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Four new *Gammarus* species from Tibetan Plateau with a key to Tibetan freshwater gammarids (Crustacea, Amphipoda, Gammaridae)

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Abstract

Four new species of the genus *Gammarus* are described and illustrated from Tibetan Plateau. *Gammarus altus* **sp. n.** and *G. limosus* **sp. n.** are characterized by pereopods III–IV with a few short setae and uropod III with marginal spines accompanied by short setae. *Gammarus kangdingensis* **sp. n.** and *G. gonggaensis* **sp. n.** are characterized by pereopods III–IV with long straight setae on posterior margins and inner ramus of uropod III 0.4 times as long as outer ramus. Detailed morphological comparisons with related species are discussed. A key to 15 *Gammarus* species from the Tibetan Plateau and a map of their distributions are provided.

Keywords

Amphipoda, diversification, freshwater, taxonomy

Introduction

The Tibetan Plateau is the highest and largest plateau in the world, and arguably the most prominent topological feature on Earth (Royden et al. 2008, Favre et al. 2015). The Tibetan Plateau is typically inhabited by highly specialized biota, which is adapted to the extreme environmental conditions, such as wild yaks and Tibetan gazelles (Hou and Li 2004). However, the freshwater diversity of the Tibetan Plateau remains poorly

understood, except fishes (He and Chen 2006, Qi et al. 2015) and mollusks (Clewing et al. 2015, 2016a). In order to better understand the biodiversity of the Tibetan Plateau, six expeditions were organized by the authors from 2001 to 2017. Following a detailed examination of the collections, crustaceans of the genus *Gammarus* Fabricius, 1775 were found widely distributed in alpine lakes and river systems. All species are cold-water adapted.

The Holarctic amphipod genus *Gammarus* contains more than 200 described species (Väinölä et al. 2008). It has been suggested that *Gammarus* originated from the ancient Tethys, and then diversified in the Eurasia driven by the Tibetan uplifting (Hou et al. 2007, 2011, Hou and Li 2017). Eleven species were described from the plateau before the current study: ten are endemic species, including *G. sinuolatus* Hou & Li, 2004, *G. frigidus* Hou & Li, 2004, *G. lasaensis* Barnard & Dai, 1988, *G. jaspidus* Hou & Li, 2004, *G. abstrusus* Hou, Platvoet & Li, 2006, *G. emeiensis* Hou, Li & Koenemann, 2002, *G. hongyuanensis* Barnard & Dai, 1988, *G. sichuanensis* Hou, Li & Zheng, 2002, *G. praecipuus* Li, Hou & An, 2013, and *G. glaber* Hou, 2017 (Zhao et al. 2017); while *G. lacustris* Sars, 1863 is widely distributed in alpine lakes (Karaman and Pinkster 1977, Clewing et al. 2016b). In the current paper, four new species are described and illustrated: *Gammarus altus* sp. n., *G. kangdingensis* sp. n., *G. gonggaensis* sp. n., and *G. limosus* sp. n. The distributions of 15 *Gammarus* species from Tibetan Plateau are presented in Figure 1, where only type localities are used for all species except *G. lacustris* Sars, 1863 based on material of Barnard and Dai (1988). A key to all these species is provided.

Materials and methods

The specimens were collected along the bank of streams flowing from high mountains with a fine-meshed hand net. Samples were preserved in 95% ethanol in the field and deposited in a -20°C refrigerator for long-term preservation. The body length of each amphipod was recorded by holding the specimen straight and measuring the distance along the dorsal side of the body from the base of the first antenna to the base of the telson. All dissected appendages were mounted in glycerol on slides. Appendages were drawn using a Leica DM2500 compound microscope equipped with a drawing tube. The specimens are lodged in the Institute of Zoology, Chinese Academy of Sciences (**IZCAS**), Beijing.

Taxonomy

Family Gammaridae Leach, 1814

Genus *Gammarus* Fabricius, 1775

Type species. *Gammarus pulex* (Linnaeus, 1758).

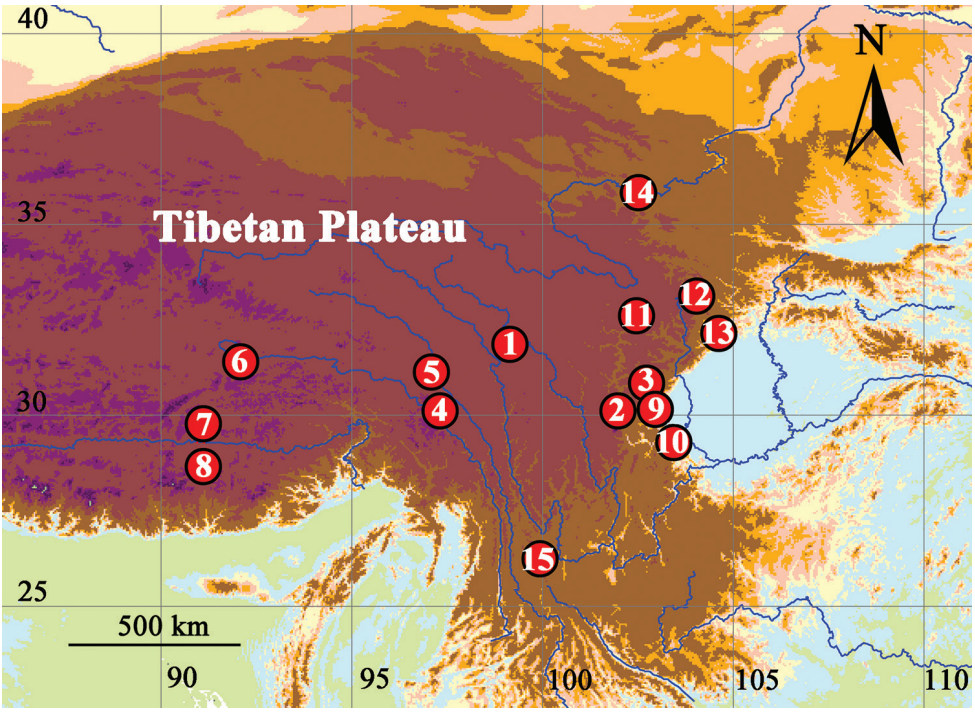

Figure 1. Distribution map of *Gammarus* species from Tibetan Plateau. Type localites are shown for species **1–14**. **1** *Gammarus altus* sp. n. **2** *G. kangdingensis* sp. n. **3** *G. gonggaensis* sp. n. **4** *G. limosus* sp. n. **5** *G. sinuolatus* Hou & Li, 2004 **6** *G. frigidus* Hou & Li, 2004 **7** *G. lasaensis* Barnard & Dai, 1988 **8** *G. jaspidus* Hou & Li, 2004 **9** *G. abstrusus* Hou, Platvoet & Li, 2006 **10** *G. emeiensis* Hou, Li & Koenemann, 2002 **11** *G. hongyuanensis* Barnard & Dai, 1988 **12** *G. sichuanensis* Hou, Li & Zheng, 2002 **13** *G. praecipuus* Li, Hou & An, 2013 **14** *G. glaber* Hou, 2017 **15** *Gammarus lacustris* Sars, 1863 based on material used in Barnard and Dai (1988).

