wrinkles on both sides along lateral bead and convex and

smooth middle; neck and blade of prosternal process evenly jointed. Abdominal ventrite 6 broadly rounded or slightly truncate apically.

Male: Antenna modified (Fig. 9); antennomeres 3–4 and 9–10 stout, antennomeres 5–8 distinctly enlarged, larger than other antennomeres. Pro- and mesotarsomeres 1–3 slightly dilated. Protarsomere 4 not modified, with large, thick, strongly curved anterolateral hook-like seta. Protarsomere 5 slightly concave ventrally, with anterior band of more than 30 and posterior row of 7 relatively long, not pointed setae (Fig. 17D). Median lobe slightly curved, narrow, with apex slightly curved downwards as very small “beak” in lateral view; with slightly concave apex and subparallel sides in ventral view. Paramere without dorsal notch, subdistal setae numerous, long, dense (forming “brash”), strong, the three most proximal of them standing isolated and slightly modified having small basal prolongations; proximal setae thin and sparse, inconspicuous (Fig. 17A–C). Abdominal ventrite 6 with 8–12 lateral strioles on each side.

Holotype: TL-H 4.45 mm, TL 4.15 mm, MW 2.2 mm.

Female: Antennomeres stout but thinner than in male. Pro- and mesotarsi not modified. Abdominal ventrite 6 without lateral strioles.

Variability. There are three specimens (see “Additional material”) of much smaller size (TL-H 3.8–3.95 mm, TL 3.2–3.6 mm, MW 1.85–1.9 mm; for *E. wigodukensis* sp. n. from Mokndoma: TL-H 4.05–4.35 mm, TL 4.3–4.7 mm, MW 2.1–2.3 mm) and with slightly different shape of the median lobe (less curved downwards apex) among the beetles of the population from Mokndoma. More material from the region is necessary to conclude whether two distinct but very similar species occur here or it is just a matter of variability.

Distribution and habitat. Papua: Puncak Jaya Regency. The species is known from two localities: Wigoduk and Mokndoma (Fig. 19).

At 2150 m, Mokndoma is an area of high cloud forest. Although this area lies within the territory of the Wano tribe, the word Mokndoma is from the neighboring Dem language. Mok means “flat” and Ndoma means “ground”. So the name of the place is literally “Flat ground”. This is the current home of the second author. In many places at Mokndoma, the ground is boggy with lots of moss and tannin stained streams and ponds. It is an almost mystical place featuring moss tunnels, bog grass, mountain rhododendrons, woody epiphytes, wild ginger and many shrubby small coniferous trees. Upon leaving the open flat area and heading into the thick jungle to the east, west or south, one finds many small streams (Fig. 1) and puddles in which *Exocelina* beetles abound.

Wigoduk is the name of a valley system to the northeast of Mokndoma. It is about onehour hike from the second author’s house site in Mokndoma. Wigoduk is located at 1800 m, right on the eastern bank of a wide bend in the Nggoduk River (Fig. 2). The Nggoduk River is approximately 6–8 m wide and most times only knee deep. In the Wigoduk valley, it meanders along, but upon exiting the valley, turns turbulent as it hurries down the mountain to the larger Yamo River at the bottom of a large east to west running valley at about 1000 m elevation. The Nggoduk River banks are made of smooth rocks and pebbles, a superb site for collecting many different Co-

leoptera. *Exocelina* beetles are found around this area and on the trail from Mokndoma to Wigoduk in many very small streams and puddles.

Etymology. The name refers to Wigoduk, the type locality. The name is an adjective in the nominative singular.

9. *Exocelina pulukensis* sp. n.

<http://zoobank.org/ABE7DB85-B0C4-4DE3-9C58-42C1CC8EFB78>

Figs 10, 18

Type locality. Papua: Puncak Jaya Regency, Puluk area, 03°37'28.5"S; 137°28'35.8"E.

Type material. *Holotype*: male “Indonesia: Papua, Wano Land, S of pass to lake plains, 1700m, 2.ix.2014, -3,6117913 137,5277983, Balke & Wild (Pap022)” (MZB). *Paratypes*: 13 males, 3 females with the same label as the holotype, one male with an additional label “M.Balke 6514” [green text] (NHMW, ZSM). 6 males, 4 female “Indonesia: Papua, Wano Land, N of pass to lake plains, 2000m, 2.ix.2014, -3,6117913 137,5277983, Balke & Wild (Pap023)”, one male with an additional label “M.Balke 6509” [green text] (NHMW, ZSM).

Additional material. 3 males, 1 female “Indonesia: Papua, Wano Land, Puluk, 1320m, 1.ix.2014, -3.660272 137.5207436, Balke & Wild (Pap020)”, one male with an additional label “M.Balke 6521” [green text] (ZSM). 1 male “Indonesia: Papua, Wano Land, red clay creek nr cave, 1100m, 3.ix.2014, nr -3.587955 137.5114945, Balke & Wild (Pap024)”, “M.Balke 6515” [green text] (ZSM).

Diagnosis. Beetle medium-sized, piceous, with pronotum paler anteriorly and laterally, dorsal punctation dense and coarse, microreticulation strongly impressed; pronotum without lateral bead; male antennomeres 3–10 stout; protarsomere 4 with large, thick, strongly curved anterolateral hook-like seta; protarsomere 5 slightly concave ventrally; median lobe slightly curved, with apex rounded, slightly curved downwards in lateral view, in ventral view narrowed subdistally, with subparallel sides and slightly asymmetrical, concave apex; paramere without dorsal notch, subdistal setae numerous, long, dense, strong, three isolated setae of the paramere with distinct basal prolongations, proximal setae thin and sparse, inconspicuous.

The species is similar to *E. wigodukensis* sp. n. but differs from it in having less modified antennae, different shape of the median lobe (broader and without apical “beak” in lateral view and narrowed subdistally and with slightly asymmetrical apex in ventral view), and in having three isolated setae of the paramere with distinct basal prolongations.

Description. *Size and shape*: Beetle medium-sized (TL-H 3.7–4.25 mm, TL 4.1–4.6 mm, MW 2–2.25 mm), with oblong-oval habitus, broadest at elytral middle. *Coloration*: as in *E. wigodukensis* sp. n. (Fig. 10).

Surface sculpture: as in *E. wigodukensis* sp. n.

Structures: as in *E. wigodukensis* sp. n. Abdominal ventrite 6 broadly rounded apically.

Male: Antenna only slightly modified (Fig. 10): antennomeres 3–10 stout. Pro- and mesotarsomeres 1–3 slightly dilated. Protarsomere 4 not modified, with large, thick,

strongly curved anterolateral hook-like seta. Protarsomere 5 slightly concave ventrally, with anterior band of ca. 30 and posterior row of six relatively long, not pointed setae (Fig. 18D). Median lobe slightly curved, with apex rounded, slightly curved downwards in lateral view; in ventral view, narrowed subdistally, with subparallel sides and slightly asymmetrical, concave apex. Paramere without dorsal notch, subdistal setae numerous, long, dense, strong, the three most proximal of them standing isolated and strongly modified having distinct basal prolongations; proximal setae thin and sparse, inconspicuous (Fig. 18A–C). Abdominal ventrite 6 with 4–7 lateral strioles on each side.

Holotype: TL-H 4.2 mm, TL 4.6 mm, MW 2.2 mm.

Female: Antennae distinctly more slender than in males. Pro- and mesotarsi not modified. Abdominal ventrite 6 without lateral strioles.

Variability. The males from the localities Pap020 and Pap024 (see “Additional material”) have thicker and shorter median lobe, with its apex distinctly broader in lateral view and more concave in ventral view. More material from the region is necessary to conclude whether two distinct but very similar species occur here or it is just a matter of variability.

Distribution. Papua: Puncak Jaya Regency. The species is known from Puluk area (Fig. 19).

At Puluk (1370 m), there are three permanent Wano families living, and near their houses, the small trees and bushes are kept trimmed back. The soil is dark, and very fertile. Off into the jungle, around their houses in a circumference of approximately 30–50 m, secondary growth is always encroaching on the hamlet site. Outwards to 250 m beyond the secondary growth, the jungle is lush, but somewhat thinned out, since they clear out smaller trees, and underbrush for firewood and materials for building houses and gardens. Their gardens are out beyond that, and are roughly made and maintained. Beyond that, the jungle is pristine. Just in the jungle to the west of the hamlet site is a small stream where *Exocelina* abound (the villagers nearest drinking and bathing source). To the north of the hamlet in the mountains, there are many smaller streams and puddles coming teeming with beetles.

Etymology. The name refers to Puluk area where the species were found. The name is an adjective in the nominative singular.

Key to species

The key is based mostly on the male characters. In many cases females cannot be assigned to species due to similarity of their external and internal structures (for female genitalia see figs 17a and 17b in Shaverdo et al. (2005)). Some species are rather similar in point of external morphology, therefore, in most cases the male genitalia need to be studied for reliable species identification. Numbers in brackets refer to an arrangement of the species descriptions above.

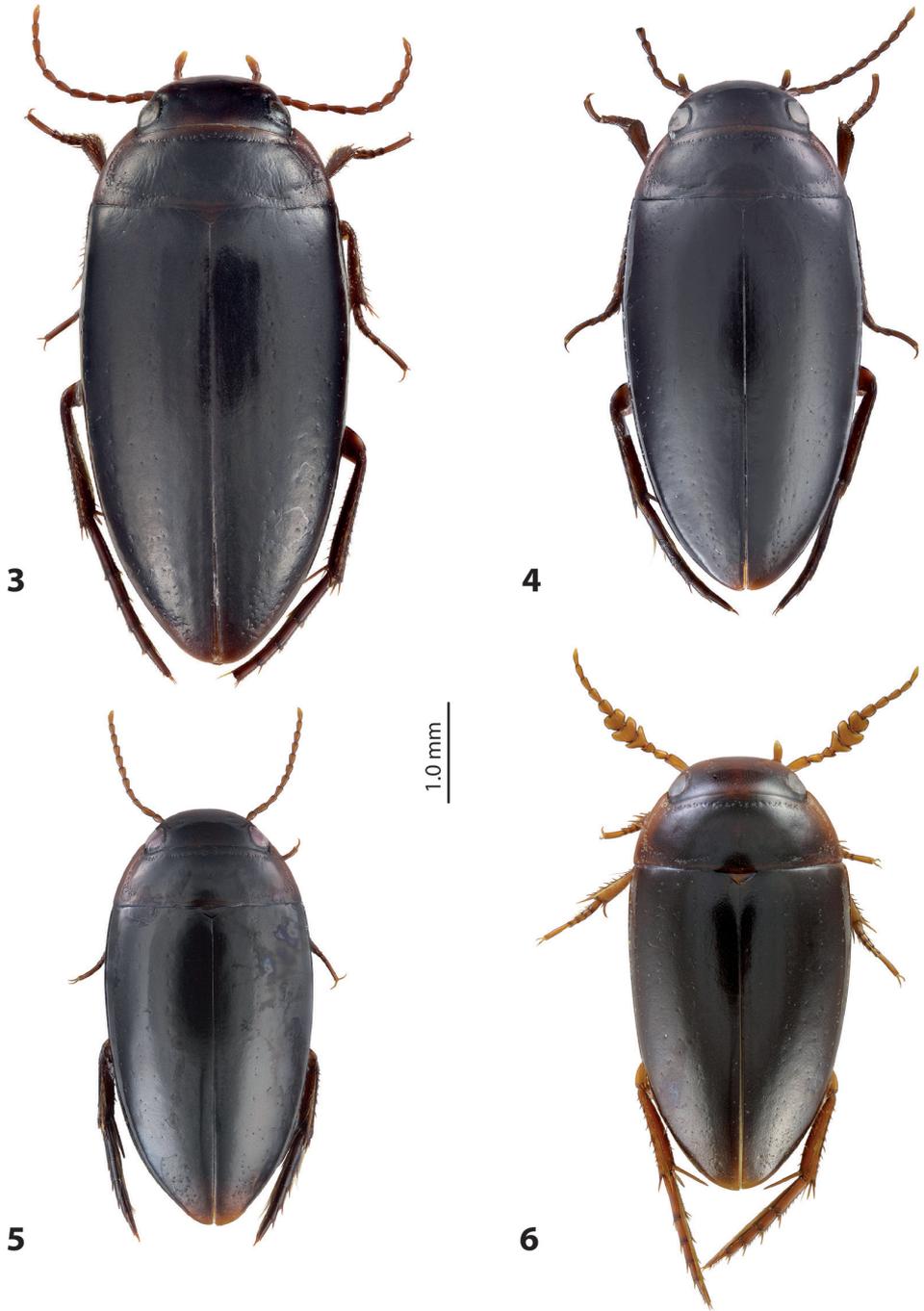
- 1 Pronotum with lateral bead..... 2
 – Pronotum without lateral bead 3
 2 Beetle larger, TL-H 5.3–5.8 mm (Fig. 3). Medial lobe with lateral setae (Fig. 11B). Paramere robust, with notch on dorsal side and very dense, strong setae on subdistal part (Fig. 11C) (1) *ascendens*
 – Beetle smaller, TL-H 2.85–3.2 mm (fig. 1 in Shaverdo et al. 2016d). Medial lobe without lateral setae (fig. 5 in Shaverdo et al. 2016d). Paramere slender, without notch on dorsal side, setae thinner (fig. 6 in Shaverdo et al. 2016d) (7) *ransikiensis*
 3 Male antennae extremely modified: antennomeres 4–6 excessively large, 3 and 7 strongly enlarged (Fig. 6) (3) *bagus*
 – Male antennae simple or differently modified 4
 4 Apex of median lobe with three small prolongations (Fig. 14A–B). Beetle small, TL-H 3.7–3.9 mm, dorsal punctation inconspicuous, microreticulation weakly impressed (Fig. 5) (4) *iratoi* sp. n.
 – Median lobe with simple apex, other characters variable 5
 5 Beetle larger, TL-H 3.7–4.75 mm 6
 – Beetle smaller, TL-H 3.2–3.6 mm 8
 6 Beetle shiny, with fine dorsal microreticulation and punctation almost invisible (Fig. 4). Male antennae not modified. Medial lobe with apex narrowly pointed in lateral view (Fig. 12B)..... (2) *tombansi* sp. n.
 – Beetle matt, with strong dorsal microreticulation and punctation. Male antennae modified: antennomeres 3–10 stout or some of them distinctly enlarged. Medial lobe with apex more or less rounded in lateral view 7
 7 Male antennomeres 3–4 and 9–10 stout, antennomeres 5–8 distinctly enlarged, larger than other antennomeres (Fig. 9). Medial lobe with apex narrower and more curved downwards in lateral view (Fig. 17B). Few last, isolated subdistal setae of paramere slightly modified having indistinct basal prolongations (Fig. 17C) (8) *wigodukensis* sp. n.
 – Male antennomeres 3–10 stout (Fig. 10). Medial lobe with apex broader and less curved downwards in lateral view (Fig. 18B). Few last, isolated subdistal setae of paramere strongly modified having distinct basal prolongations (Fig. 18C)..... (9) *pulukensis* sp. n.
 8 Dorsal punctation dense, coarse (Fig. 7). Medial lobe apically more pointed in lateral view, without lateral setae (Fig. 15B)..... (5) *likui* sp. n.
 – Dorsal punctation very fine (Fig. 8). Medial lobe apically truncate in lateral view, with lateral setae (Fig. 16B) (6) *pui* sp. n.



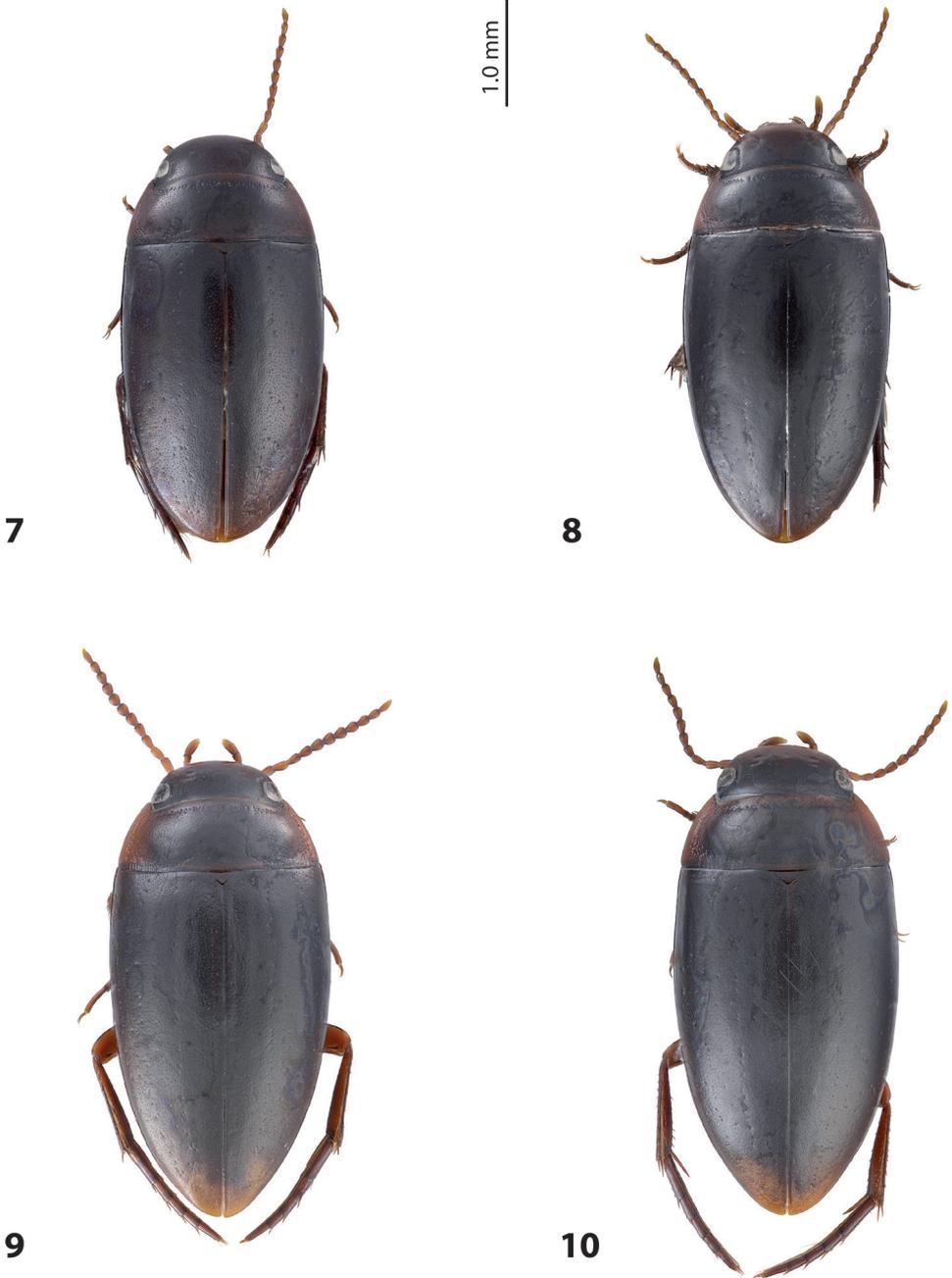
Figure 1. Wano Land, Mokndoma, small forest stream; photo by M. Wild.



Figure 2. Wano Land, Wigoduk, Nggoduk River; photo by M. Wild.



Figures 3–6. Habitus and coloration **3** *Exocelina ascendens* (Balke, 1998) **4** *E. tombansi* sp. n. **5** *E. iratoi* sp. n. **6** *E. bagus* (Balke & Hendrich, 2001).



Figures 7–10. Habitus and coloration **7** *Exocelina likui* sp. n. **8** *E. pui* sp. n. **9** *E. wigodukensis* sp. n. **10** *E. pulukensis* sp. n.

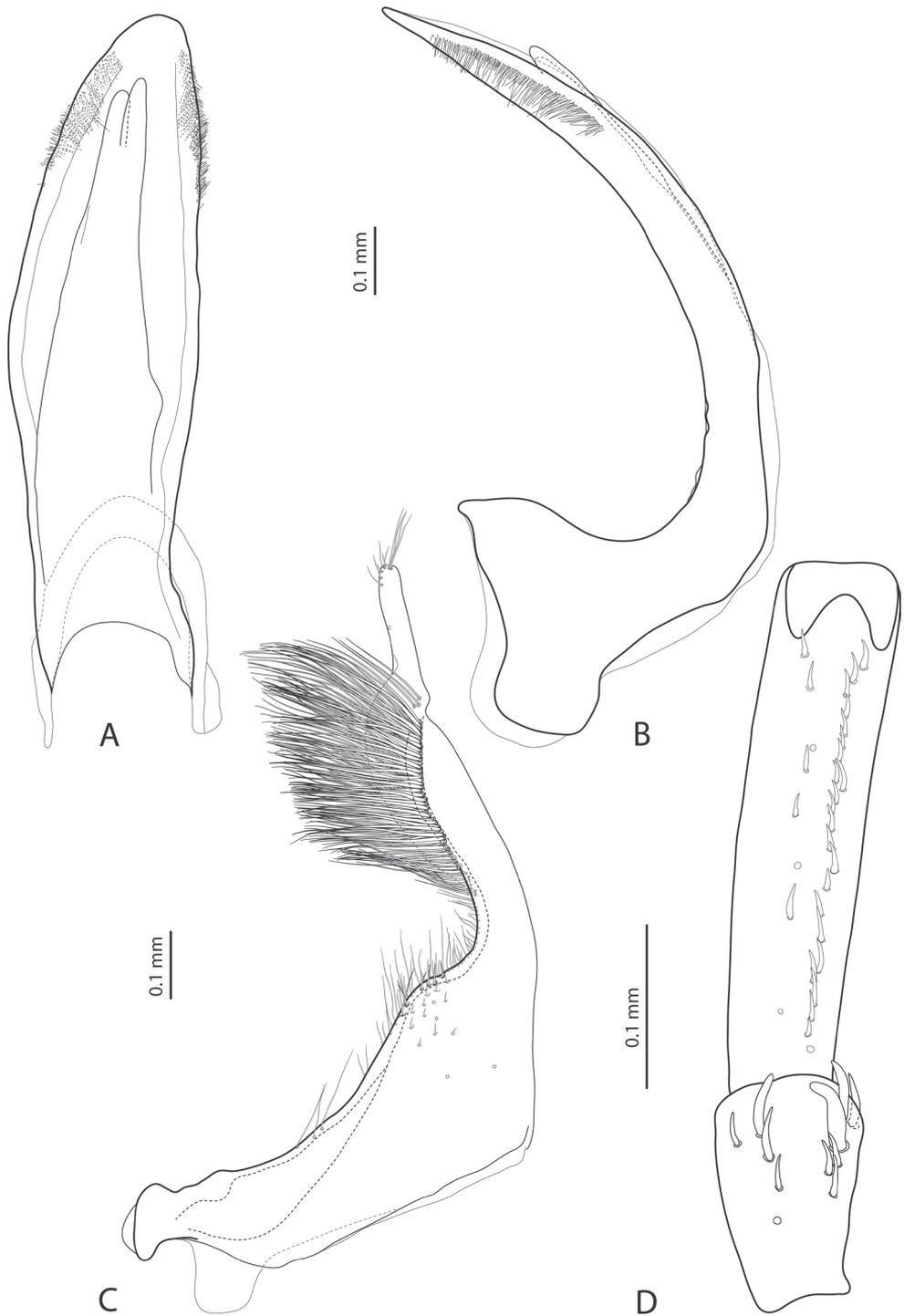


Figure 11. *Exocelina ascendens* (Balke, 1998) **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.

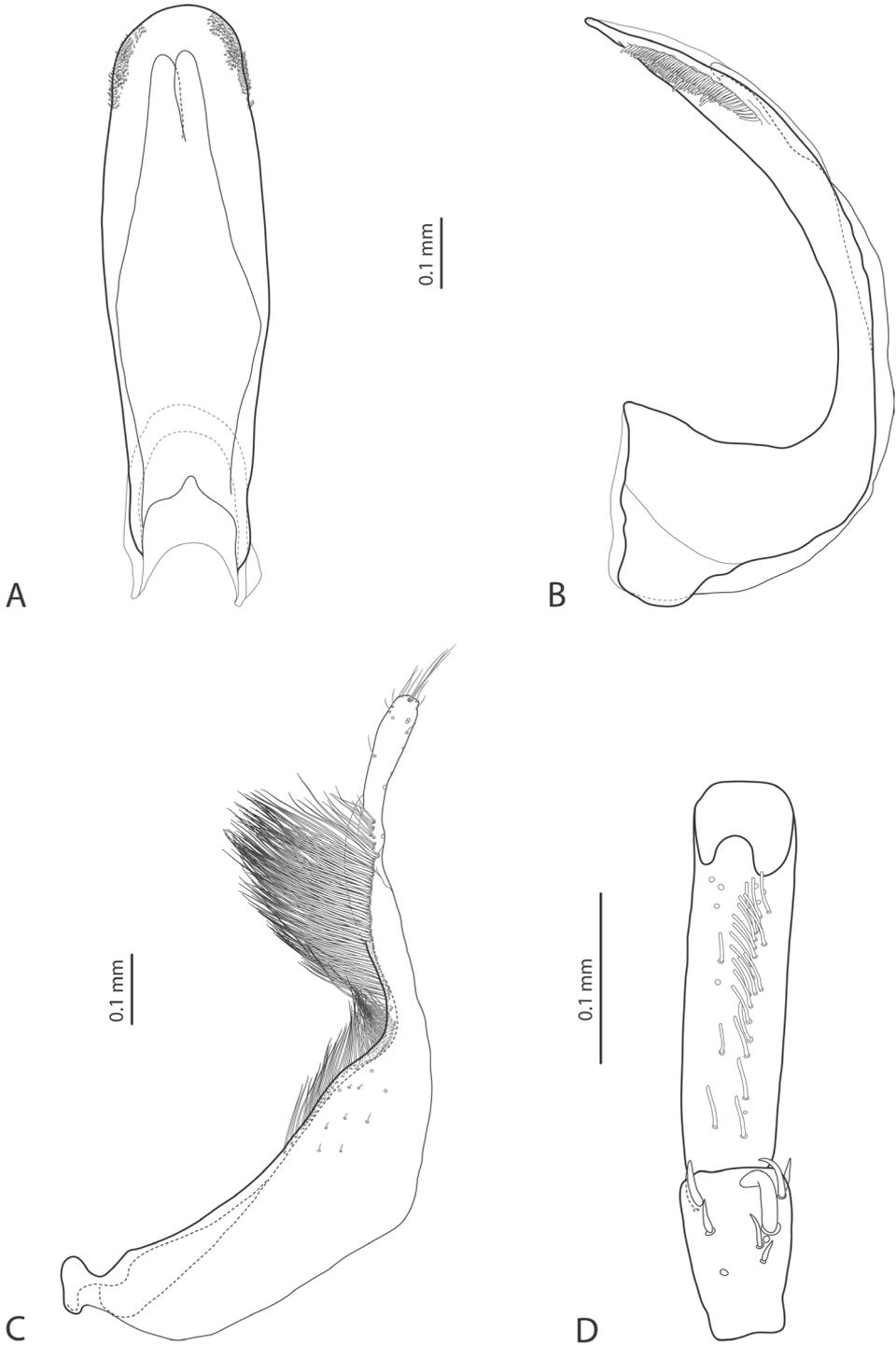
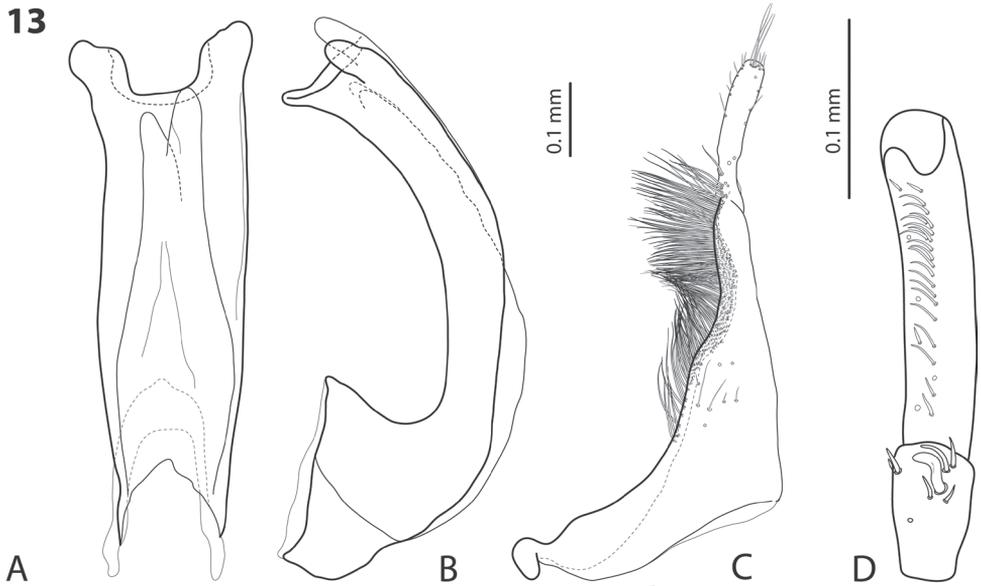


Figure 12 *Exocelina tombansi* sp. n. **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.

13



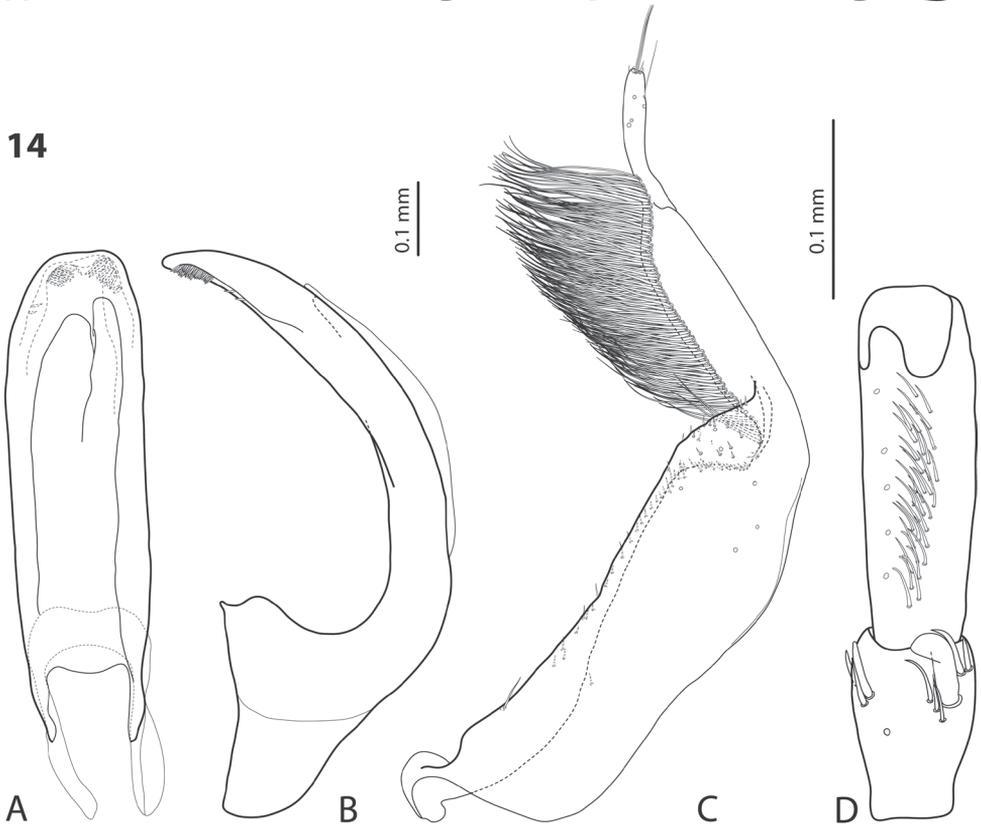
A

B

C

D

14



A

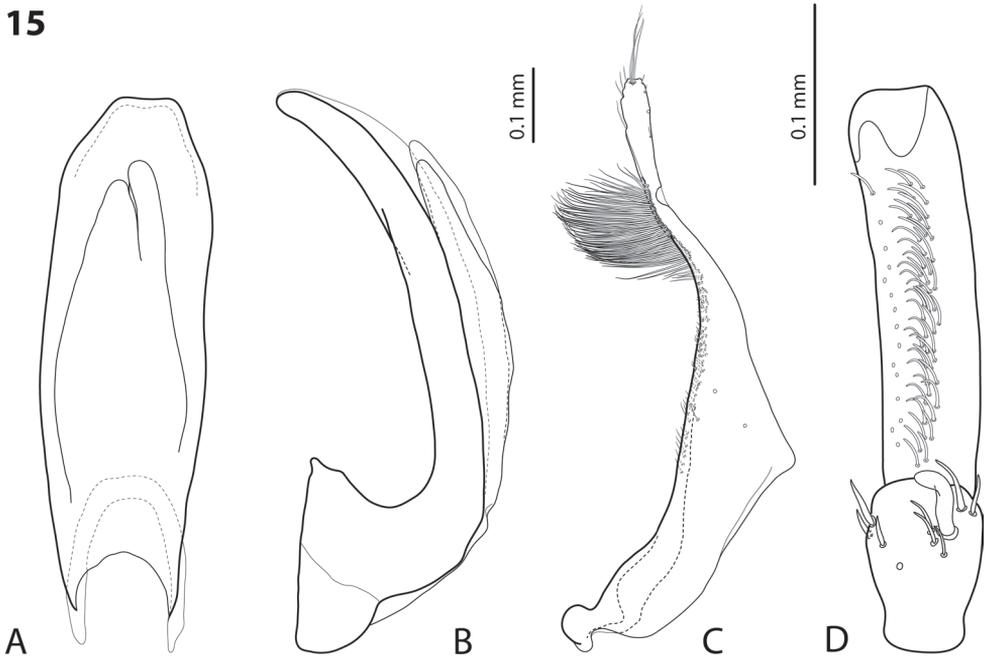
B

C

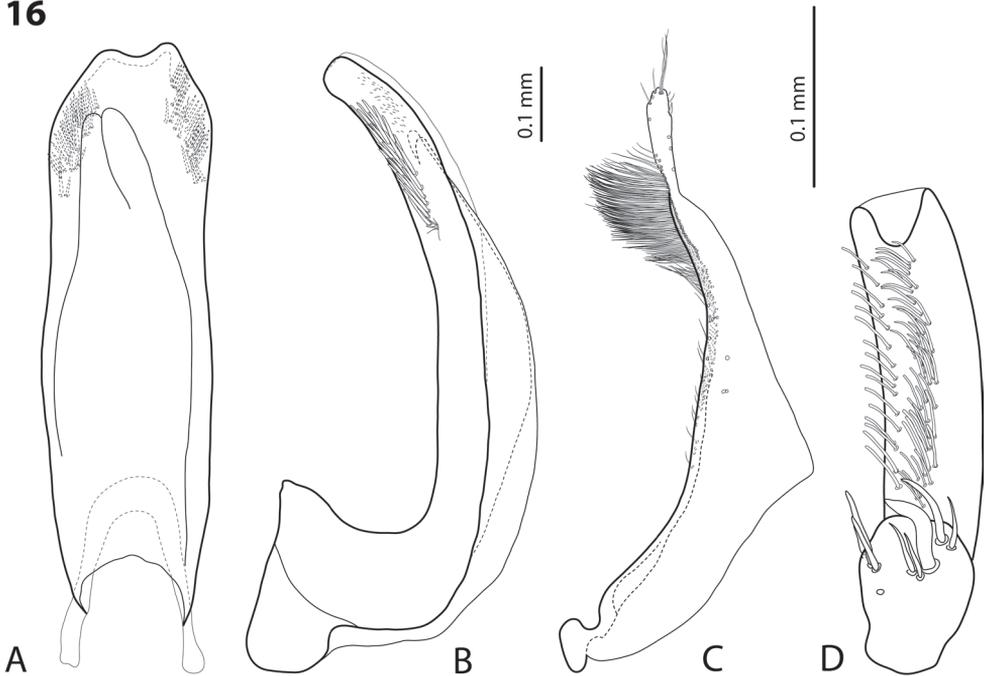
D

Figures 13–14. 13 *Exocelina iratoi* sp. n. 14 *E. bagus* (Balke & Hendrich, 2001) **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.