Gammarus altus sp. n.

http://zoobank.org/B32F6C92-AEAB-4A62-BD6F-4916FCC73377
Figs 2–6

Material examined. Holotype: male (IZCAS-I-A0061-1), 11.6 mm, Maniganggo Town (31.9°N, 99.2°E), Dege County, Sichuan Province, altitude 4000 m, August 12, 2001, collected by Xianjin Peng. Paratype: female (IZCAS-I-A0061-2), 10.1 mm; paratypes: five males and five females (IZCAS-I-A0061-3), same data as holotype.

Etymology. The specific name alludes to its typical biotope, living in high altitude; adjective.

Diagnosis. Pereopods III and IV with a few setae on posterior margins; pereopods V–VII slender, bases elongated, carpus and propodus with spines on anterior margins but few setae; epimeral plates with blunt posterodistal corners; uropod III inner ramus length approx. one-third of outer ramus length, both rami with marginal spines but with few marginal setae.

Description of male holotype. (IZCAS-I-A0061-1), 11.6 mm.

Head. (Fig. 4D): cephalic lateral lobe truncated, inferior antennal sinus deep, eyes ovate.

Antenna I (Fig. 4A): peduncle articles I–III in length ratio 1.0 : 0.7 : 0.4, with some setae on posterior margin; primary flagellum with 28 articles, most with aesthetascs, accessory flagellum with three articles.

Antenna II (Fig. 4B): gland cone reaching peduncle article III, article IV a little shorter than article V, bearing one to three clusters of setae on lateral and medial margins; flagellum with ten articles, proximal seven articles with calceoli.

Upper lip (Fig. 2C): convex, with minute setae.

Mandible (Fig. 2A, B, H): incisor of left mandible with five teeth; lacinia mobilis with four teeth; spine row with six plumose setae; second article of palp with 15 marginal setae and four medial setae, third article 83% length of second article, with six A-setae on outer face, two groups of B-setae on inner face, approx. 17 D-setae and four E-setae apically. Incisor of right mandible with four teeth; lacinia mobilis bifurcate, with small teeth.

Lower lip (Fig. 2D): inner lobes lacking, outer lobes covered with thin setae.

Maxilla I (Fig. 2F, G): asymmetrical, left inner plate with 18 plumose setae; outer plate with eleven serrated apical spines; second article of left palp with seven slender spines and two stiff setae; second article of right palp with five blunt spines and one stiff seta.

Maxilla II (Fig. 2E): inner plate with 16 plumose setae in an oblique row; inner and outer plates with long setae apically.

Maxilliped (Fig. 2I): inner plate with three apical spines and 12 plumose marginal setae; outer plate with a row of 14 blade spines on medial margin and four plumose setae apically; third article of palp with long setae, terminal article hooked, with a group of setae at hinge of unguis.

Pereon. Gnathopod I (Fig. 3A, B): coxal plate bearing a seta on anterior and posterior corners each; basis with long setae on anterior and posterior margins; carpus sub-parallel, 71% length of propodus, posterior margin with groups of setae; propodus pyriform, palm oblique, with one medial spine, seven spines on posterior margin and six spines on inner face; dactylus more than half of posterior margin in length, with one seta on outer margin.

Gnathopod II (Fig. 3C, D): coxal plate with two setae on anterior corner and one seta on posterior corner; basis with setae on anterior and posterior margins; carpus almost as long as propodus, with subparallel margins, bearing seven clusters of setae along ventral margin, a group of setae on dorsal margin; propodus subrectangular, palm transverse, with one medial spine and four spines on posterior corner; dactylus beyond the palm margin, with one seta on outer margin.

Pereopod III (Fig. 4F, G): coxal plate with two setae and one seta on anterior and posterior margins, respectively; basis with setae along anterior and posterior margins; merus with two spines on anterior margin and four clusters of setae on posterior margin, anterodistal corner with one spine accompanied by setae; carpus with three groups of spines accompanied by setae on posterior margin, anterodistal corner with one spine and posterodistal corner with two spines accompanied by setae; propodus

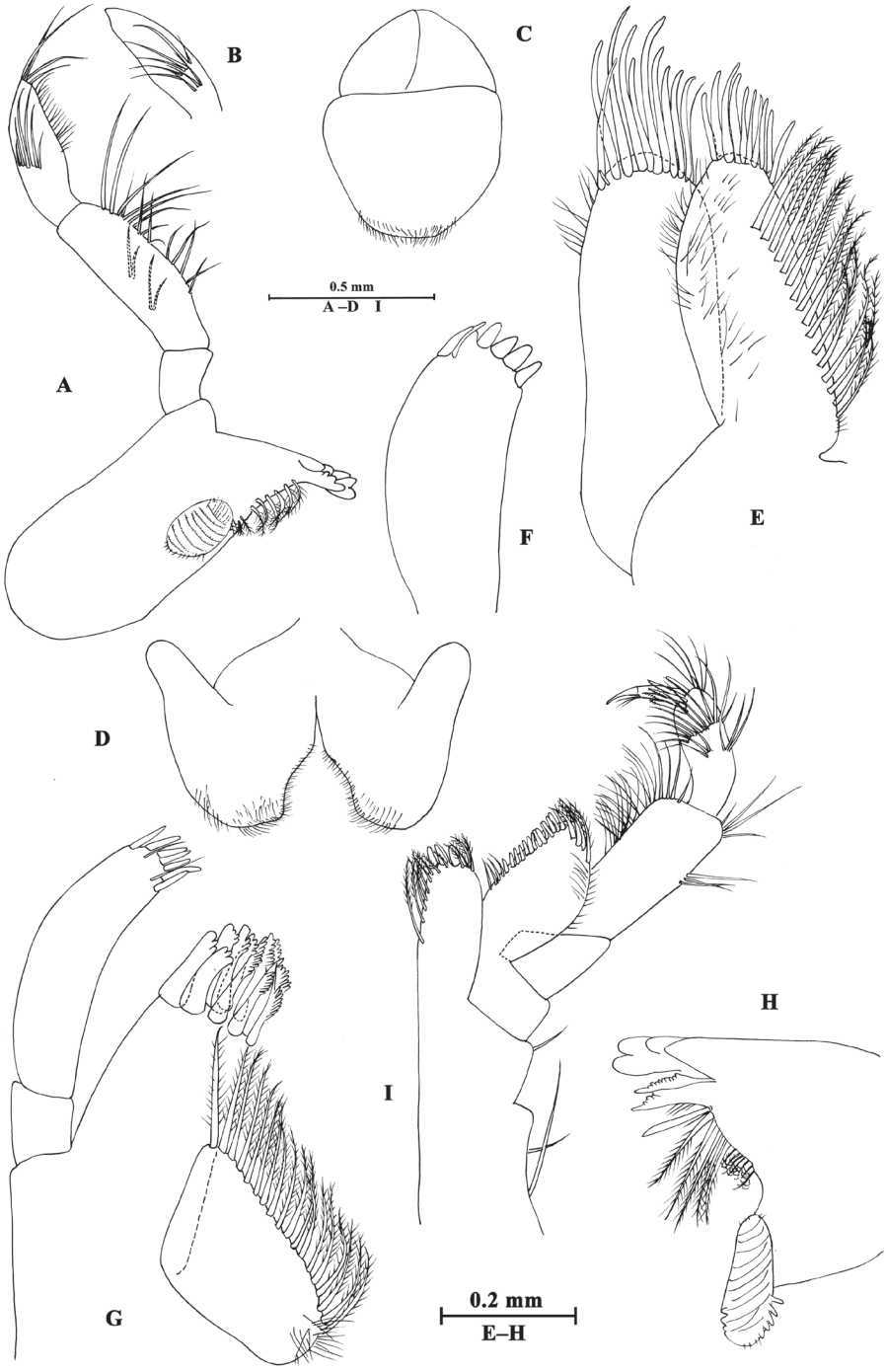

Figure 2. *Gammarus altus* sp. n., male holotype. **A** left mandible **B** inner face of article III of left palp **C** upper lip **D** lower lip **E** maxilla II **F** palp of right maxilla I **G** left maxilla I **H** incisor of right palp **I** maxilliped.

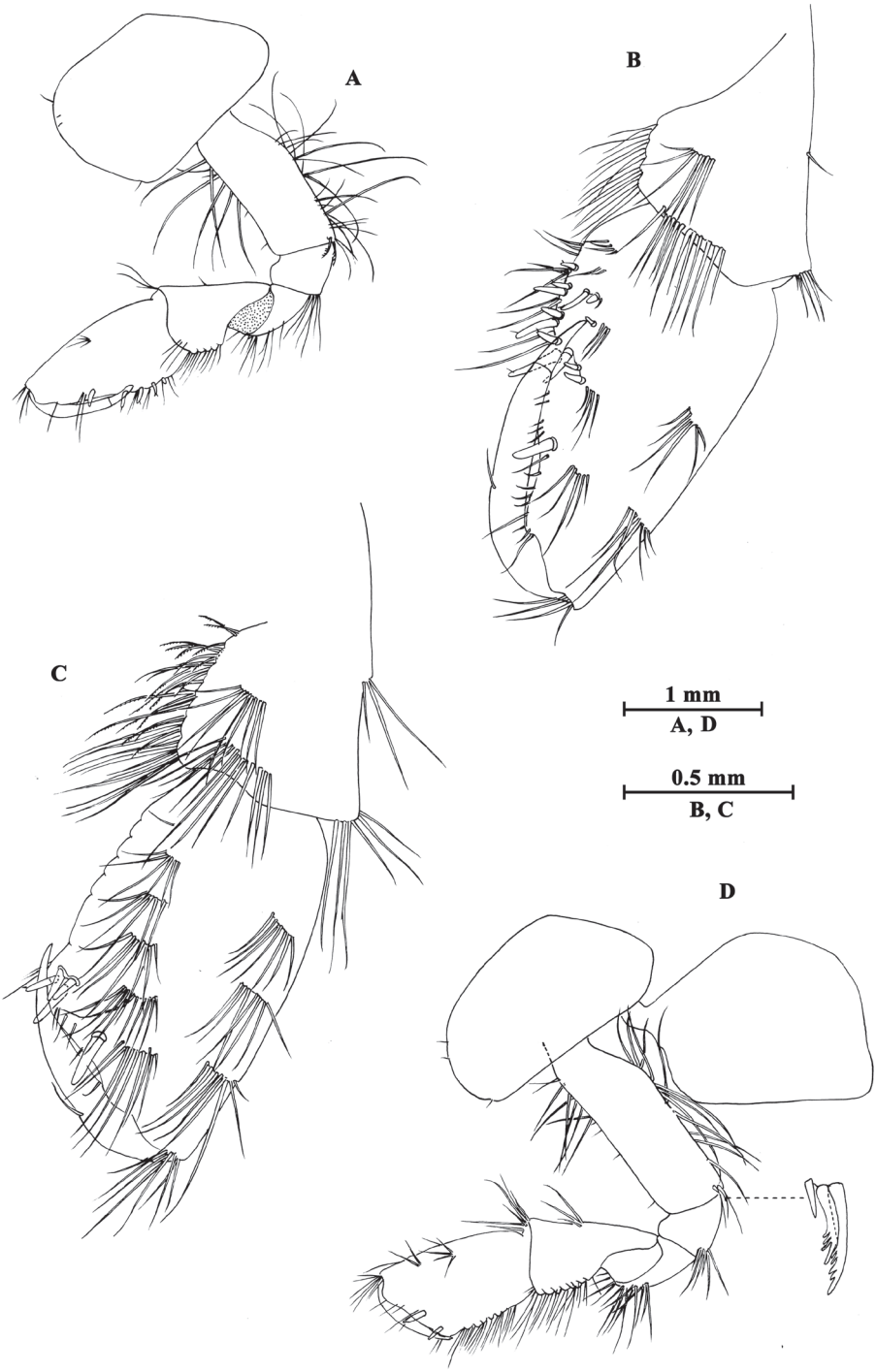

Figure 3. *Gammarus altus* sp. n., male holotype. **A** gnathopod I **B** propodus of gnathopod I (medial view) **C** propodus of gnathopod II (medial view) **D** gnathopod II.