15

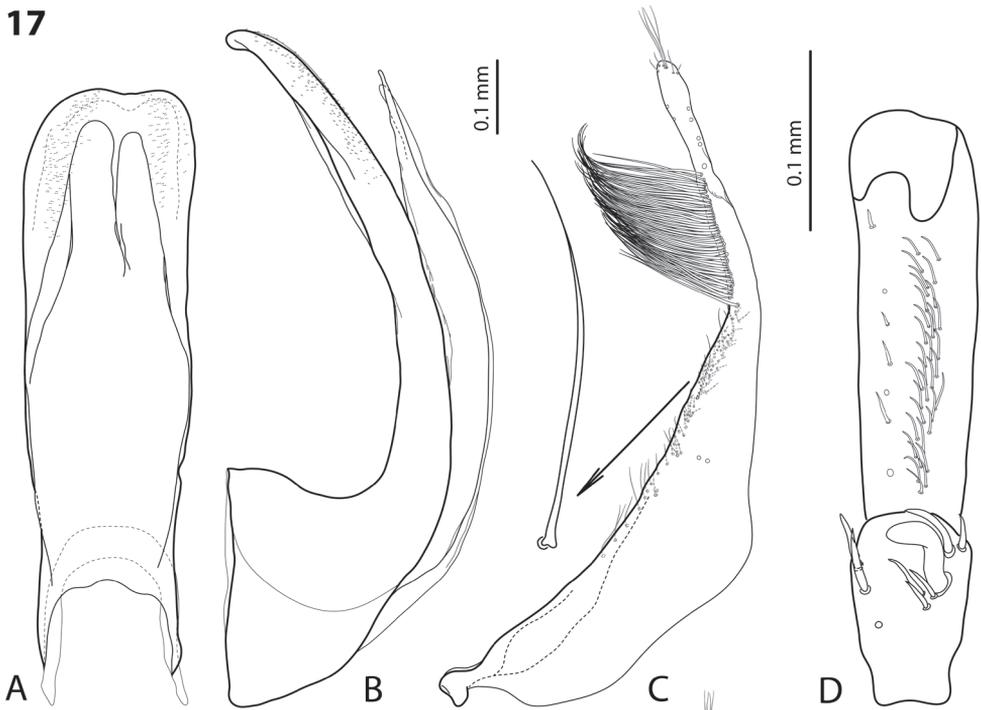


16

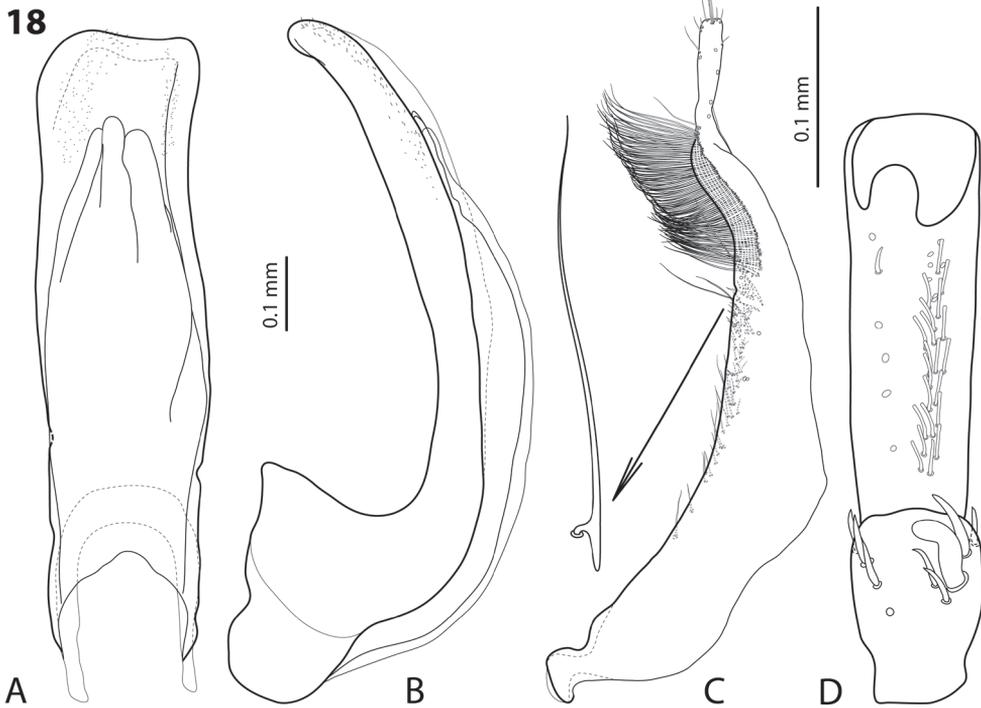


Figures 15–16. 15 *Exocelina likui* sp. n. 16 *E. pui* sp. n. **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.

17



18



Figures 17–18. 17 *Exocelina wigodukensis* sp. n. 18 *E. pulukensis* sp. n. **A** median lobe in ventral view **B** median lobe in lateral view **C** paramere in external view **D** male protarsomeres 4–5 in ventral view.

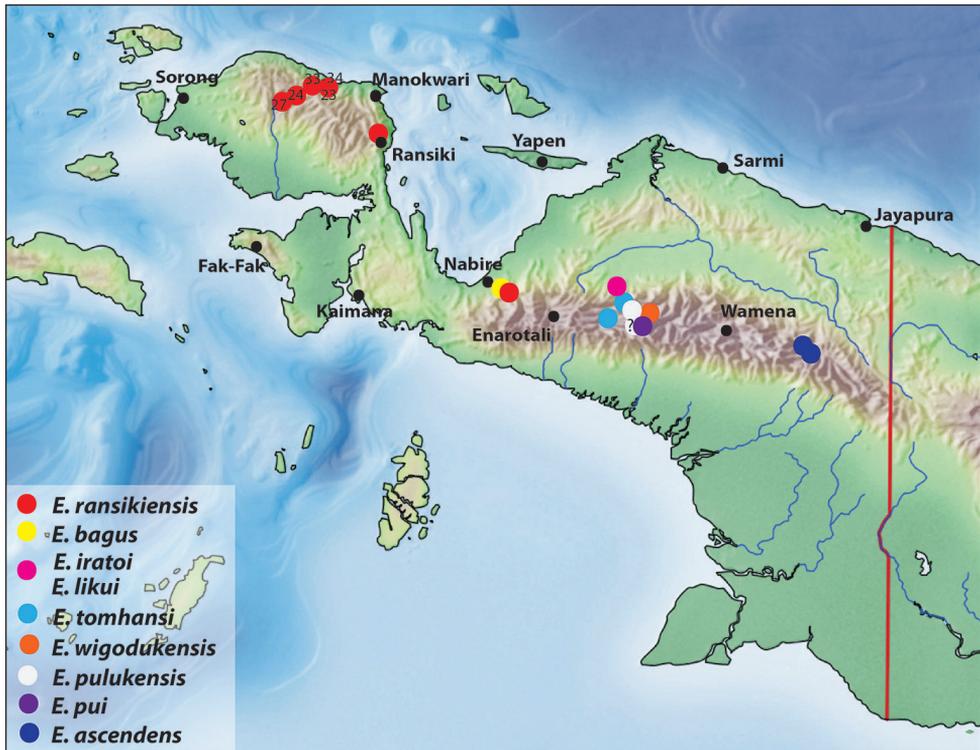


Figure 19. Map of the western part of New Guinea showing the species distributions.

Acknowledgements

We are grateful Dr. H. Schillhammer (Vienna) for the habitus photos and Prof. D. Bilton (Plymouth) for a linguistic review of the manuscript.

Financial support for the study was provided by the FWF (Fonds zur Förderung der wissenschaftlichen Forschung – the Austrian Science Fund) through a project P 24312-B17 to Helena Shaverdo. Michael Balke was supported by the German Science Foundation (DFG BA2152/11-1, 11-2, 19-1).

References

- Balfour-Browne J (1939) On *Copelatus* Er. and *Leiopterus* Steph. (Coleoptera: Dytiscidae) with descriptions of new species. Transactions of the Royal entomological Society of London 88: 57–88. <https://doi.org/10.1111/j.1365-2311.1939.tb00250.x>
- Balke M (1998) Revision of New Guinea *Copelatus* Erichson, 1832 (Insecta: Coleoptera: Dytiscidae): The running water species, Part I. Annalen des Naturhistorischen Museum Wien 100B: 301–341.

- Balke M (1999) Two new species of the genus *Copelatus* Erichson, 1832, subgenus *Papuadytes* Balke, 1998, from Papua New Guinea (Insecta: Coleoptera: Dytiscidae). *Annalen des Naturhistorischen Museum Wien* 101B: 273–276.
- Balke M (2001) Replacement names for three New Guinea species of *Copelatus*, subgenus *Papuadytes* Balke, 1998 (Coleoptera: Dytiscidae). *Annalen des Naturhistorischen Museum Wien* 103B: 361–362.
- Broun T (1886) *Manual of the New Zealand Coleoptera*. Parts III and IV. Wellington, Government Printer, 817–973.
- Nilsson AN (2001) Dytiscidae. *World catalogue of insects*. Vol. 3. Stenstrup, Apollo Books, 395 pp.
- Nilsson AN (2007) *Exocelina* Broun, 1886, is the valid name of *Papuadytes* Balke, 1998. *Latissimus* 23: 33–34.
- Nilsson AN, Fery H (2006) *World Catalogue of Dytiscidae – corrections and additions*, 3 (Coleoptera: Dytiscidae). *Koleopterologische Rundschau* 76: 55–74.
- Shaverdo HV, Balke M (2014) *Exocelina kinibeli* sp.n. from Papua New Guinea, a new species of the *E. ullrichi*-group (Coleoptera: Dytiscidae). *Koleopterologische Rundschau* 84: 31–40.
- Shaverdo HV, Sagata K, Balke M (2005) Five new species of the genus *Papuadytes* Balke, 1998 from New Guinea (Coleoptera: Dytiscidae). *Aquatic Insects* 27: 269–280. <https://doi.org/10.1080/01650420500290169>
- Shaverdo HV, Surbakti S, Hendrich L, Balke M (2012) Introduction of the *Exocelina ekari*-group with descriptions of 22 new species from New Guinea (Coleoptera, Dytiscidae, Copelatinae). *ZooKeys* 250: 1–76. <https://doi.org/10.3897/zookeys.250.3715>
- Shaverdo HV, Hendrich L, Balke M (2013) *Exocelina baliem* sp. n., the only known pond species of New Guinea *Exocelina* Broun, 1886 (Coleoptera, Dytiscidae, Copelatinae). *ZooKeys* 304: 83–99. <https://doi.org/10.3897/zookeys.304.4852>
- Shaverdo H, Sagata K, Panjaitan R, Menufandu H, Balke M (2014) Description of 23 new species of the *Exocelina ekari*-group from New Guinea, with a key to all representatives of the group (Coleoptera, Dytiscidae, Copelatinae). *ZooKeys* 468: 1–83. <https://doi.org/10.3897/zookeys.468.8506>
- Shaverdo H, Panjaitan R, Balke M (2016a) A new, widely distributed species of the *Exocelina ekari*-group from West Papua (Coleoptera, Dytiscidae, Copelatinae). *ZooKeys* 554: 69–85. <https://doi.org/10.3897/zookeys.554.6065>
- Shaverdo H, Sagata K, Balke M (2016b) Description of two new species of the *Exocelina broschii*-group from Papua New Guinea, with revision and key to all representatives of this species group (Coleoptera, Dytiscidae, Copelatinae). *ZooKeys* 577: 125–148. <https://doi.org/10.3897/zookeys.577.7254>
- Shaverdo H, Panjaitan R, Balke M (2016c) *Exocelina ransikiensis* sp. nov. from the Bird's Head of New Guinea (Coleoptera: Dytiscidae: Copelatinae). *Acta Entomologica Musei Nationalis Pragae* 56: 103–108.
- Shaverdo H, Sagata K, Balke M (2016d) Taxonomic revision of New Guinea diving beetles of the *Exocelina danae* group, with description of ten new species (Coleoptera, Dytiscidae, Copelatinae). *ZooKeys* 619: 45–102. <https://doi.org/10.3897/zookeys.619.9951>

- Toussaint EFA, Hall R, Monaghan MT, Sagata K, Ibalim S, Shaverdo HV, Vogler AP, Pons J, Balke M (2014) The towering orogeny of New Guinea as a trigger for arthropod megadiversity. *Nature Communications* 1: 1–10 [+ 10 supplements, 5: 4001]. <https://doi.org/10.1038/ncomms5001>
- Toussaint EFA, Henrich L, Shaverdo H, Balke M (2015) Mosaic patterns of diversification dynamics following the colonization of Melanesian islands. *Scientific Reports* 5, 16016. <https://doi.org/10.1038/srep16016>

A new species group in the genus *Dichaetophora*, with descriptions of six new species from the Oriental region (Diptera, Drosophilidae)

Jin-Hua Yang¹, Masanori J. Toda², Awit Suwito³, Rosli Hashim⁴, Jian-Jun Gao¹

1 State Key Laboratory for Conservation and Utilization of Bioresources in Yunnan, Yunnan University, 2 Cuihubeilu, Kunming 650091, China **2** Hokkaido University Museum, Hokkaido University, N10, W8, Kita-ku, Sapporo 060-0810, Japan **3** Zoology Division (Museum Zoologicum Bogoriense), Research Center for Biology-LIPI, Cibinong, Bogor 16911, Indonesia **4** Institute of Biological Science, University of Malaya, 50603 Kuala Lumpur, Malaysia

Corresponding author: Jian-Jun Gao (gaojj@ynu.edu.cn)

Academic editor: R. Meier | Received 23 December 2016 | Accepted 13 March 2017 | Published 4 April 2017

<http://zoobank.org/222DBEEE-143E-4E0B-BA4F-C3484A230961>

Citation: Yang J-H, Toda MJ, Suwito A, Hashim R, Gao J-J (2017) A new species group in the genus *Dichaetophora*, with descriptions of six new species from the Oriental region (Diptera, Drosophilidae). ZooKeys 665: 121–146. <https://doi.org/10.3897/zookeys.665.11609>

Abstract

The genus *Dichaetophora* Duda comprises 61 described species classified into four species groups: *agbo*, *tenuicauda*, *acutissima* and *sinensis*. This genus is distributed exclusively in the Old World, and is rich in species in the tropical and subtropical areas of the Oriental, Australasian, and Afrotropical regions. In this paper, a new species group, the *trilobita* group, is established for six new species discovered from the Oriental region. The delimitation of these species is firstly performed in light of morphology and further with the aid of DNA sequences of the mitochondrial *COI* and *COII* (cytochrome *c* oxidase, subunits I and II, respectively) genes, considering also their respective geographical origins. Then, the new species (*trilobita* Yang & Gao, **sp. n.**, *heterochroma* Yang & Gao, **sp. n.**, *flatosternata* Yang & Gao, **sp. n.**, *borneoensis* Yang & Gao, **sp. n.**, *javaensis* Yang & Gao, **sp. n.**, and *sumatraensis* Yang & Gao, **sp. n.**) are described, and a key, based on not only morphological but also molecular information, is provided.

Keywords

DNA barcoding, geographical isolation, mitochondrial DNA, taxonomy

Introduction

The genus *Dichaetophora* is widely distributed in the Old World, especially its tropical and subtropical regions. This genus was originally established by Duda (1940) as a subgenus in the genus *Drosophila* Fallén, for the Seychellean species, *Drosophila aberrans* Lamb. Burla (1954) supplemented three African new species (including an informally named one) into *Dichaetophora* and revised its diagnostic characters. Since then, the species composition of this subgenus [genus since Grimaldi's (1990) upgrading] had been altered time and again in relation to the genus *Nesiodrosophila* Wheeler & Takada (see Hu and Toda 2002). Hu and Toda (2002) examined the relationships among the genera *Dichaetophora*, *Nesiodrosophila*, the *Lordiphosa tenuicauda* species group and some presumably related genera by a cladistic analysis of morphological characters. As a result, the revised and enlarged genus *Dichaetophora* was proposed and subdivided into three species groups, i.e., the *agbo*, *acutissima* and *tenuicauda* groups. Hu and Toda (2005) established the fourth (*sinensis*) species group for four species newly described from China, raising the number of known *Dichaetophora* species to 61. In the present study, a new species group is established for six new species of *Dichaetophora* recently discovered from the Oriental region, the *trilobita* group. The species delimitation is based on not only morphological but also geographical and DNA sequence data. A key to the six species is provided.

Materials and methods

Specimens

A summary of the specimens employed in the present study is shown in Table 1. The flies were mostly captured by net sweeping on herbs growing along watersides in open forests or at forest edges. Specimens were preserved in either 70% (after fixing with Kahle's solution for morphological observation) or 100% ethanol (for DNA sequencing).

Species delimitation

The specimens were first identified as of *Dichaetophora* in light of morphology referring to Hu and Toda's (2005) diagnosis of this genus. Then, they were examined for external morphology, morphometric characters and detailed structures of some dissected organs by the same methods as in Li et al. (2014), and sorted into morpho-species. For each of these morpho-species, representative specimens suitable for DNA sequencing were selected, considering also the numbers, geographical origins, and genders of available specimens. For each of the selected specimens, the total DNA was extracted from a hind-leg (usually the right one) or small piece(s) of abdominal tissue picked from the dissection cut of terminalia, using the TIANamp® Genomic DNA Kit. DNA

Table 1. Summary of new species and specimens of *Dichaetophora* employed in the present study.

Code of morpho-species	Formal name	Voucher # ^a	Distribution / collection site	Collection date
sp.K1	<i>trilobita</i> sp. n.	#03876 (♂)	Park Headquarters, Mt. Kinabalu, Sabah, Malaysia	11.iii.2008
		#03877 –8 (♂, ♀)	Ulu Gombak, Selangor, Malaysia	8.xii.2013
		#03882 (♀)	Poring, Mt. Kinabalu, Sabah, Malaysia	20.iii.2008
		unnumbered (1♂, 1♀)	Kubah, Sarawak, Malaysia	19.i.1999
sp.K2	<i>heterochroma</i> sp. n.	#03879 –81 (2♂, 1♀), (1♂)	Poring, Mt. Kinabalu, Sabah, Malaysia	20.iii.2008
		#03883 (♀)	Poring, Mt. Kinabalu, Sabah, Malaysia	13.iii.2008
		#03884–6 (1♂, 2♀)	Ulu Senagang, Crocker Range, Sabah, Malaysia	18.x.1999
		unnumbered (1♂)	Poring, Mt. Kinabalu, Sabah, Malaysia	19.iii.2008
		unnumbered (1♂)	Poring, Mt. Kinabalu, Sabah, Malaysia	3.x.1999
		unnumbered (3♀)	Mahua, Crocker Range, Sabah, Malaysia	14.x.1999
sp.K2-like	<i>flatosternata</i> sp. n.	#04171–8 (6♂, 2♀)	Guanlei, Xishuangbanna Nature Reserve, Yunnan, China	14–15.x.2012
sp.K3	<i>borneoensis</i> sp. n.	#03893–4 (♀)	Park Headquarters, Mt. Kinabalu, Sabah, Malaysia	11.iii.2008
		#03895 (♂)	Park Headquarters, Mt. Kinabalu, Sabah, Malaysia	16.viii.2011
		#03896 (♂)	Park Headquarters, Mt. Kinabalu, Sabah, Malaysia	17.viii.2011
		unnumbered (8♂, 4♀)	Park Headquarters, Mt. Kinabalu, Sabah, Malaysia	2.i.1999
		unnumbered (1♂)	Poring, Mt. Kinabalu, Sabah, Malaysia	28.xii.1998
		unnumbered (1♂)	Mahua, Crocker Range, Sabah, Malaysia	14.x.1999
	<i>javaensis</i> sp. n.	#03887–89 (♀)	Cikaniki, Mt. Halimun, West Java, Indonesia	6.xi.2009
		#03892 (♂)	Cikaniki, Mt. Halimun, West Java, Indonesia	7.xi.2009
		unnumbered (1♀)	Cikaniki, Mt. Halimun, West Java, Indonesia	10.xi.2009
		unnumbered (1♂)	Cibodas, West Java, Indonesia	16.xi.2013
		unnumbered (1♂)	Mt. Patuha, Sugihmukti, West Java, Indonesia	13.x.2004
	<i>sumatraensis</i> sp. n.	#03890 –1 (♂, ♀)	Mt. Kerinci, Jambi, Sumatra, Indonesia	7.x.2004
unnumbered (1♀)		Mt. Kerinci, Jambi, Sumatra, Indonesia	6.x.2004	

^a Numbers in bold indicate holotypes of new species.

sequences of the 658-bp barcoding region of the mitochondrial *COI* (cytochrome *c* oxidase subunit I) gene were then amplified and sequenced with the Folmer primers (Folmer et al. 1994; Table 2), using the same PCR cycle program as in Li et al. (2014). In addition, we determined the DNA sequences of the whole 688-bp region of the mitochondrial *COII* (cytochrome *c* oxidase subunit II) gene, using the primer pair designed by Simon et al. (1994; Table 2), with the same PCR cycle program used in Gao et al. (2007). The sequences obtained were edited in the SeqMan module of the DNASTar package, version 7.1.0 (DNASTar, Inc., Madison, WI), and aligned in MEGA7 (Kumar et al. 2016). We performed a tree-based DNA barcoding with the *COI* and *COII* sequences, respectively, with Bayesian trees constructed using MrBayes 3.1 (Ronquist and Huelsenbeck 2003). For this, the sequence alignment of each gene was partitioned into two subsets (codon positions 1 plus 2, and codon position 3), with choice of substitution models justified via model testing (Srivathsana and Meier 2012) in MEGA7 using the Bayesian Information Criterion. In Bayesian inference, sampling frequency was set as every 1000 generations, and numbers of chains = 4. Two analyses were run simultaneously till the average deviation of split frequencies fell well below 0.01. Therefore, in all analyses, full runs of 5,000,000 generations were performed. In each analysis, 1000 early-phase samples were discarded as burn-in for each run, yielding a total of 8,002 trees to construct a 50% majority consensus tree with nodes characterized by posterior probability (PP). We then summarized the information of intra- and interspecific p-distances calculated without data partitioning. The morpho-species were then reconsidered by integrating information from the morphology, the geographical distribution (Fig. 1) and DNA barcodes.

Descriptions

In species illustration, a DinoLite® Digital Eyepiece Camera was used to microphotograph some organs for representative specimens. McAlpine (1981) was followed for the morphological terminology, and Zhang and Toda (1992) for the definitions of measurements and indices. The examined specimens are deposited in the following institutes:

- UMKL** Zoological Museum, Institute of Biological Science, University of Malaya, Kuala Lumpur, Malaysia
- KPSP** Kinabalu Park, Sabah Parks, Sabah, Malaysia
- ITBC** Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Kota Kinabalu, Sabah, Malaysia
- MZB** Museum Zoologicum Bogoriense, Bogor, Indonesia
- SEHU** Systematic Entomology, The Hokkaido University Museum, Hokkaido University, Sapporo, Japan
- KIZ** Kunming Natural History Museum of Zoology, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming, China

Table 2. Primer sequences for PCR/sequencing.

Target region	Primer name	Primer sequence (5'–3')	Reference
<i>COI</i>	LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. (1994)
	HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	ditto
<i>COII</i>	COII-1	ATGGCAGATTAGTGCAATGG	Simon et al. (1994)
	COII-2	GTTTAAGAGACCAGTACTTG	Ditto

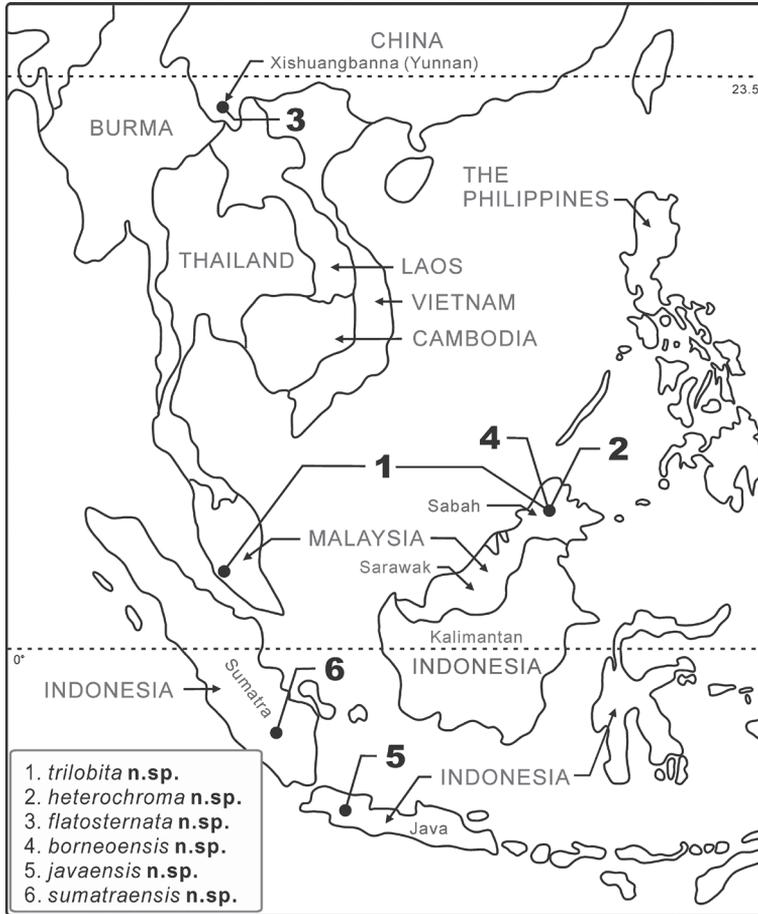


Figure 1. Geographical distribution of the *Dichaetophora trilobita* species group. See the text for the detailed information of the collection sites on the map.

Results

Species delimitation

The specimens examined were first sorted into four morpho-species (Table 1). We got 23 *COI* and 26 *COII* sequences. The GenBank accession numbers are KY809802–KY809824 for the *COI*, and KY809825–KY809850 for the *COII* sequences. Table 3

shows the result of model selection. The *COI* and *COII* Bayesian trees (both unrooted) are shown in Fig. 2. Each of the morpho-species sp.K1 [from Peninsular Malaysia and Borneo (Sarawak and Sabah)], sp.K2 (Sabah) and sp.K2-like (Xishuangbanna, Yunnan, southwestern China) was strongly suggested to be monophyletic. Sp.K2 and sp.K2-like formed a well-supported clade (PPs = 1.00 in both of the *COI* and *COII* trees, respectively). Sp.K1, which is sympatric with sp.K2 in Sabah, formed a clade independent from the clade of sp.K2+sp.K2-like. Thus, these three morpho-species, spp.K1, K2 and K2-like, were recognized as independent species, i.e., *trilobita* sp. n., *heterochroma* sp. n. and *flatosternata* sp. n., respectively.

Specimens of the morpho-species sp.K3 clustered into three more or less diverged, allopatric lineages each endemic to Borneo (Sabah), West Java, or Sumatra (Jambi) in the *COII* tree (PP = 1.00 for each lineage). While the former two lineages were recovered in the *COI* tree (PPs = 0.99 and 1.00, respectively), the last one was not supported in this tree. Table 4 shows the summary of intra- and interspecific p-distances for the six putative species. The interspecific mean p-distances for *COI* sequences among these three lineages of sp.K3 varied from 0.0349 (Java vs. Sumatra) to 0.0751 (Borneo vs. Java), coinciding with the smallest interspecific distance variability of $5.9 \pm 4.1\%$ (uncorrected divergence) for *COI* sequences in Diptera (Meier et al. 2008) and being larger than their intraspecific mean distances ranging from 0.0045 (Java) to 0.0185 (Sumatra). However, these lineages are morphologically very similar, differing from each other in so few morphological characters that it is hard to distinguish between them (see descriptions). On the other hand, comparison of the *COI* and *COII* nucleotide sequences among these lineages has revealed that there are fixed, lineage-specific nucleotides at more than one sites, where nucleotides remain unchanged in the other three species (Table 5). Such sites can therefore be used as pure molecular diagnostic characters (Sarkar et al. 2002, DeSalle et al., 2005) for respective lineages. Taking into account their geographically isolated situations as well, we regard these lineages as three independent, cryptic species, i.e., *borneoensis* sp. n., *javaensis* sp. n. and *sumatraensis* sp. n.

Taxonomy

In the following descriptions of the new species group and new species, and also the key to species, some figures in Hu and Toda (2005) are referred to, with their original numbers given in double quotation marks.

The six new species to be described here certainly belong to the genus *Dichaetophora*, according to its diagnosis revised by Hu and Toda (2002): cibarium only slightly protruded at anterolateral corners; oviscapt with apical ovisensillum robust and largest, distinguishable from the others; basal lobe of palpus without setulae; hypopharyngeal apodeme expanded anteriorly; labellum with less than six pseudotracheae; ocellar setae outside triangle made by ocelli. Within *Dichaetophora*, they should be related to the

Table 3. Models selected for sequence subsets^a.

Gene	Data set	Model selected	BIC score	lnL	Invariant	Gamma	R
<i>COI</i>	whole	GTR+G	4417.9362	-1962.0299	n/a	0.2057	2.1514
	CP ₁₊₂	K2+G	2057.0568	-823.9557	n/a	0.0500	18.7827
	CP ₃	T92+G	2322.3495	-967.9958	n/a	1.0658	3.3825
<i>COII</i>	whole	T92+G	4745.1717	-2118.2231	n/a	0.1231	4.6468
	CP ₁₊₂	T92+G	2250.9406	-881.6321	n/a	0.0500	4.4687
	CP ₃	T92+G	2525.5613	-1037.0171	n/a	0.9274	9.6084

^a Abbreviations: CP₁₊₂, codon positions 1 plus 2; CP₃, codon position 3; GTR, general time reversible; G, discrete Gamma distribution; K2, Kimura 2-parameter; T92, Tamura 3-parameter; BIC score, Bayesian Information Criterion score; lnL, maximum likelihood value; Invariant, estimated fraction of invariant sites; Gamma, gamma shape parameter; R, estimated value of transition/transversion bias.

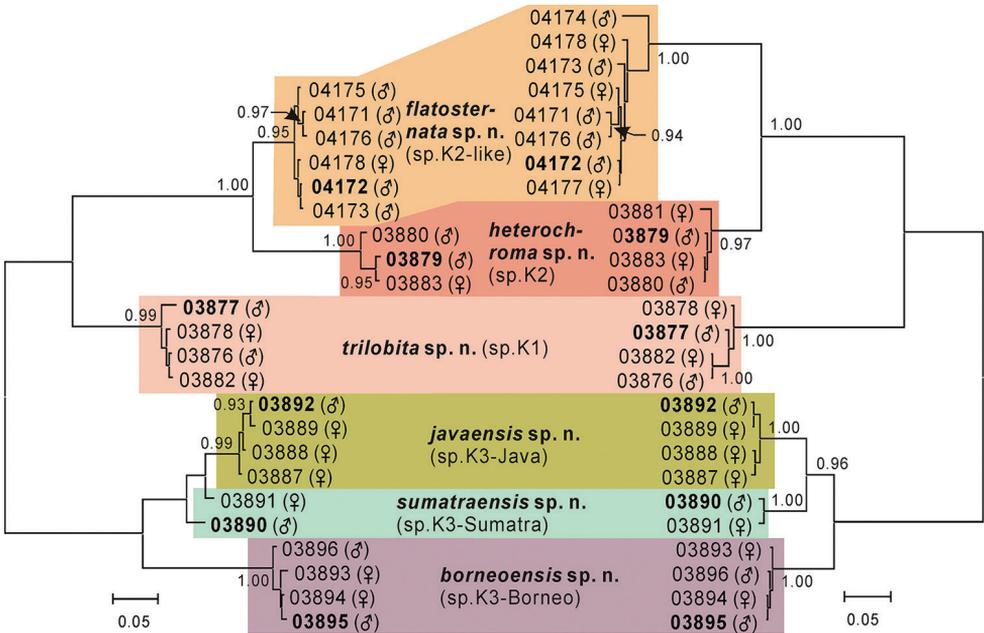


Figure 2. Bayesian trees deduced with *COI* (left) and *COII* (right) gene sequences. Label of each operational taxonomic unit (OUT) is given in the format of “voucher number (sex)”. Numbers beside nodes are posterior probabilities (when ≥ 0.90). Bold voucher numbers indicate holotype specimens.

sinensis group, sharing some characters regarded by Hu and Toda (2005) as diagnostic for the latter group: very large ocellar triangle (“Fig. 1”); large number (≥ 40 per side) of medial sensilla on cibarium (“Fig. 6”); ventral surface of prementum forming discrete bump (Fig 4E, J, O, T, Y, D’; “Figs 8–11A”). However, they lack some other diagnostic characters of the *sinensis* group: foreleg tibia with stout apical seta distinctly thicker than preapical dorsal seta (“Fig. 2”); aedeagus apically with membranous, trumpet-like

Table 4. Summary of intra- and interspecific p-distances.