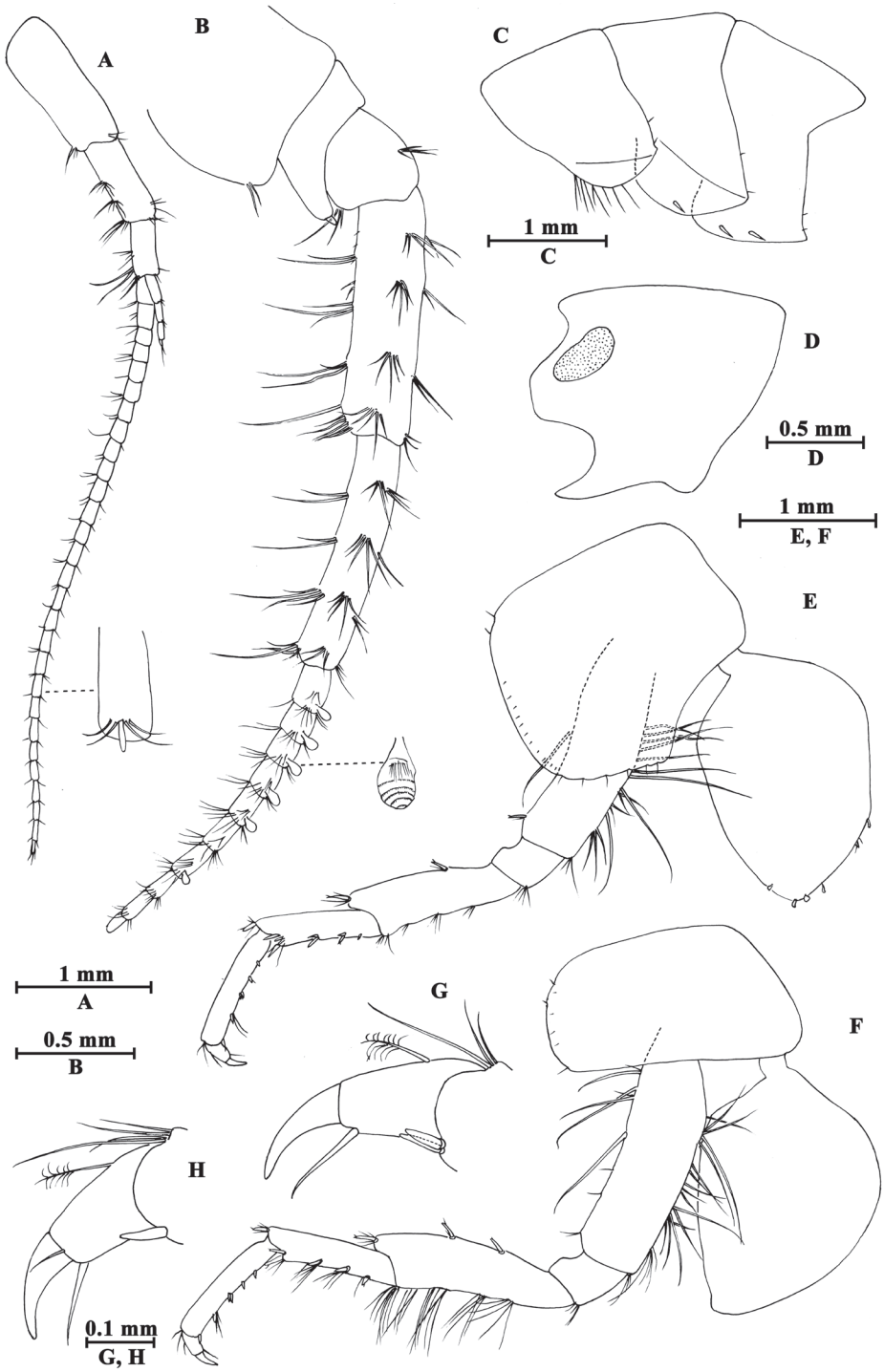

Figure 4. *Gammarus altus* sp. n., male holotype. **A** antenna I **B** antenna II **C** epimeral plates I–III **D** head **E** pereopod IV **F** pereopod III **G** dactylus of pereopod III **H** dactylus of pereopod IV.

with four groups of spines accompanied by setae on posterior margin, and two spines on posterodistal corner; dactylus stout, with one plumose seta on anterior margin and one seta at joint of unguis.

Pereopod IV (Fig. 4E, H): coxal plate concave posteriorly, with two setae on anterior corner and six setae on posterior margin; basis with one spine on anterodistal corner, and clusters of setae on posterior margin; merus with a spine on anterior margin, a spine accompanied with setae on anterodistal corner, three clusters of short setae on posterior margin; carpus and propodus with groups of spines accompanied by a few setae on posterior margins; dactylus with one plumose seta on anterior margin, and two setae at hinge of unguis.

Pereopod V (Fig. 5A): coxal plate with one seta on anterior lobe and four setae on posterior margin; basis posterior margin nearly straight, with four spines on anterior margin and one spine on anterodistal corner, and a row of 13 setae on posterior margin; merus with two spines on anterior margin and two spines on posterior margin, anterodistal and posterodistal corners with two spines each; carpus and propodus with groups of spines accompanied by fine setae on anterior margin, posterior margin of carpus with three groups of spines accompanied with setae; dactylus with two setae at hinge of unguis.

Pereopod VI (Fig. 5C, G): coxal plate with one seta and three setae on anterior and posterior margins, respectively; basis elongated, with one long seta and four spines on anterior margin, anterodistal corner with one spine accompanied by setae; posterior margin narrowing distally, with a row of 14 fine setae; merus with two groups of spines on anterior margin and two spines on posterior margin, anterodistal and posterodistal corners with two spines each; carpus and propodus with groups of spines on anterior margin, posterior margin of carpus with two pairs of spines accompanied by setae; dactylus with one seta at hinge of unguis.

Pereopod VII (Fig. 5B, H): coxal plate with five setae on posterior margin; basis expanded, with two long setae and four spines on anterior margin, anterodistal corner with two spines accompanied by setae, posterior margin with a row of 15 setae, and a spine on inner surface; merus with two pairs of spines on anterior margin and two single spines on posterior margin, anterodistal and posterodistal corners with two spines each; carpus and propodus with three or four pairs of spines on anterior margins, posterior margin of carpus with two pairs of spines, and posterior margin of propodus with two clusters of setae; dactylus with one plumose seta on posterior margin and two setae at hinge of unguis.

Coxal gills (Figs 3D, 4E, F, 5A–C): present on gnathopod II and pereopods III–VII, sac-like.

Pleon. Epimeral plates (Fig. 4C): plates I–III truncated to weakly acute, bearing two short setae on posterior margins. Plate I ventrally rounded, with nine setae on ventral margin; plate II with one spine on ventral margin; plate III with two spines on ventral margin.

Pleopods (Fig. 5D–F): subequal in length, peduncle with some marginal setae and two retinacula accompanied by two setae; inner and outer rami with approximately 20 segments, armed with plumose setae.

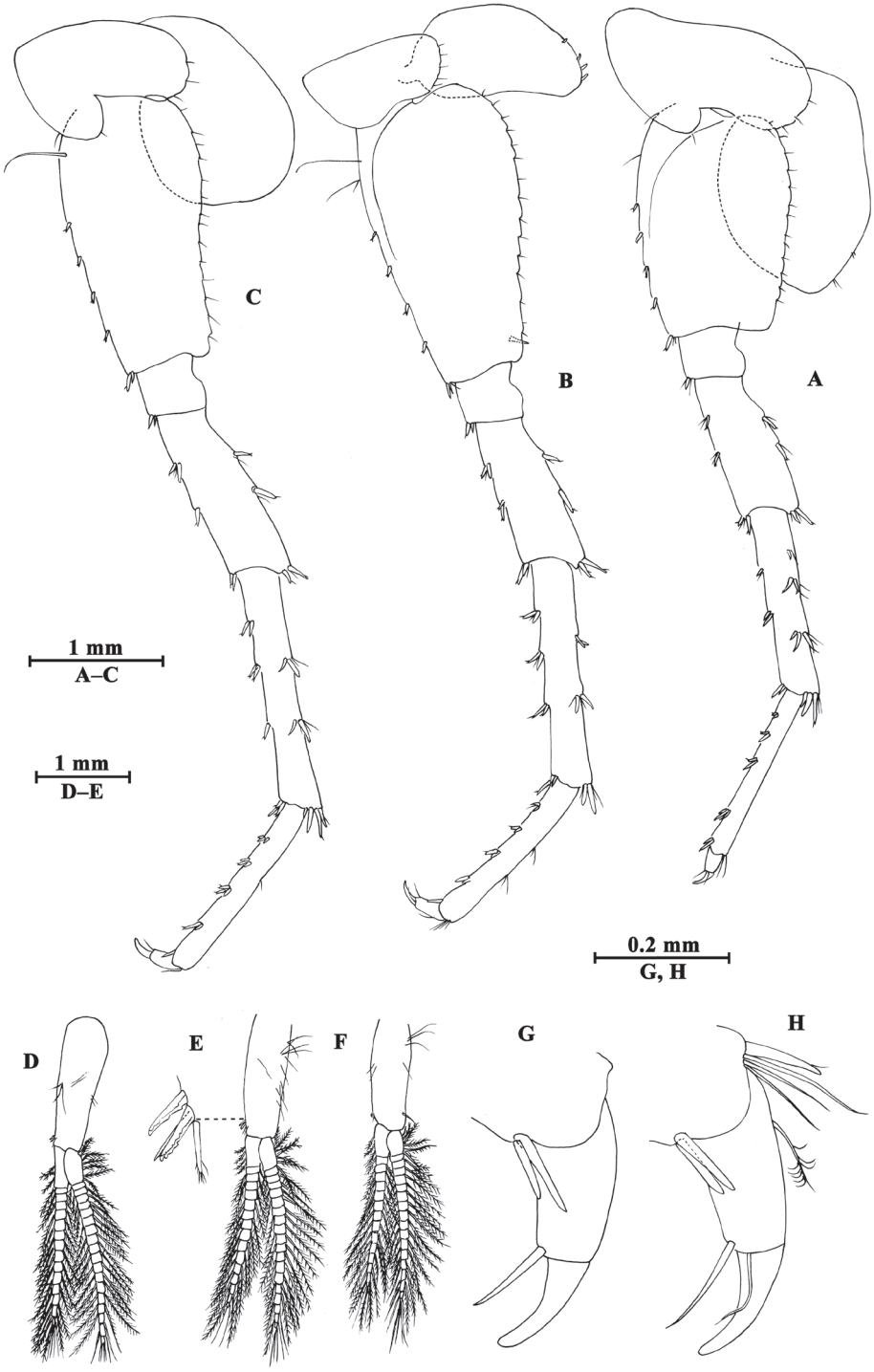

Figure 5. *Gammarus altus* sp. n., male holotype. **A** pereopod V **B** pereopod VII **C** pereopod VI **D** pleopod I **E** pleopod II **F** pleopod III **G** dactylus of pereopod VI **H** dactylus of pereopod VII.

Urosome. Urosomites (Fig. 6E): non-humped, urosomites I–II bearing two-one-one-two spines on dorsal margin; urosomite III with two-one spines on lateral margins and two setae on dorsal margin.

Uropod I (Fig. 6C): peduncle longer than rami, with one basofacial spine, one spine on outer margin and two spines on inner margin, two spines and one spine on outer and inner distal corners respectively; inner ramus with one spine on inner margin, outer ramus with one spine on inner and outer margins each, both rami with five terminal spines.

Uropod II (Fig. 6A): peduncle with one spine on outer margin and one spine on outer distal corner; inner ramus with one spine on inner margin; outer ramus with one spine on outer margin, both rami with five terminal spines.

Uropod III (Fig. 6D): peduncle with one marginal spine and some setae; inner ramus length nearly one-third of outer ramus length, with three spines accompanied by setae on inner margin, outer margin bare; proximal article of outer ramus slender, with four pairs of spines on outer margin, six groups of spines and setae on inner margin, and four distal spines, terminal article cone-shaped, with simple setae distally; both rami with few short setae.

Telson (Fig. 6B): cleft, each lobe with three distal spines, one basolateral spine and some facial setae.

Description of paratype female. (IZCAS-I-A0061-2), 10.1mm.

Pereon. Gnathopod I (Fig. 6F): propodus of gnathopod I ovate, palm slant, with seven spines on posterior corner, dactylus with one seta on outer margin.

Gnathopod II (Fig. 6G): propodus subrectangular, with two spines on posterior corner.

Oostegite: present on gnathopod II and pereopods III–V.

Urosome. Uropod III (Fig. 6H): inner ramus less than 30% length of outer ramus, with two spines on inner ramus and one distal spine accompanied by setae; outer ramus with four or five groups of spines accompanied by setae on inner and outer margins; both rami armed with few marginal setae.

Habitat. This species was collected from a stream with altitude 4000 m, water clear and cold. There are a few water plants in the locality.

Remarks. *Gammarus altus* sp. n. is most similar to *G. glaber* Hou, 2017 in having some setae on posterior margins of pereopods III and IV , and uropod III inner ramus length around one-third of outer ramus length, both rami with spines but few setae. The new species can be distinguished from *G. glaber* by the following characters (*G. glaber* in parentheses): second article of palp with two groups of B-setae (a group of B-setae); bases of pereopods V–VII elongated (broad), narrowing distally (posterior margin of pereopods V and VI nearly straight); uropod III with spines accompanied by simple setae on inner margin (uropod III with spines accompanied by plumose setae); and telson with no medial spines on surface (with one or two spines on medial surface).

This species is similar to *G. sichuanensis* Hou, Li & Zheng, 2002 in peduncle of antenna I and II with two or three groups of setae along anterior and posterior margins, and pereopod IV with a few setae on posterior margin. It differs from *G. sichuanensis* (*G. sichuanensis* in parentheses) by pereopod III with short setae on posterior margins