Species (Morpho-species code)	Intraspecific mean distance (\pm SE) ^a		Interspecific mean distance (<i>COI</i> / <i>COII</i>) ^b					
	<i>COI</i>	<i>COII</i>	1	2	3	4	5	6
1. <i>trilobita</i> sp. n. (sp.K1)	0.0078 \pm 0.0028	0.0098 \pm 0.0033		0.0112 / 0.0117	0.0101 / 0.0098	0.0127 / 0.0128	0.0122 / 0.0115	0.0123 / 0.0114
2. <i>heterochroma</i> sp. n. (sp. 2)	0.0076 \pm 0.0026	0.0044 \pm 0.0018	0.1123 / 0.1054		0.0082 / 0.0076	0.0128 / 0.0103	0.0114 / 0.0104	0.0125 / 0.0114
3. <i>flatosternata</i> sp. n. sp.K2-like)	0.0041 \pm 0.0017	0.0111 \pm 0.0021	0.1105 / 0.1148	0.0573 / 0.0707		0.0128 / 0.0112	0.0127 / 0.0110	0.0123 / 0.0106
4. <i>borneensis</i> sp. n. (sp.K3, Borneo)	0.0063 \pm 0.0024	0.0007 \pm 0.0007	0.1256 / 0.1273	0.1412 / 0.1159	0.1448 / 0.1355		0.0082 / 0.0075	0.0085 / 0.0076
5. <i>jauensis</i> sp. n. (sp.K3, Java)	0.0045 \pm 0.0019	0.0044 \pm 0.0020	0.1118 / 0.1170	0.1295 / 0.1136	0.1271 / 0.1280	0.0751 / 0.0607		0.0079 / 0.0072
6. <i>sumatruensis</i> sp. n. (sp.K3, Sumatra)	0.0185 \pm 0.0065	0.0060 \pm 0.0027	0.1007 / 0.1178	0.1184 / 0.1129	0.1175 / 0.1223	0.0713 / 0.0576	0.0349 / 0.0468	

^a SE, standard error;^b Values of p-distance below diagonal, values of standard error above diagonal.

dilation (“Figs 8F, 9–11D”). And, three of them, *trilobita* sp. n., *heterochroma* sp. n. and *flatosternata* sp. n., share a particular character, i.e., 4 pseudotracheae varying in thickness (“Fig. 4”), with the *agbo* species group (Hu and Toda 2005). Furthermore, all the six new species possess some characters specific to themselves: there are two or three prominent setae on the anteromedial portion of cercus (Figs 5–10B); the cercus is strongly sclerotized along the anterior to caudoventral margin, which seems to be homologous with the strong sclerotization of the caudoventral portion of cercus seen in three species of the *sinensis* group (“Figs 9–11B”), but the sclerotized plates of cerci are fused with each other caudoventrally and to epandrium anteroventrally (Figs 5–10A,B). Based on these morphological characteristics, we establish a new species group, the *trilobita* species group, in *Dichaetophora*, for the six new species.

Dichaetophora trilobita species group

Diagnosis. Cercus anteromedially with two or three prominent setae on anteromedial portion, strongly sclerotized along anterior to caudoventral margin; sclerotized plates of curci fused with each other caudoventrally and to epandrium anteroventrally (Figs 5–10A, B).

Common characters. *Head* (Fig. 4): Eye red, with dense interfacetal setulae; longest axis nearly orthogonal to body axis. Frons, face, gena, occiput, postgena and clypeus glossy black; facial carina blackish brown. Ocellar very large, nearly rectangular, anteriorly reaching to ptilinal fissure; frontal vitta narrow, without interfrontal setulae. Pedicel grayish brown; arista with 6–7 dorsal and 2–3 ventral branches in addition to terminal fork. Subvibrissal seta not differentiated, as small as other orals. Palpus slender, apically with one prominent ventral and one subprominent dorsal setae. Cibarium not thickened on anterior margin, with four anterior sensilla arranged square; dorsal wall pear-shaped, anteriorly somewhat dilated in dorsal view and strongly convex in lateral view; anterior portion of hypopharynx shorter than posterior tubular portion. Prementum with 5–6 (one proximal, one central, 2–3 lateral, and one distal longest) pairs of setae. Labellum with four pseudotracheae per side.

Thorax (Fig. 3A, B, E, F, H, I, K, L, N, O, Q, R): Scutum and scutellum matt, entirely black. Postpronotum, thoracic pleura and notopleural portion blackish brown to black. Acrostichal setulae in six rows. Mid katapisternal seta minute, indistinguishable from a few underneath others.

Legs (Fig. 3A, E, H, K, N, Q): Preapical dorsal setae present on all tibiae; foreleg apical seta as thick as preapical dorsal one. Foreleg first tarsomere slightly shorter than total length of four succeeding tarsomeres; all tarsi narrowing distally, with small, apical claws.

Abdomen (Fig. 3A, D, E, H, K, N, Q): Tergites blackish brown. Sternites grayish yellow.

Male terminalia (Figs 5A–H, 6A–I, 7A–I, 8A–G, 9A–G, 10A–H): Surstylus basally narrowly fused to epandrium, with 8–10 peg-like prenisetae on caudal margin. Hypandrium pale brown, submedially with a pair of small, pubescent lobes apically

bearing short paramedian seta. Paramere broad, plate-like, not pubescent, partly fused to hypandrium, articulated with aedeagus, with two sensilla. Aedeagus apically without pale, membranous trumpet-like dilation; basal processes absent; aedeagal guide present, apically fused to hypandrium; apodeme as long as aedeagus.

Female terminalia (Figs 5I–K, 6J–L, 7J–L, 8H–J, 9H–J, 10I–K): Oviscapt valve yellowish brown, apically pointed and slightly bent outward, with four (three dorsal, one ventral) subterminal, trichoid ovisensilla.

Included species. *trilobita* Yang & Gao, sp. n., *heterochroma* Yang & Gao, sp. n., *flatosternata* Yang & Gao, sp. n., *borneoensis* Yang & Gao, sp. n., *javaensis* Yang & Gao, sp. n., and *sumatraensis* Yang & Gao, sp. n.

Key to the species

In the following key, not only morphological characters but also the selected pure diagnostic nucleotide sites of *COI* and *COII* sequences (Table 5) are used to identify the three cryptic species, *borneoensis* sp. n., *javaensis* sp. n. and *sumatraensis* sp. n.

- 1 Postocellar setae absent; ocellar plate granulose; posteromost pseudotrachea of labellum thicker than the others; mid-leg first tarsomere with one subproximal and one apical, short, blackish brown spines, and hindleg first tarsomere with one apical, short spine; prenisetae on surstylus apically blunt (Figs 5–7C); cercus with three prominent setae on anteromedial portion (Figs 5–7B); sclerotized, caudoventral bridge of cerci with a pair of lateral, broad, apically rounded lobes (Figs 5A, 6C, 7C); aedeagus apically hooked (Figs 5G, 6H, 7H); spermathecal capsule pale brown, spherical, slightly broader than long, without apical indentation (Figs 5K, 6L, 7L) **2**
- Postocellar setae present (Fig. 4W); ocellar plate smooth, glossy; posteromost pseudotrachea of labellum as thick as the others; first tarsomeres of mid- and hindlegs without short, blackish brown spines; prenisetae on surstylus apically somewhat pointed (Figs 8–10C); cercus with two prominent setae on anteromedial portion (Figs 8–10B); sclerotized, caudoventral bridge of cerci without lateral lobes (Figs 8–10C); aedeagus apically not hooked (Figs 8F, 9F, 10G); spermathecal capsule small, less sclerotized, with apical indentation (Figs 8J, 9J, 10K) **4**
- 2 Wing nearly entirely, lightly fuscous, without distinct cloud (Fig. 3C); sclerotized, caudoventral bridge of cerci with small, narrow, apically pointed, median process (Fig. 5A); aedeagus apically curved, hook-like, and finely wrinkled all over, subapically with numerous, coarse serrations, submedially not swollen dorsally (Fig. 5G); spermatheca without distinct introvert (Fig. 5K) ***Di. trilobita* Yang & Gao, sp. n.**
- Wing largely clouded, except for central pale patch around dm-cu vein and periphery (Fig. 3G,J); sclerotized, caudoventral bridge of cerci without me-

- dian process (Figs 6C, 7C); aedeagus apically bearing a pair of strongly recurved, smooth hooks, subapically densely spinose, submedially swollen dorsally (Figs 6F,H, 7F,H); spermatheca with introvert 1/5–1/4 as deep as capsule height (Figs 6L, 7L) **3**
- 3 Dorsolateral tentorial apodemes nearly parallel in basal half but strongly divergent in distal half (Fig. 4H); tenth sternite mediolaterally with a pair of round depressions (seen in anterior view; Fig. 6E); oviscapt valve 2/5 as broad as long (Fig. 6J)..... ***Di. heterochroma* Yang & Gao, sp. n.**
- Dorsolateral tentorial apodemes slightly divergent in basal half but strongly divergent in distal half (Fig. 4M); tenth sternite nearly flat (Fig. 7E); oviscapt valve half as broad as long (Fig. 7J) ... ***Di. flatosternata*, Yang & Gao, sp. n.**
- 4 Spermathecal capsule somewhat cylindrical, apically flat; introvert 7/10 as deep as capsule height (Fig. 8J); *COI* = C, C, T, T, C and C at sites 235, 499, 519, 532, 541 and 544, respectively; *COII* = G, T, C, A and G at sites 309, 389, 441, 513 and 636, respectively (Table 5).....
- ***Di. borneoensis* Yang & Gao, sp. n.**
- Spermathecal capsule somewhat dome-shaped, apically roundish; introvert 2/5 as deep as capsule height (Figs 9J, 10K); *COI* = T, T, C, A, T and T at sites 235, 499, 519, 532, 541 and 544, respectively; *COII* = A, C, T, G and A at sites 309, 389, 441, 513 and 636, respectively (Table 5) **5**
- 5 Hypandrium sparsely pubescent in small, medial patch on caudolateral plate (Fig. 9G); *COI* = C and T at sites 142 and 205, respectively; *COII* = T, C, C, C, G and C at sites 18, 69, 270, 303, 381 and 393, respectively (Table 5)....
- ***Di. javaensis* Yang & Gao, sp. n.**
- Hypandrium without pubescence on caudolateral plate (Fig. 10H); *COI* = T and C at sites 142 and 205, respectively; *COII* = C, T, T, T, A and T at sites 18, 69, 270, 303, 381 and 393, respectively (Table 5).....
- ***Di. sumatraensis* Yang & Gao, sp. n.**

Description of new species

The characters described above for the genus, the species group, and the key are not referred to in the following descriptions.

***Dichaetophora trilobita* Yang & Gao, sp. n.**

<http://zoobank.org/BAF11C36-EB50-4E98-A8A1-537AE7AD715A>

Figs 3A–D, 4A–E, 5

Type material. Holotype ♂ (#03877): MALAYSIA: Ulu Gombak, Selangor, 8.xii.2013, MJ Toda (UMKL).

Paratypes: same data as holotype (1♀: #03878, UMKL); Kubah, Sarawak, Malaysia, 19.i.1999 (1♂, 1♀, SEHU); Park Headquarters, Mt. Kinabalu, Sabah, Malaysia, 11.iii.2008, MJ Toda (1♂: #03876, KIZ); Poring, Mt. Kinabalu, Sabah, Malaysia, 20.iii.2008, MJ Toda (1♀: #03882, KIZ).

Diagnosis. Postocellar setae absent; wing without distinct cloud (Fig. 3C); sclerotized, caudoventral bridge of cerci with small, narrow, apically pointed, median process and a pair of lateral, broad, apically rounded lobes (Fig. 5A); aedeagus apically curved, hook-like, and finely wrinkled all over, subapically with numerous, coarse serrations, submedially not swollen dorsally (Fig. 5G); spermatheca without distinct introvert (Fig. 5K).

Description. *Head* (Figs 3A, B, 4A–E): First flagellomere grayish yellow. Dorsolateral tentorial apodemes slightly divergent in basal 2/5 but strongly divergent in distal 3/5; supracervical setae 21–23 per side; postocular setae 22–23 per side. Palpus with two subprominent, lateromedial setae. Cibarium with ca. 70 medial and ca. 8 posterior sensilla per side.

Wings (Fig. 3C): Veins pale brown to brown. Halter pale gray; stem darker.

Legs (Fig. 3A) pale grayish yellow; mid- and hindleg femora distally, foreleg tibia and tarsi proximally to medially darker. Apical setae present on all tibiae; hindleg apical seta short, stout. Mid-leg first tarsomere longer than total length of four succeeding tarsomeres; hindleg first tarsomere as long as total length of four succeeding tarsomeres.

Male terminalia (Fig. 5A–H): Epandrium pubescent except for anterior to ventral margin, with 1–3 dorsal and ca. 22 ventral, long setae per side. Surstylus with peg-like prenisetae in sinuate row on caudal margin, 2–5 apically pointed spines and medial patch of pubescence on outer surface and ca. 26 apically pointed spines (ventral ones shorter, thicker and straight, but medial to dorsal ones trichoid and recurved) on inner, caudal portion. Tenth sternite nearly flat. Cercus pubescent except for caudal margin, with 11–12 long setae near dorsal to posterior margin and 7–11 short setae in cluster on ventral portion of sclerotized marginal plate. Paramere with sensilla apically.

Female terminalia (Fig. 5I–K): Oviscapt valve dorsomedially narrowly extended, with 3–4 lateral and 9–13 marginal, peg-like ovisensilla.

Measurements (in mm): BL (straight distance from anterior edge of pedicel to tip of abdomen) = 2.03 in holotype (1♂ paratype: 2.00; range in 2♀ paratypes: 2.00–2.21), ThL (distance from anterior notal margin to apex of scutellum) = 0.84 (0.82; 0.86–0.88), WL (distance from humeral cross vein to wing apex) = 1.62 (1.69; 1.72–1.73), WW (maximum wing width) = 0.71 (0.72; 0.74–0.79).

Indices: FW/HW (frontal width/head width) = 0.53 (range in 1♂, 2♀, or less if noted, paratypes: 0.38–0.50), ch/o (maximum width of gena/maximum diameter of eye) = 0.18 (0.19–0.26), prorb (proclinate orbital seta/posterior reclinate orbital seta in length) = 0.72 (2♀: 0.71–0.80), rcorb (anterior reclinate orbital seta/posterior reclinate orbital seta in length) = 0.30 (2♀: 0.31–0.33), orbito (distance between proclinate and posterior reclinate orbital setae / distance between inner vertical and posterior reclinate orbital setae) = 0.60 (0.58–0.68), dcl (anterior dorsocentral seta/posterior

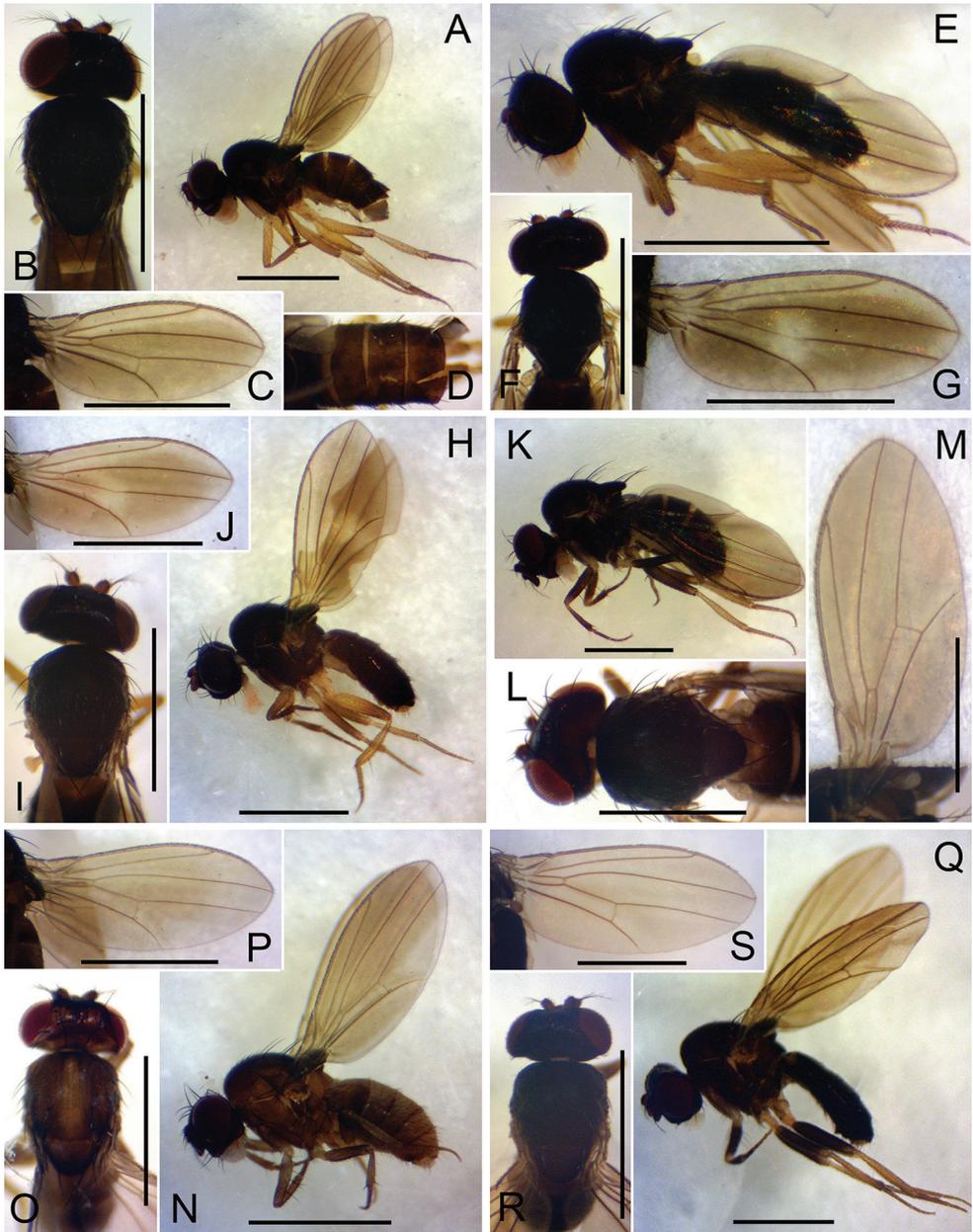


Figure 3. Left lateral habitus, head and thorax (dorsal view), wing (left, ventral view), and abdomen (dorsal view). **A–D** *Dichaetophora tirlobita* sp. n. (#03877) **E–G** *D. heterochroma* sp. n. (#03879) **H–J** *D. flatosternata* sp. n. (#04172) **K–M** *D. borneoensis* sp. n. (#03895) **N–P** *D. javaensis* sp. n. (#03892) **Q–S** *D. sumatraensis* sp. n. (#03890). Scale bars: 1.0 mm.