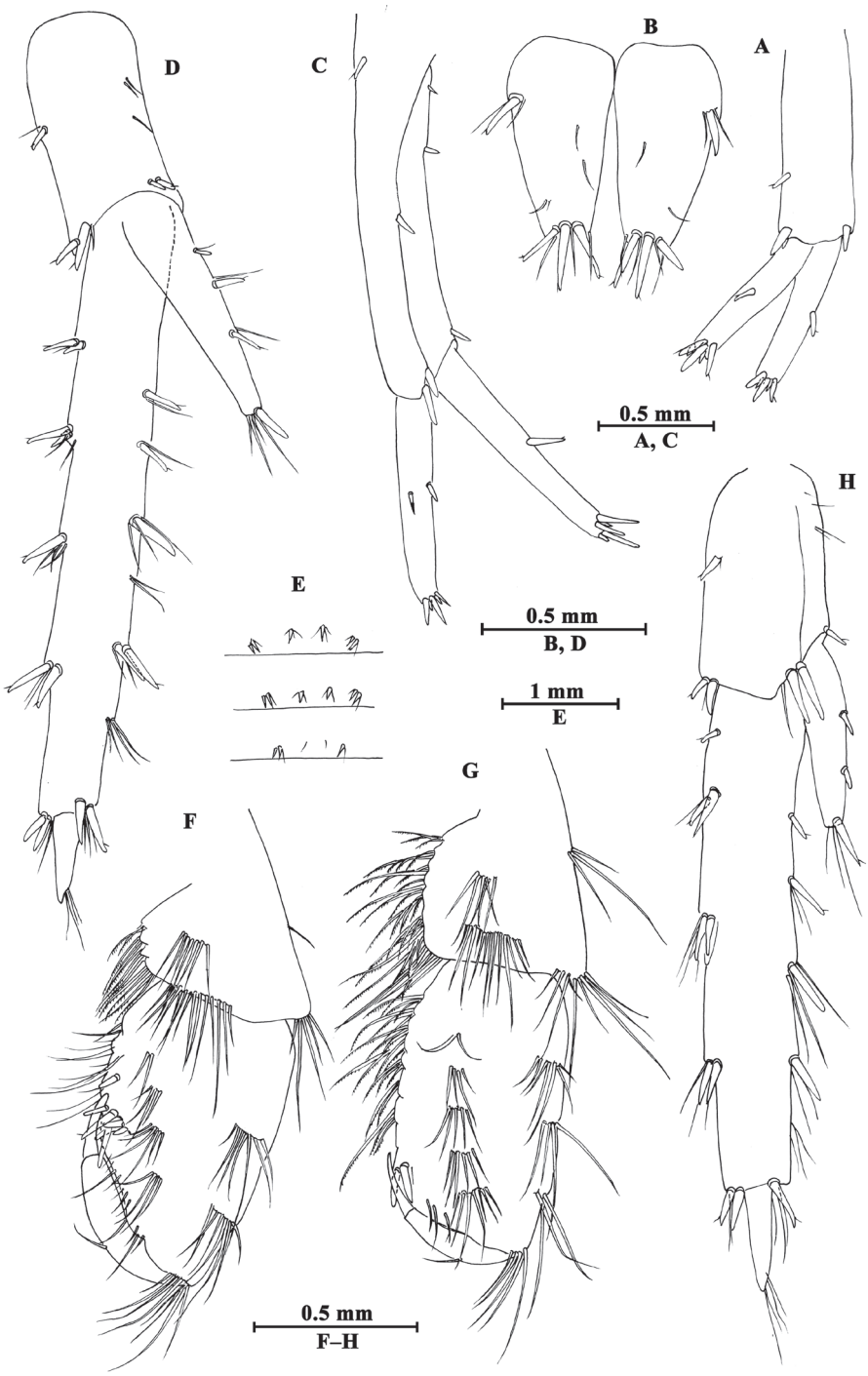

Figure 6. *Gammarus altus* sp. n., **A–E** male, holotype **F–H** female, paratype. **A** uropod II **B** telson **C** uropod I **D** uropod III **E** urosomites I–III (dorsal view) **F** propodus of gnathopod I (medial view) **G** propodus of gnathopod II (medial view) **H** uropod III.

of merus and carpus (with long setae on posterior margins of merus and carpus); bases of pereopods V–VII elongated (broad in *G. sichuanensis*); uropod III with no plumose setae (both rami with plumose setae on inner and outer margins).

***Gammarus kangdingensis* sp. n.**
http://zoobank.org/2883210F-54D8-4945-95C0-9C9DEE5D0DA2
Figs 7–11

Material examined. Holotype: male (IZCAS-I-A0059-1), 11.8 mm, Erdaohe, Kangding County (30.0°N, 101.9°E), altitude 2470 m, August 19, 2001, collected by Xianjin Peng. Paratype: female (IZCAS-I-A0059-2), 8.5 mm; paratypes: two males and three females (IZCAS-I-A0059-3), same data as holotype.

Etymology. The specific name is derived from the type locality; adjective.

Diagnosis. Pereopods III and IV with long setae on posterior margins; epimeral plates blunt; uropod III inner ramus length less than half of outer ramus length, outer margin of outer ramus with few plumose setae.

Description of male holotype. (IZCAS-I-A0059-1), 11.8 mm, slender.

Head. (Fig. 7A, B): cephalic lateral lobe truncated, inferior antennal sinus deep, eyes ovate.

Antenna I (Fig. 7F, G): peduncle articles I–III in length ratio 1.0 : 0.7 : 0.4, each article with distal setae; primary flagellum with 22 articles, most with aesthetascs; accessory flagellum with five articles.

Antenna II (Fig. 8F): gland cone reaching peduncle article III, peduncle articles VI and V in length ratio 1.0 : 0.7, with one or two groups of setae on ventral margin, flagellum with nine articles, each with short setae, calceoli present on articles II–V.

Upper lip (Fig. 7M): convex, with minute setae.

Mandible (Fig. 7H–J): incisor of left mandible with five teeth; lacinia mobilis with four teeth; second article of palp with 14 stiff setae, third article 77% the length of second article, with three groups of A-setae on outer face, seven B-setae on inner face, a row of 25 D-setae and five E-setae apically. Incisor of right mandible with four teeth; lacinia mobilis bifurcate, with small teeth.

Lower lip (Fig. 8E): inner lobes lacking, outer lobes covered with thin setae.

Maxilla I (Fig. 7K, L): asymmetrical, left inner plate with 18 plumose setae, outer plate with eleven serrated spines, second article of left palp with eight slender spines and three stiff setae; second article of right palp with five blunt spines and two stiff setae.

Maxilla II (Fig. 8G): inner plate with 15 plumose setae in an oblique row, outer plate broad, with apical setae.

Maxilliped (Fig. 8H): inner plate with three blunt spines and one subapical spine; outer plate broad, with 13 blade spines on medial margin and four plumose setae apically; palp with four articles, terminal article unguis-form, with setae at hinge of unguis.

Pereon. Gnathopod I (Fig. 8A, D): coxal plate weakly dilated distally, with two and one seta on anterior and posterior corners, respectively; basis with long setae along

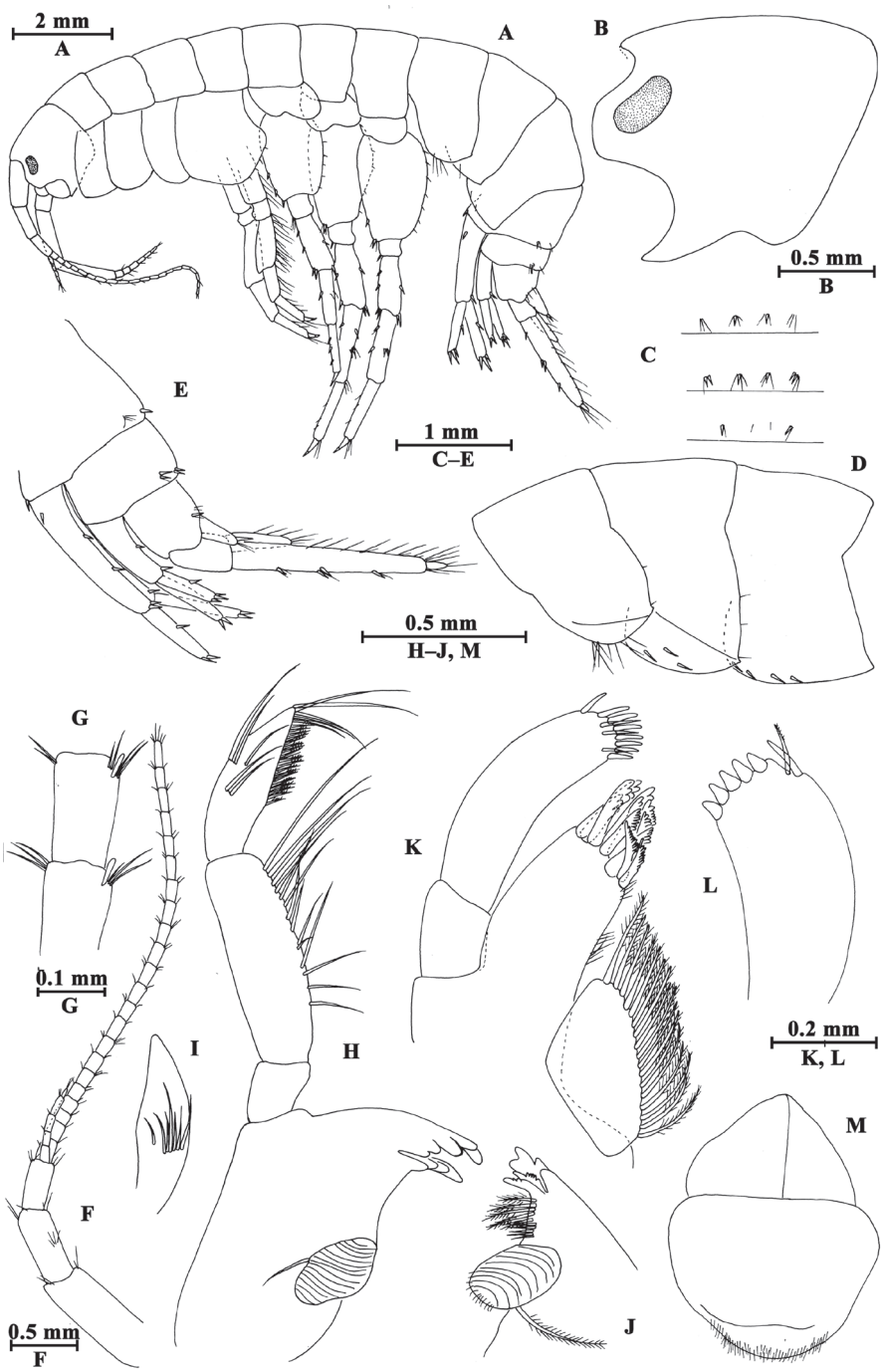

Figure 7. *Gammarus kangdingensis* sp. n., male holotype. **A** body (lateral view) **B** head **C** urosomites (dorsal view) **D** epimeral plates I–III **E** urosomites (lateral view) **F** antenna I **G** flagellum of antenna I **H** left mandible **I** inner face of article III of right palp **J** incisor of right palp **K** left maxilla **L** palp of right maxilla **M** upper lip.

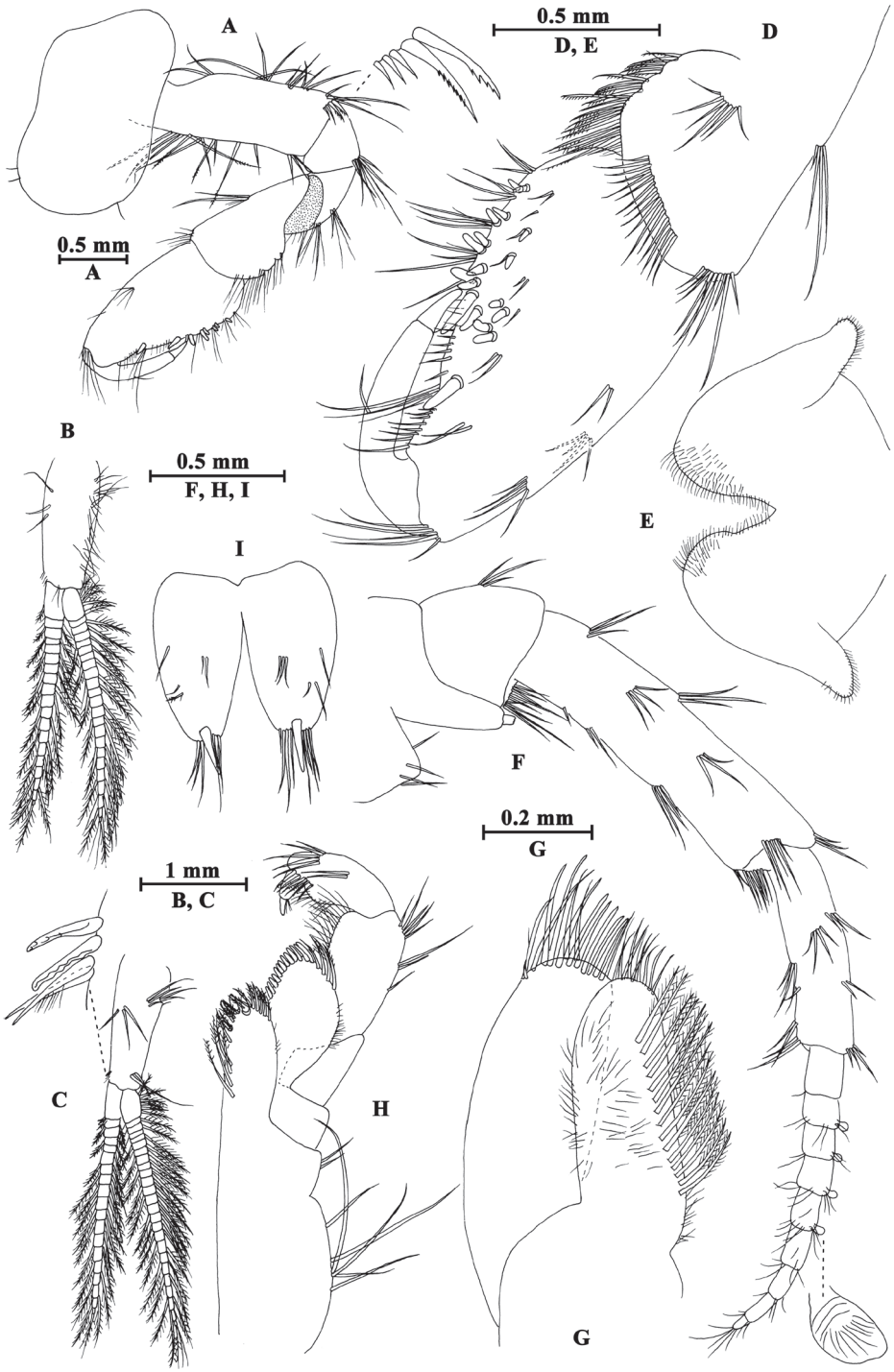

Figure 8. *Gammarus kangdingensis* sp. n., male holotype. **A** gnathopod I **B** pleopod II **C** pleopod I **D** propodus of gnathopod I (medial view) **E** lower lip **F** antenna II **G** maxilla II **H** maxilliped **I** telson.

anterior and posterior margins; carpus a little shorter than propodus, with four groups of setae on posterior margin; propodus pyriform, palm oblique, bearing a median spine, ten spines on posterior margin and seven spines on inner face; dactylus reaching half of posterior margin of propodus, with one seta on outer margin.