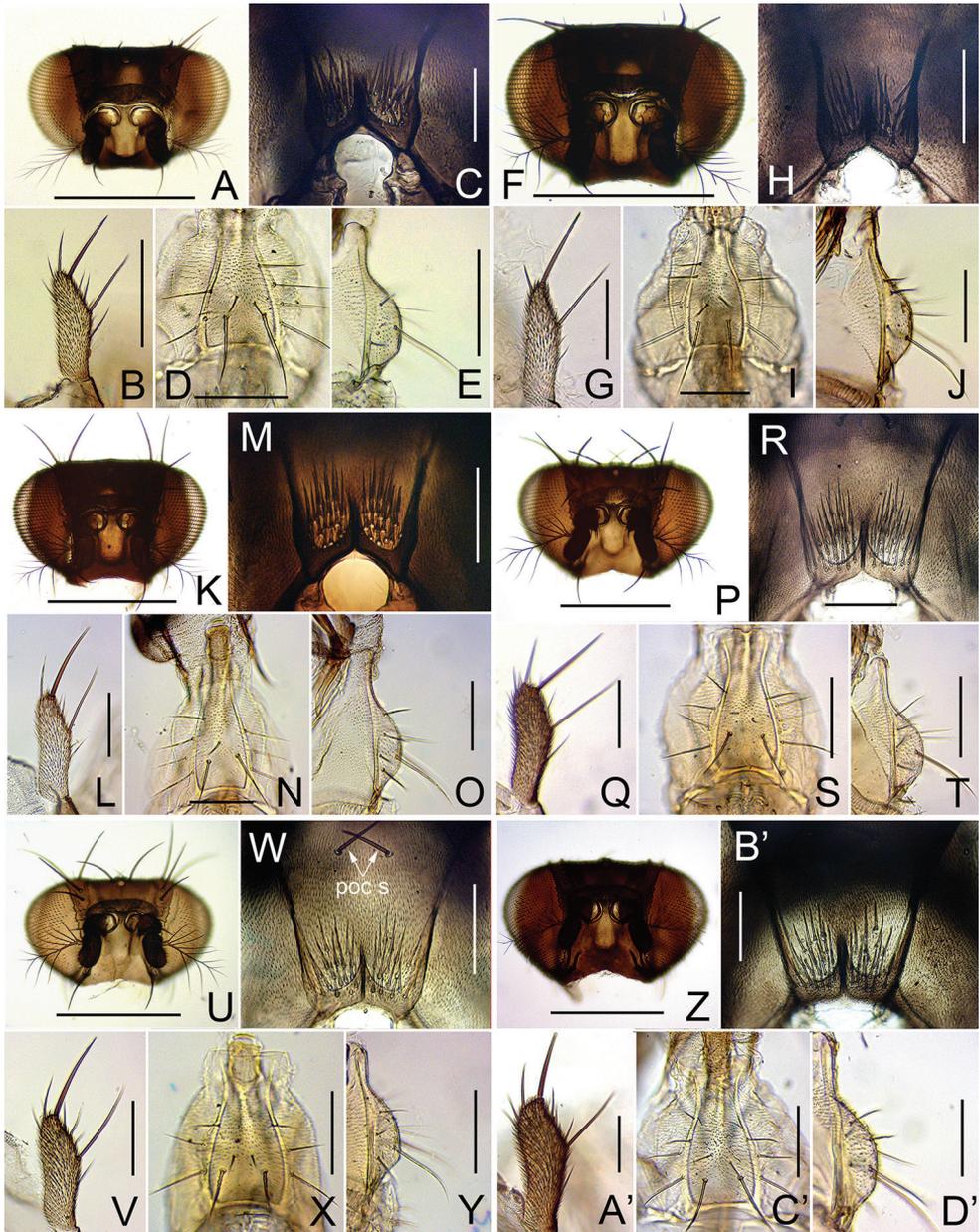


Figure 4. Head (anterior view), postociput, palpus, and prementum (ventral and lateral view, respectively). **A-E** *Dichaetophora tirlobita* sp. n. (#03877) **F-J** *D. heterochroma* sp. n. (#03879) **K-O** *D. flatosternata* sp. n. (#04172) **P-T** *D. borneoensis* sp. n. (#03895) **U-Y** *D. javaensis* sp. n. (#03892) **Z-D'** *D. sumatraensis* sp. n. (#03890). Scale bars: 0.1 mm except for **A, F, K, P, U, Z** (0.5 mm).

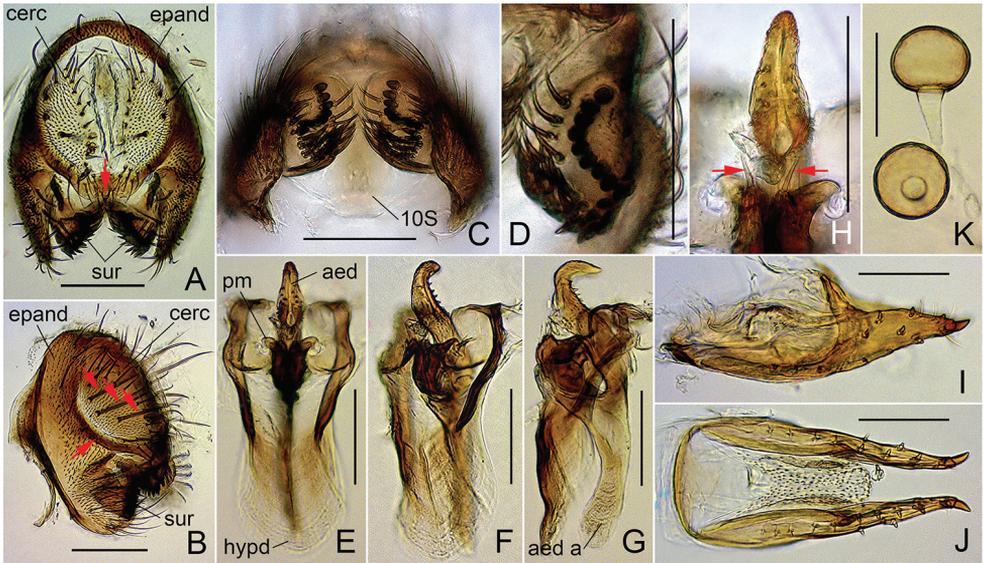


Figure 5. *Dichaetophora trilobita* sp. n. (A–H #03877 I–K paratype #03878). **A**Periphallallic organs (posterior view), with red arrow indicating the median process on the caudoventral bridge of cerci **B** periphallallic organs (posterolateral view), with red arrows indicating the prominent setae on the cercus and the anteroventral fusion of cercus (sclerotized, marginal plate) with the epandrium **C** surstyli (ventral view) **D** surstylus (inner side) **E–G** phallic organs (ventral, ventrolateral and lateral view, respectively) **H** paramedian setae (indicated with red arrows), and apical portion of paramere **I, J** ovisclap (lateral and ventral view, respectively) **K** spermathecae. Abbreviations: aed = aedeagus, aed a = aedeagal apodeme, cerc = cercus, epand = epandrium, hypd = hypandrium, pm = paramere, sur = surstylus, 10S = tenth sternite. Scale bars: 0.1 mm.

dorsocentral seta in length) = 0.78 (2♀: 0.64–0.74), sctl (basal scutellar seta/apical scutellar seta in length) = 0.67 (1♀: 0.60), sterno (anterior katepisternal seta/posterior katepisternal seta in length) = 0.51 (0.57–0.60), dcp (distance between ipsilateral dorsocentral setae/distance between anterior dorsocentral setae) = 0.49 (0.53–0.60), sctlp (distance between ipsilateral scutellar setae/distance between apical scutellar setae) = 0.79 (0.68–0.77), C (2nd costal section between subcostal break and R_{2+3} /3rd costal section between R_{2+3} and R_{4+5}) = 1.57 (1.35–1.53), 4c (3rd costal section between R_{2+3} and R_{4+5} / M_1 between r-m and dm-cu) = 1.54 (1.46–1.66), 4v (M_1 between dm-cu and wing margin/ M_1 between r-m and dm-cu) = 2.19 (2.11–2.33), 5x (CuA_1 between dm-cu and wing margin/dm-cu between M_1 and CuA_1) = 2.19 (2.00–2.38), ac (3rd costal section between R_{2+3} and R_{4+5} /distance between distal ends of R_{4+5} and M_1) = 3.58 (3.66–3.76), M (CuA_1 between dm-cu and wing margin/ M_1 between r-m and dm-cu) = 0.72 (0.66–0.70), C3F (length of heavy setation in 3rd costal section/length of 3rd costal section) = 0.70 (0.66–0.68).

Etymology. Referring to the trilobed, caudoventral bridge of cercal sclerotized plates.

Distribution. Malaysia (Peninsular Malaysia, Sarawak, Sabah).

***Dichaetophora heterochroma* Yang & Gao, sp. n.**

<http://zoobank.org/4C4A707B-EFFC-474D-A485-381B40B879E8>

Figs 3E–G, 4F–J, 6

Type material. Holotype ♂ (#03879): MALAYSIA: Poring, Mt. Kinabalu, Sabah, 20.iii.2008, MJ Toda (KPSP).

Paratypes: same data as holotype (1♂, 1♀: #03880, #03881, KIZ; 1♂, SEHU); same data as holotype except for 13.iii.2008 (1♀: #03883, KIZ); same data as holotype except for 19.iii.2008 (1♂, SEHU); same data as holotype except for 3.x.1999 (1♂, SEHU); Mahua, Crocker Range, Sabah, Malaysia, 14.x.1999, MJ Toda (1♀, KPSP; 2♀, SEHU); Ulu Senagang, Crocker Range, Sabah, Malaysia, 18.x.1999, MJ Toda (1♂, 2♀: #03884–3886, ITBC).

Diagnosis. Wing largely clouded, except for central pale patch around dm-cu vein and periphery (Fig. 3G); dorsolateral tentorial apodemes nearly parallel in basal half (Fig. 4H); tenth sternite mediolaterally with a pair of round depressions (seen in anterior view; Fig. 6E); oviscapt valve 2/5 as broad as long (Fig. 6J).

Description. *Head* (Figs 3E, F, 4F–J): First flagellomere grayish yellow. Supracervical setae 15–22 per side; postocular setae 17–21 per side. Palpus with one subprominent lateromedial seta. Cibarium with 78–79 medial and ca. 8 posterior sensilla per side.

Wings (Fig. 3G): Veins pale brown to dark brown, but pale within central pale patch. Halter pale gray; stem darker.

Legs (Fig. 3E) pale grayish yellow; foreleg coxa, tibia and tarsus, except for fifth tarsomere, dark brown. Mid-leg first tarsomere longer than total length of four succeeding tarsomeres; hindleg first tarsomere as long as total length of four succeeding tarsomeres.

Male terminalia (Fig. 6A–I): Epandrium pubescent except for anterior portion, with 3–4 dorsal and 9–12 ventral, long setae per side. Surstylus with prensisetae in nearly straight row on caudal margin, 2–4 apically pointed spines but no pubescence on outer surface and ca. 20 apically pointed, recurved spines on inner, caudal portion. Cercus pubescent except for caudal margin, with 6–12 long setae near dorsal to posterior margin and 6–7 short setae in cluster on ventral portion of sclerotized marginal plate. Paramere with sensilla subapically.

Female terminalia (Fig. 6J–L): Oviscapt valve with ca. five lateral and 12–14 marginal, peg-like ovisensilla. Introvert of spermathecal capsule 1/5 as deep as capsule height.

Measurements (in mm): BL = 2.18 in holotype (range in 2♂ paratypes: 1.99–2.21; range in 4♀ paratypes: 2.31–2.77), ThL = 0.79 (0.81–0.85; 0.92–0.97), WL = 1.64 (1.60–1.64; 1.80–2.30), WW = 0.68 (0.69–0.70; 0.75–0.97).

Indices: FW/HW = 0.59 (2♂, 4♀, or less if noted, paratypes: 0.50–0.54), ch/o = 0.20 (0.25–0.28), prorrb = 0.74 (2♂, 1♀: 0.76–0.87), rcorb = 0.29 (2♂, 3♀: 0.31–0.36), orbito = 0.54 (0.48–0.76), dcl = 0.71 (1♂, 2♀: 0.60–0.73), sctl = n/a (1♂, 3♀: 0.88–0.94), sterno = 0.54 (0.50–0.61), dcp = 0.55 (0.55–0.65), sctlp = 0.62 (0.75–0.95), C = 1.69 (1.99–2.08), 4c = 1.54 (1.41–1.54), 4v = 2.50 (2.28–2.51), 5x = 1.79 (1.25–1.56), ac = 2.86 (2.38–3.09), M = 0.70 (0.62–0.64), C3F = 0.78 (0.73–0.87).

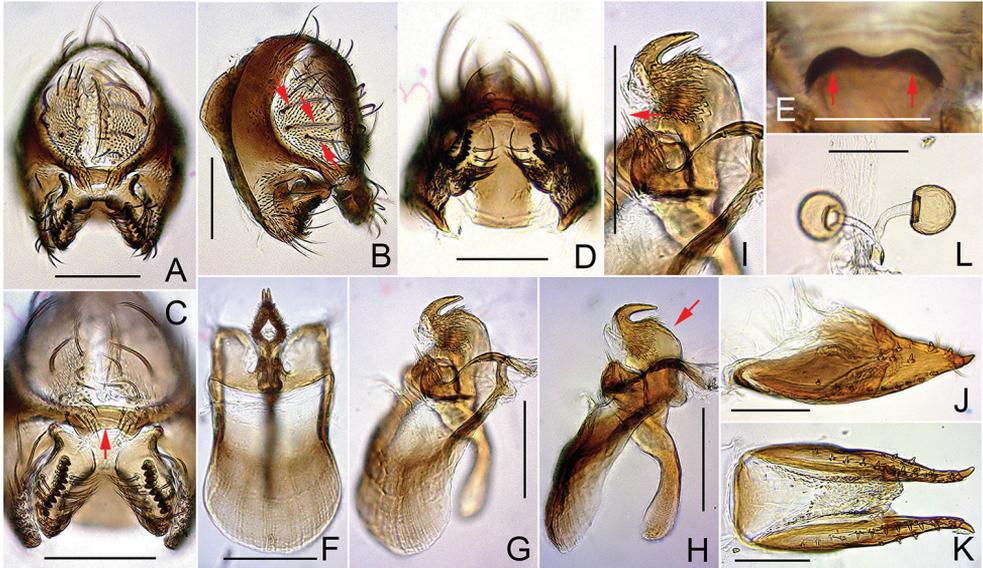


Figure 6. *Dichaetophora heterochroma* sp. n. (A–I #03879 J–L paratype #03881). **A, B**Periphallallic organs (posterior and posterolateral view, respectively) **C** surstyli and cerci, with red arrow indicating the caudoventral bridge of cerci **D, E** tenth sternite (ventral and anterior view, respectively), with red arrows (**E**) indicating a pair of depressions **F–H** phallic organs (ventral, ventrolateral and lateral view, respectively), with red arrow (**H**) indicating the dorsally swollen, submedial portion of aedeagus **I** paramedian setae **J, K** oviscapt (lateral and ventral view, respectively) **L** spermathecae (lateral view). Scale bars: 0.1 mm.

Etymology. Referring to the heterochromatic legs.

Distribution. Malaysia (Sabah).

***Dichaetophora flatosternata* Yang & Gao, sp. n.**

<http://zoobank.org/2BAD2A68-B183-4781-AF74-A103DEF614F4>

Figs 3H–J, 4K–O, 7

Type material. Holotype. ♂ (#04172), CHINA: Mengyuan Substation, Mengla Station, Xishuangbanna National Nature Reserve, Guanlei, Mengla, Xishuangbanna, Yunnan, 14–15.xi.2012, JJ Gao (KIZ).

Paratypes: same data as holotype (5♂, 2♀: #04171, #04173–4178, KIZ, SEHU).

Diagnosis. Wing largely clouded, except for central pale patch around dm-cu vein and periphery (Fig. 3J); dorsolateral tentorial apodemes slightly divergent in basal half (Fig. 4M); tenth sternite nearly flat (Fig. 7E); oviscapt valve half as broad as long (Fig. 7J).

Description. *Head* (Figs 3H, I, 4K–O): First flagellomere grayish yellow. Supercervical setae 17–18 per side; postocular setae 20–22 per side. Palpus with one subprominent lateromedial seta. Cibarium with 77–79 medial and ca. 10 posterior sensilla per side.

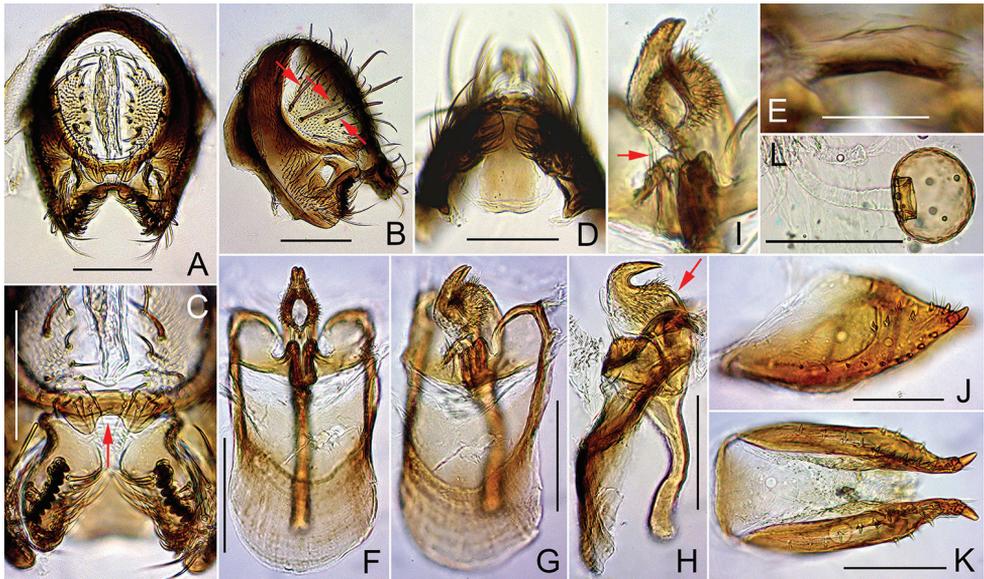


Figure 7. *Dichaetophora flatosternata* sp. n. (A–I #04172 J–L paratype #04177). **A, B**Periphallal organs (posterior and posterolateral view, respectively) **C** surstyli and cerci **D, E** tenth sternite (ventral and anterior view, respectively) **F–H** phallic organs (ventral, ventrolateral and lateral view, respectively) **I** paramedian setae **J, K** oviscapt (lateral and ventral view, respectively) **L** spermatheca (lateral view). Scale bars: 0.1 mm.

Wings (Fig. 3J): Veins pale brown to dark brown, but pale within central pale patch. Halter pale gray; stem darker.

Legs (Fig. 3H) pale grayish yellow; foreleg tibia and tarsus, mid-leg femur and distal portion of hindleg femur darker. Hindleg tibia lacking apical seta. Mid-leg first tarsomere longer than total length of four succeeding tarsomeres; hindleg first tarsomere as long as total length of four succeeding tarsomeres.

Male terminalia (Fig. 7A–I): Epandrium pubescent except for anterior portion, with ca. three dorsal and 10–11 ventral, long setae per side. Surstylus with prenisetae in slightly concave row on caudal margin, 2–3 apically pointed spines but no pubescence on outer surface and ca. 16 apically pointed, recurved spines on inner, caudal portion. Cercus pubescent except for caudal margin, with 10–13 long setae near dorsal to posterior margin and 8–10 short setae in cluster on ventral portion of sclerotized marginal plate. Paramere with sensilla subapically.

Female terminalia (Fig. 7J–L): Oviscapt valve with ca. four lateral and 12–13 marginal, peg-like ovisensilla. Introvert of spermathecal capsule 1/4 as deep as capsule height.

Measurements (in mm): BL = 2.10 in holotype (range in 5♂ paratype: 2.08–2.32; range in 2♀ paratypes: 2.21–2.31), ThL = 0.87 (0.83–0.88; 0.83–0.93), WL = 1.78 (1.67–1.81; 1.71–1.81), WW = 0.81 (1.79–1.82; 0.81–0.83).

Indices: FW/HW = 0.54 (5♂, 2♀, or less if noted, paratypes: 0.49–0.54), ch/o = 0.23 (0.27–0.29), prorb = 0.71 (0.79–0.87), rcorb = n/a (0.33–0.39), orbito = 0.54

(0.55–0.74), dcl = 0.64 (0.62–0.78), sctl = n/a (4♂, 2♀: 0.89–0.97), sterno = 0.65 (0.54–0.63), dcp = 0.55 (0.54–0.62), sctlp = 0.73 (0.74–0.80), C = 1.53 (1.63–1.71), 4c = 1.45 (1.22–1.36), 4v = 1.96 (1.42–1.60), 5x = 1.89 (1.79–1.94), ac = 3.04 (2.53–2.76), M = 0.64 (0.57–0.64), C3F = 0.69 (0.62–0.71).

Etymology. Referring to the flat male tenth sternite.

Distribution. China (Yunnan).

***Dichaetophora borneoensis* Yang & Gao, sp. n.**

<http://zoobank.org/20778512-6C3C-4BC2-99A6-83A02C6FBCC4>

Figs 3K–M, 4P–T, 8

Type material. Holotype ♂ (#03895), MALAYSIA: Park Headquarters, Mt. Kinabalu, Sabah, 16.viii.2011, K Akutsu (KPSP).

Paratypes: same data as holotype except for 17.viii.2011 (1♂: #03896, KIZ); same data as holotype except for 11.iii.2008 (2♀: #03893, #03894, KIZ); same data as holotype except for 2.i.1999, MJ Toda (8♂, 2♀, SEHU; 1♀, KPSP; 1♀, ITBC); Poring, Mt. Kinabalu, Sabah, Malaysia, 28.xii.1998 (1♂); Mahua, Crocker Range, Sabah, Malaysia, 14.x.1999, MJ Toda (1♂, ITBC).

Diagnosis. Postocellar setae present; spermathecal capsule somewhat cylindrical, apically flat; introvert 7/10 as deep as capsule height (Fig. 8J); *COI* = C, C, T, T, C and C at sites 235, 499, 519, 532, 541 and 544, respectively; *COII* = G, T, C, A and G at sites 309, 389, 441, 513 and 636, respectively (Table 5).

Description. *Head* (Figs 3K, L, 4P–T): First flagellomere grayish brown. Dorsolateral tentorial apodemes slightly divergent in basal 2/5 but strongly divergent in distal 3/5; supracervical setae 21–25 per side; postocular setae 23–24 per side. Palpus with one subprominent, lateromedial seta. Cibarium with ca. 80 medial and 9–12 posterior sensilla per side.

Wings (Fig. 3M) slightly fuscous; veins yellowish brown to brown. Halter and stem gray.

Legs (Fig. 3K): All femora blackish brown; foreleg coxa, tibia and tarsus (except 5th tarsomere) grayish brown; rest grayish yellow. Apical setae present on foreleg and mid-leg tibiae. Mid-leg first tarsomere as long as total length of four succeeding tarsomeres; hindleg first tarsomere longer than total length of four succeeding tarsomeres.

Male terminalia (Fig. 8A–G): Epandrium pubescent except for anterior margin, with 1–2 dorsal and 7–11 ventral, long setae per side. Surstylus with 1–3 short spines and medial patch of pubescence on outer surface and 7–10 recurved spines on inner, caudal portion. Tenth sternite lingulate, slightly curved. Cercus pubescent except for dorsal to caudal margin, with 15–17 long setae distributed nearly all over; sclerotized, caudoventral bridge of cerci medially with narrowly elongated process. Paramere some-

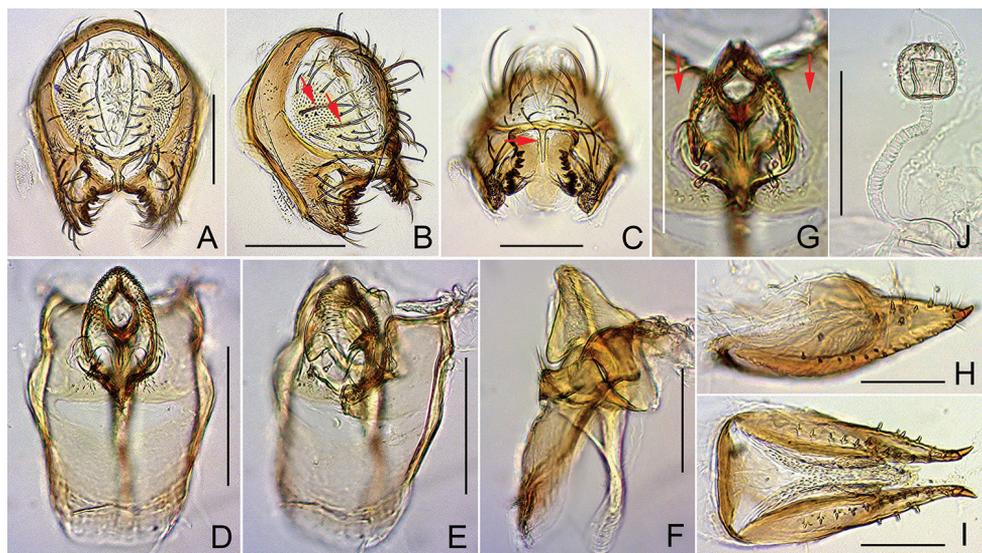


Figure 8. *Dichaetophora borneoensis* sp. n. (A–G #03895 H–J paratype #03894). A, BPeriphallitic organs (posterior and posterolateral view, respectively) C surstyli and cerci, with red arrow indicating the median, elongated process on the caudoventral bridge of cerci D–F phallic organs (ventral, ventrolateral and lateral view, respectively) G distal portion of hypandrium (posteroventral view), showing the caudolateral plates not pubescent (red arrows) and the paramedian setae H, I ovisclat (lateral and ventral view, respectively) J spermatheca (lateral view). Scale bars: 0.1 mm.

what triangular in lateral view, apically round, with sensilla on inner surface. Aedeagus apically trilobed, densely hirsute on outer lobes, dorsosubapically with a pair of small, marginally serrated flaps.

Female terminalia (Fig. 8H–J): Ovisclat valve dorsomedially narrowly extended, with 4–5 lateral and 12–15 marginal, peg-like ovisensilla. Spermathecal capsule with fine spinules on distal half of outer surface.

Measurements (in mm): BL = 2.42 in holotype (1♂ paratype: 2.10; range in 2♀ paratypes: 2.34–2.57), ThL = 1.01 (0.87; 0.93–0.96), WL = 2.19 (1.84; 1.82–2.14), WW = 0.97 (0.85; 0.92–0.94).

Indices: FW/HW = 0.50 (1♂, 2♀, or less if noted, paratypes: 0.48–0.51), ch/o = 0.19 (0.25–0.29), prob = 0.66 (1♂, 1♀: 0.63–0.73), rcorb = 0.23 (1♂, 1♀: 0.24–0.30), orbito = 0.62 (0.53–0.60), dcl = 0.76 (1♀: 0.77), sclt = 0.86 (0.84–0.87), sterno = 0.59 (1♂, 1♀: 0.58–0.62), dcp = 0.49 (0.49–0.52), scltp = 0.90 (0.84–0.89), C = 1.82 (1.82–2.01), 4c = 1.47 (1.31–1.51), 4v = 2.51 (2.22–2.70), 5x = 2.16 (2.11–2.32), ac = 2.81 (2.88–3.15), M = 0.79 (0.71–0.87), C3F = 0.59 (0.57–0.63).

Etymology. Pertaining to the type locality.

Distribution. Malaysia (Sabah).

***Dichaetophora javaensis* Yang & Gao, sp. n.**

<http://zoobank.org/09DA1C1A-C0A2-4025-99FB-6AAAC123F295>

Figs 3N–P, 4U–Y, 9

Type material. Holotype. ♂ (#03892), INDONESIA: Cikaniki, Mt. Halimun, West Java, 7.x.2009, MJ Toda (MZB).

Paratypes: same as holotype except for 6.xi.2009 (1♀: #03887, MZB; 2♀: #03888–9, KIZ); same as holotype except for 10.xi.2009 (1♀, SEHU); Cibodas, West Java, Indonesia, 16.xi.2013, MJ Toda (1♂, SEHU); Mt. Patuha, Sugihmukti, West Java, Indonesia, 13.x.2004 (1♂, SEHU).

Diagnosis. Postocellar setae present; spermathecal capsule somewhat dome-shaped, apically roundish; introvert 2/5 as deep as capsule height (Fig. 9J); hypandrium sparsely pubescent in small, medial patch on caudolateral plate (Fig. 9G); *COI* = C and T at sites 142 and 205, respectively; *COII* = T, C, C, C, G and C at sites 18, 69, 270, 303, 381 and 393, respectively (Table 5).

Description. *Head* (Figs 3N, O, 4U–Y): First flagellomere grayish brown. Dorsolateral tentorial apodemes slightly divergent in basal 2/5 but strongly divergent in distal 3/5; supercervical setae 18–22 per side; postocular setae 19 per side. Palpus with one subprominent, lateromedial seta. Cibarium with ca. 90 medial and 10–12 posterior sensilla per side.

Wings (Fig. 3P) slightly fuscous; veins yellowish brown to brown. Halter and stem gray.

Legs (Fig. 3N): All femora blackish brown; foreleg coxa, tibia and tarsus (except 5th tarsomere) grayish brown; rest grayish yellow. Apical setae present on foreleg and mid-leg tibiae. Mid-leg first tarsomere as long as total length of four succeeding tarsomeres; hindleg first tarsomere longer than total length of four succeeding tarsomeres.

Male terminalia (Fig. 9A–G): Epandrium pubescent except for anterior margin, with 2–3 dorsal and 9–10 ventral, long setae per side. Surstylus with 2–3 short spines and medial patch of pubescence on outer surface and 10–11 recurved spines on inner, caudal portion. Tenth sternite lingulate, slightly curved. Cercus pubescent except for dorsal to caudal margin, with 14–17 long setae; sclerotized, caudoventral bridge of cerci medially with narrowly elongated process. Paramere somewhat triangular in lateral view, apically round, with sensilla on inner surface. Aedeagus apically trilobed, densely hirsute on outer lobes, dorsosubapically with a pair of small, marginally serrated flaps.

Female terminalia (Fig. 9H–J): Oviscapt valve dorsomedially narrowly extended, with 4–5 lateral and 12–15 marginal, peg-like ovisensilla. Spermathecal capsule without spinules on outer surface.

Measurements (in mm): BL = 1.94 in holotype (range in 3♀ paratypes: 2.08–2.50), ThL = 0.86 (0.97–1.03), WL = 1.81 (1.99–2.07), WW = 0.82 (0.86–0.92).

Indices: FW/HW = 0.56 (3♀, or less if noted, paratypes: 0.49–0.52), ch/o = 0.21 (0.34–0.41), prorb = 0.76 (0.72–0.79), rcorb = 0.24 (0.29–0.31), orbito = 0.60 (0.54–0.69), dcl = 0.74 (1♀: 0.71), sclt = 0.81 (1♀: 0.81), sterno = 0.60 (0.50–0.54), dcp = 0.52 (0.53–0.60), sclp = 0.71 (0.52–0.71), C = 1.85 (1.78–1.98), 4c = 1.54 (1.35–1.40),

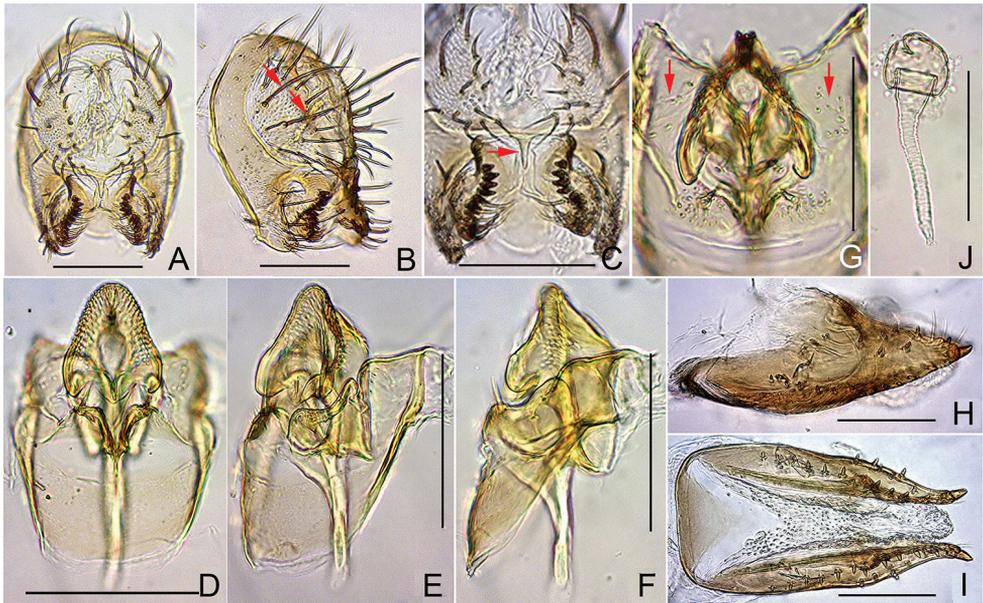


Figure 9. *Dichaetophora javaensis* sp. n. (A–G #03892 H–J paratype #03888). **A, B** Periphallic organs (posterior and posterolateral view, respectively) **C** surstyli and ventral portions of cerci **D–F** phallic organs (ventral, ventrolateral and lateral view, respectively) **G** distal portion of hypandrium (posteroventral view), showing a pair of small patches of sparse pubescence on the caudolateral plates (red arrows) and the paramedian setae **H, I** oviscapt (lateral and ventral view, respectively) **J** spermatheca (lateral view). Scale bars: 0.1 mm.

$4v = 2.62$ (2.26–2.28), $5x = 2.28$ (1.73–1.91), $ac = 3.03$ (2.95–3.24), $M = 0.76$ (0.71–0.90), $C3F = 0.58$ (0.50–0.60).

Etymology. Pertaining to the type locality.

Distribution. Indonesia (West Java).

***Dichaetophora sumatraensis* Yang & Gao, sp. n.**

<http://zoobank.org/8F7EB4F2-3B81-4D2F-9AAC-3ABD144F8BC7>

Figs 3Q–S, 4Z–D’, 10

Type material. Holotype ♂ (#03890): INDONESIA: Mt. Kerinci., Jambi, Sumatra, 7.x.2004, MJ Toda (MZB).

Paratypes: same as holotype (1♀: #03891, MZB); same as holotype except for 6.x.2004 (1♀, SEHU).

Diagnosis. Postocellar setae present; spermathecal capsule somewhat dome-shaped, apically roundish; introvert 2/5 as deep as capsule height (Fig. 10K); hypandrium without pubescence on caudolateral plate (Fig. 10H); *COI* = T and C at sites 142 and 205, respectively; *COII* = C, T, T, T, A and T at sites 18, 69, 270, 303, 381 and 393, respectively (Table 5).

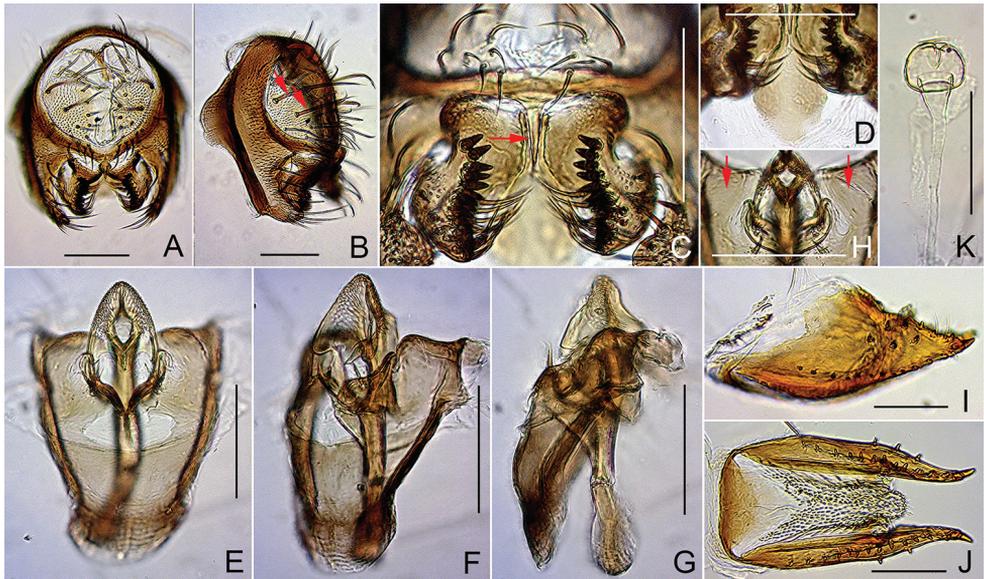


Figure 10. *Dichaetophora sumatraensis* sp. n. (A–H #03890 I–K paratype #03891). **A, B**Periphallal organs (posterior and posterolateral view, respectively) **C** surstyli and ventral portions of cerci **D** tenth sternite (posteroventral view) **E–G** phallic organs (ventral, ventrolateral and lateral view, respectively) **H** distal portion of hypandrium (posteroventral view), showing the caudolateral plates not pubescent (red arrows) and the paramedian setae **I, J** oviscapit (lateral and ventral view, respectively) **K** spermatheca (lateral view). Scale bars: 0.1 mm.

Description. *Head* (Figs 3Q, R, 4Z–D’): First flagellomere grayish brown. Dorsolateral tentorial apodemes slightly divergent in basal 2/5 but strongly divergent in distal 3/5; supercervical setae 19–22 per side; postocular setae 20–24 per side. Palpus with one subprominent, lateromedial seta. Cibarium with numerous (> 60) medial and 8–9 posterior sensilla per side.

Wing (Fig. 3S) slightly fuscous; veins yellowish brown to brown. Halter and stem gray.

Legs (Fig. 3Q): All femora blackish brown; foreleg coxa, tibia and tarsus (except 5th tarsomere) grayish brown; rest grayish yellow. Apical setae present on foreleg and mid-leg tibiae. Mid-leg first tarsomere as long as total length of four succeeding tarsomeres; hindleg first tarsomere longer than total length of four succeeding tarsomeres.

Male terminalia (Fig. 10A–H): Epandrium pubescent except for anterior margin, with three dorsal and 11–13 ventral, long setae per side. Surstylus with 9–10 prenisetae caudal margin, 2–3 short spines and medial patch of pubescence on outer surface and ca. 15 recurved spines on inner, caudal portion. Tenth sternite linguulate, slightly curved. Cercus pubescent except for dorsal to caudal margin, with 20–21 long setae; sclerotized, caudoventral bridge of cerci medially with narrowly elongated process. Paramere somewhat triangular in lateral view, apically round, with sensilla on inner surface. Aedeagus apically trilobed, densely hirsute on outer lobes, dorsosubapically with a pair of small, marginally serrated flaps.

Female terminalia (Fig. 10I–K): Oviscapt valve dorsomedially narrowly extended, with 5–6 lateral and 14–17 marginal, peg-like ovisensilla. Spermathecal capsule without spinules on outer surface.

Measurements (in mm): BL = 2.33 in holotype (1♀ paratype: 2.70), ThL = 1.04 (1.13), WL = 2.17 (2.46), WW = 1.10 (1.00).

Indices: FW/HW = 0.36 (1♀ paratype: 0.40), ch/o = 0.39 (0.33), prorb = n/a (n/a), rcorb = n/a(n/a), orbito = 0.75 (0.78), dcl = 0.72 (n/a), sclt = n/a (n/a), sterno = n/a (0.61), dcp = 0.62 (0.60), scltp = 0.80 (0.75), C = 1.90 (2.00), 4c = 1.29 (1.34), 4v = 2.18 (2.23), 5x = 2.18 (1.84), ac = 2.37 (2.57), M = 0.79 (0.75), C3F = 0.58 (0.60).

Etymology. Pertaining to the type locality.

Distribution. Indonesia (Sumatra).

Remarks. The last three species somewhat resemble *trilobita* sp. n. in having the following morphological characters: wing without distinct, dark cloud; surstylus with medial patch of pubescence on outer surface; sclerotized, caudoventral bridge of cerci with narrow, median process; and oviscapt valve dorsomedially narrowly extended. However, the three species are very hard to distinguish from each other because of their least morphological differentiation. To overcome this difficulty, we employed 19 nucleotide sites of *COI* and *COII* genes as molecular diagnostic characters to identify these cryptic species (Table 5). Nucleotide substitutions at two of these sites are nonsynonymous, i.e., causing changes of amino acids, and specific to *borneoensis* sp. n. (Table 5), thus providing more reliable (less changeable) characters for this species.

Acknowledgments

We thank Dr Maklarin B. Lakim and Dr Maryati Bte Mohamed for their help in field works in Sabah, Malaysia under research permissions (UPE:40/200/19 SJ. 732 and UPE: 40/200/19 SJ.1194 and 1195) of Economic Planning Unit of Malaysian Government. This work was supported by NSFC (Nos 31160429, 31572238), the fund of the Ministry of Science and Technology of China (No. 2011FY120200 and 2012FY110800).

References

- Burla H (1954) Zur Kenntnis der Drosophiliden der Elfenbeinküste (Französisch West-Afrika). *Revue Suisse de Zoologie* 61: 1–218. <https://doi.org/10.5962/bhl.part.75413>
- Duda O (1940) Revision der afrikanischen Drosophiliden (Diptera). II. *Annales Historico-Naturales Musei Nationalis Hungarici* 33: 19–53.
- DeSalle R, Egan MG, Siddall M (2005) The unholy trinity: taxonomy, species delimitation and DNA barcoding. *Philosophical Transactions of the Royal Society B* 360: 1905–1916. <https://doi.org/10.1098/rstb.2005.1722>

- Gao JJ, Watabe H, Aotsuka T, Pang JF, Zhang YP (2007) Molecular phylogeny of the *Drosophila obscura* species group, with emphasis on the Old World species. BMC Evolutionary Biology 7: article no. 87. <https://doi.org/10.1186/1471-2148-7-87>
- Grimaldi DA (1990) A phylogenetic, revised classification of genera in the Drosophilidae (Diptera). Bulletin of the American Museum of Natural History 197: 1–139.
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome *c* oxidase subunit I for diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3: 294–299.
- Hu YG, Toda MJ (2002) Cladistic analysis of the genus *Dichaetophora* Duda (Diptera: Drosophilidae) and a revised classification. Insect Systematics and Evolution 33: 91–102. <https://doi.org/10.1163/187631202X00064>
- Hu YG, Toda MJ (2005) A new species group in the genus *Dichaetophora* Duda (Diptera: Drosophilidae) based on a phylogenetic analysis, with descriptions of four new species from China. Zoological Science 22: 1266–1276. <http://dx.doi.org/10.2108/zsj.22.1265>
- Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33: 1870–1874. <https://doi.org/10.1093/molbev/msw054>
- Li NN, Toda MJ, Fu Z, Li SH, Gao JJ (2014) Taxonomy of the *Colocasiomyia gigantea* species group (Diptera, Drosophilidae), with descriptions of four new species from Yunnan, China. ZooKeys 406: 41–64. <https://doi.org/10.3897/zookeys.406.7176>
- McAlpine JF (1981) Morphology and terminology: adults. In: McAlpine JF, Peterson BV, Shewell GE, Teskey HJ, Vockeroth JR, Wood DM (Eds) Manual of Nearctic Diptera, Vol 1. Biosystematics Research Institute, Ottawa, 9–63.
- Meier R, Zhang G, Ali F (2008) The use of mean instead of smallest interspecific distances exaggerates the size of the “barcoding gap” and leads to misidentification. Systematic Biology 57: 809–813. <https://doi.org/10.1080/10635150802406343>
- Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574. <https://doi.org/10.1093/bioinformatics/btg180>
- Sarkar IN, Thornton JW, Planet PJ, Figurski DH, Schierwater B, DeSalle R (2002) An automated phylogenetic key for classifying homeoboxes. Molecular Phylogenetics and Evolution 24: 388–399. [https://doi.org/10.1016/S1055-7903\(02\)00259-2](https://doi.org/10.1016/S1055-7903(02)00259-2)
- Simon C, Frati F, Beckenbach A, Crespi B, Liu H, Flook P (1994) Evolution, weighting, and phylogenetic utility of mitochondrial gene sequences and a compilation of conserved polymerase chain reaction primers. Annals of the Entomological Society of America 87: 651–701. <https://doi.org/10.1093/aesa/87.6.651>
- Srivathsan A, Meier R (2012) On the inappropriate use of Kimura-2-parameter (K2P) divergences in the DNA-barcoding literature. Cladistics 28: 190–194. <https://doi.org/10.1111/j.1096-0031.2011.00370.x>
- Zhang WX, Toda MJ (1992) A new species-subgroup of the *Drosophila immigrans* species-group, with description of two new species from China and revision of taxonomic terminology. Japanese Journal of Entomology 60: 839–850.

**Corrigenda: *Cherax warsamsonicus*, a new species of crayfish from the Kepala Burung (Vogelkop) peninsula in West Papua, Indonesia (Crustacea, Decapoda, Parastacidae) ZooKeys 660: 151–167.
<https://doi.org/10.3897/zookeys.660.11847>**

Christian Lukhaup¹, Rury Eprilurahman², Thomas von Rintelen³

1 Waldstrasse 5a, 66999 Hinterweidenthal, Germany **2** Animal Systematics Laboratory, Faculty of Biology, Universitas Gadjah Mada Jl. Teknika Selatan, Sekip Utara Yogyakarta 55281, Indonesia **3** Museum für Naturkunde -Leibniz Institute for Evolution and Biodiversity Science, Invalidenstrasse 43, 10115 Berlin, Germany

Corresponding author: *Christian Lukhaup* (craykeeper@gmx.de)

Academic editor: *P. Stoev* | Received 21 March 2017 | Accepted 23 March 2017 | Published 4 April 2017

<http://zoobank.org/9283383B-CC1F-49DF-B1D2-B81B07150000>

Citation: Lukhaup C, Eprilurahman R, Rintelen T (2017) Corrigenda: *Cherax warsamsonicus*, a new species of crayfish from the Kepala Burung (Vogelkop) peninsula in West Papua, Indonesia (Crustacea, Decapoda, Parastacidae) ZooKeys 660: 151–167. <https://doi.org/10.3897/zookeys.660.11847>. ZooKeys 665: 147–148. <https://doi.org/10.3897/zookeys.665.12850>

It has come to our attention that in the work referenced above Table 1 is incomplete. Furthermore, Figure 7 as printed therein is not the final version of that figure.

The correct versions of both Table 1 and Figure 7 are reproduced here below.

Table 1. Material studied with GenBank accession numbers.

Species/sample	Location	GenBank acc. nos	
		COI	16S
<i>Cherax albertisii</i>	Bensbach River, Papua New Guinea (Queensland Museum)	–	KJ920770
<i>C. boesemani</i>	Ajamaru Lake, Papua Barat; 1°17'19.97"S, 132°14'49.14"E; January 23, 2016	KY654084 KY654085	KY654089 KY654090
<i>C. holthuisi</i>	Papua Barat	KU821419	KU821433
<i>C. misolicus</i>	Misool Island, South of Papua Barat (Leiden Museum)	-	KJ920813
<i>C. monticola</i>	Baliem River, Wamena, Papua	KF649851 –	KF649851 KJ920818
<i>C. paniaicus</i>	Lake Tage, Papua (Field collection)	KJ950528	KJ920830
<i>C. peknyi</i>	Pet Shop	KU821422	KU821435
<i>C. pulcher</i>	Hoa Creek (Teminabuan), Papua Barat; 1°28'32.73"S, 132°3'54.94"E; January 23, 2016	KY654083	KY654088
<i>C. 'pulcher'</i>	Papua Barat (Pet Shop)	KU821424 KU821426	KU821438 KU821437
<i>C. rhynchotus</i>	Lake Wicheura, Cape York, Queensland (Queensland Museum)	–	KJ920765
<i>C. snowden</i>	Oinsok (Ainsok River Drainage), Papua Barat; 1°11'40.07"S, 131°50'1.14"E; January 24, 2016	KY654082	KY654087
<i>C. warsamsonicus</i>	Small tributary to Warsamson River, 0°49'16.62"S, 131°23'3.34"E; January 20, 2016	KY654086	KY654091
<i>Engaeus strictifrons</i>	Crawford River, Victoria, Australia	AF493633	AF492812
<i>Euastacus bispinosus</i>	Crawford River, Victoria, Australia	AF493634	AF492813

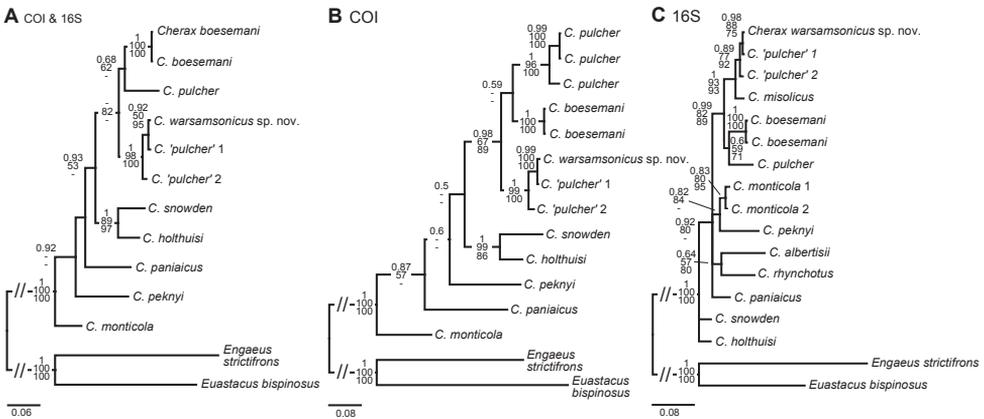


Figure 7. Phylogenetic position of *Cherax warsamsonicus* sp. n. within closely related New Guinean *Cherax* species, reconstructed by BI analyses of two mitochondrial gene fragments. Number on branches show, from top, Bayesian posterior probabilities and ML/MP bootstrap values. The scale bar indicates the substitution rate. See Table 1 for information on the sequenced specimens. **A** Topology based on concatenated COI and 16S dataset **B** Topology based on COI dataset **C** Topology based on 16S dataset.