Gnathopod II (Fig. 9A, D), coxal plate subrectangular, with one seta on anterior corner and one seta on posterior corner, basis slender than that of gnathopod I, bearing four serrated setae distally; carpus as long as propodus, with subparallel margins; propodus subrectangular, palm with a median blunt spine, and six spines on posterior corner; dactylus beyond the palm margin, with one seta on posterior margin.

Pereopod III (Fig. 9C, F): coxal plate with two setae on anterior corner and one seta on posterior corner; basis with long straight setae on posterior margin, merus with one spine accompanied by setae on anterior margin, and long setae on posterior margin; carpus with four groups of spines accompanied by long setae on posterior margin; propodus with four pairs of spines accompanied by few setae on posterior margin; dactylus short, with one plumose seta on anterior margin and one stiff seta at hinge of unguis.

Pereopod IV (Fig. 9B, E): shorter than pereopod III, coxal plate concave, with two setae on anterior corner and six setae on posterior margin; basis with long straight setae on posterior margin; merus with one spine accompanied by one seta on anterior margin and six clusters of long setae on posterior margin; carpus with three pairs of spines accompanied by long setae on posterior margin, posterodistal corner with two spines accompanied by long setae; propodus with four groups of spines accompanied by a few setae on posterior margin; dactylus with one seta at hinge of unguis.

Pereopod V (Fig. 10A, H): coxal plate with one seta on anterior lobe and three setae on posterior lobe; basis weakly expanded, with three groups of long setae and a row of five spines on anterior margin, anterodistal corner with a spine accompanied by setae, posterior margin with a row of 15 fine setae; merus with three groups of setae and spines on anterior margin, and a spine accompanied by setae on posterior margin; carpus with two groups of spines on anterior and posterior margins each; propodus with three groups of spines on anterior margin; dactylus with one plumose seta on posterior margin and two setae at hinge of unguis.

Pereopod VI (Fig. 10B, I): coxal plate with three setae on posterior margin; basis expanded, tapered distally, with six long setae and five spines on anterior margin, anterodistal corner with one spine accompanied with setae, posterior margin with 16 setae, and two setae on inner surface; merus and carpus with spines on anterior and posterior margins; propodus with four spines on anterior margin; dactylus with one plumose seta on posterior margin and two setae at hinge of unguis.

Pereopod VII (Fig. 10C, J): coxal plate with five setae on posterior margin; basis expanded, anterior margin with three groups of long setae and five spines, anterodistal corner with a spine accompanied by setae, posterior margin with a row of 15 setae, inner surface with a spine accompanied by setae; merus and carpus with spines on anterior and posterior margins; propodus with four pairs of spines on anterior margin; dactylus with one plumose seta on posterior margin and a seta at hinge of unguis.

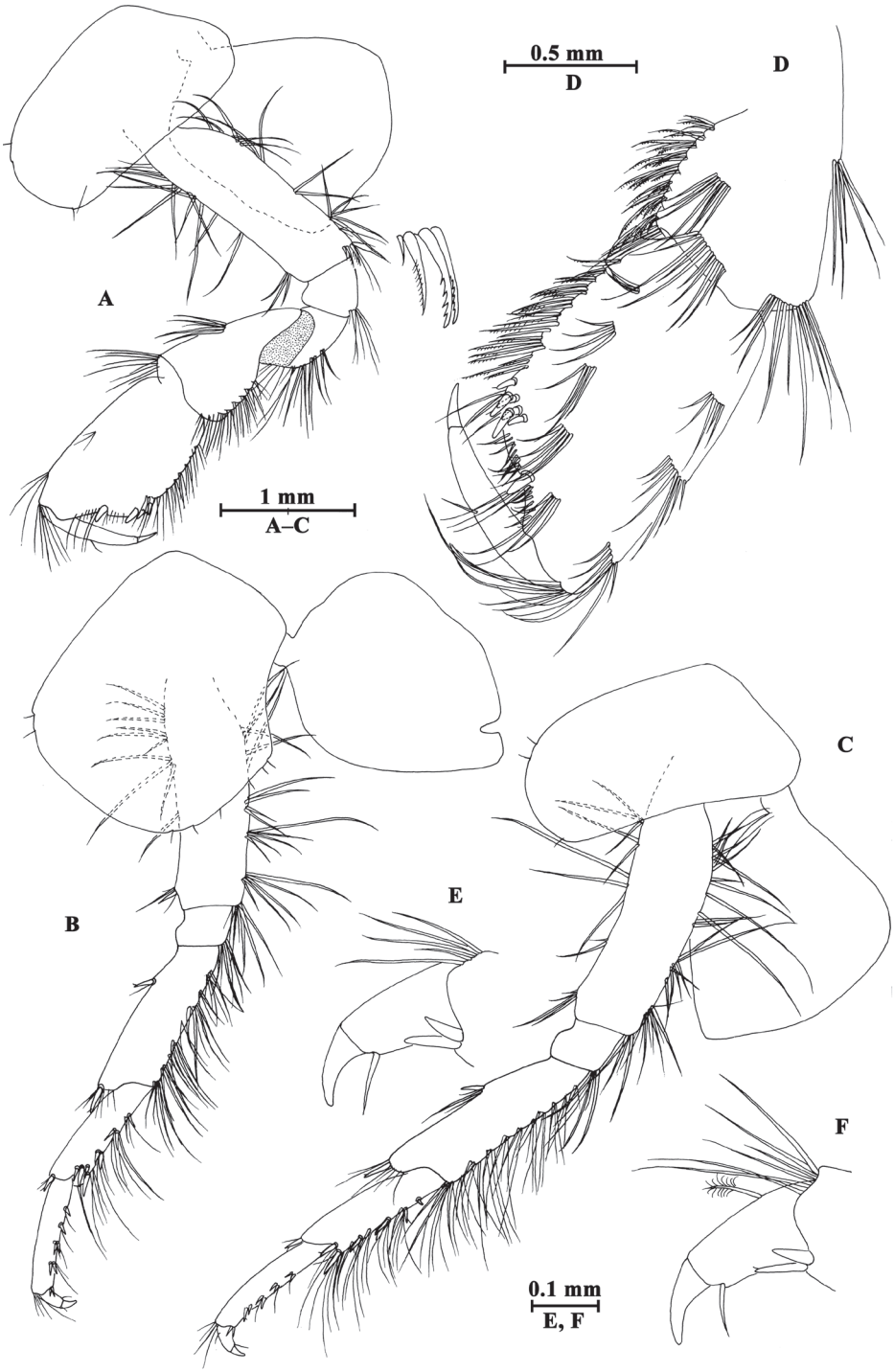

Figure 9. *Gammarus kangdingensis* sp. n., male holotype. **A** gnathopod II **B** pereopod IV **C** pereopod III **D** propodus of gnathopod (medial view) II **E** dactylus of pereopod IV **F** dactylus of pereopod III.

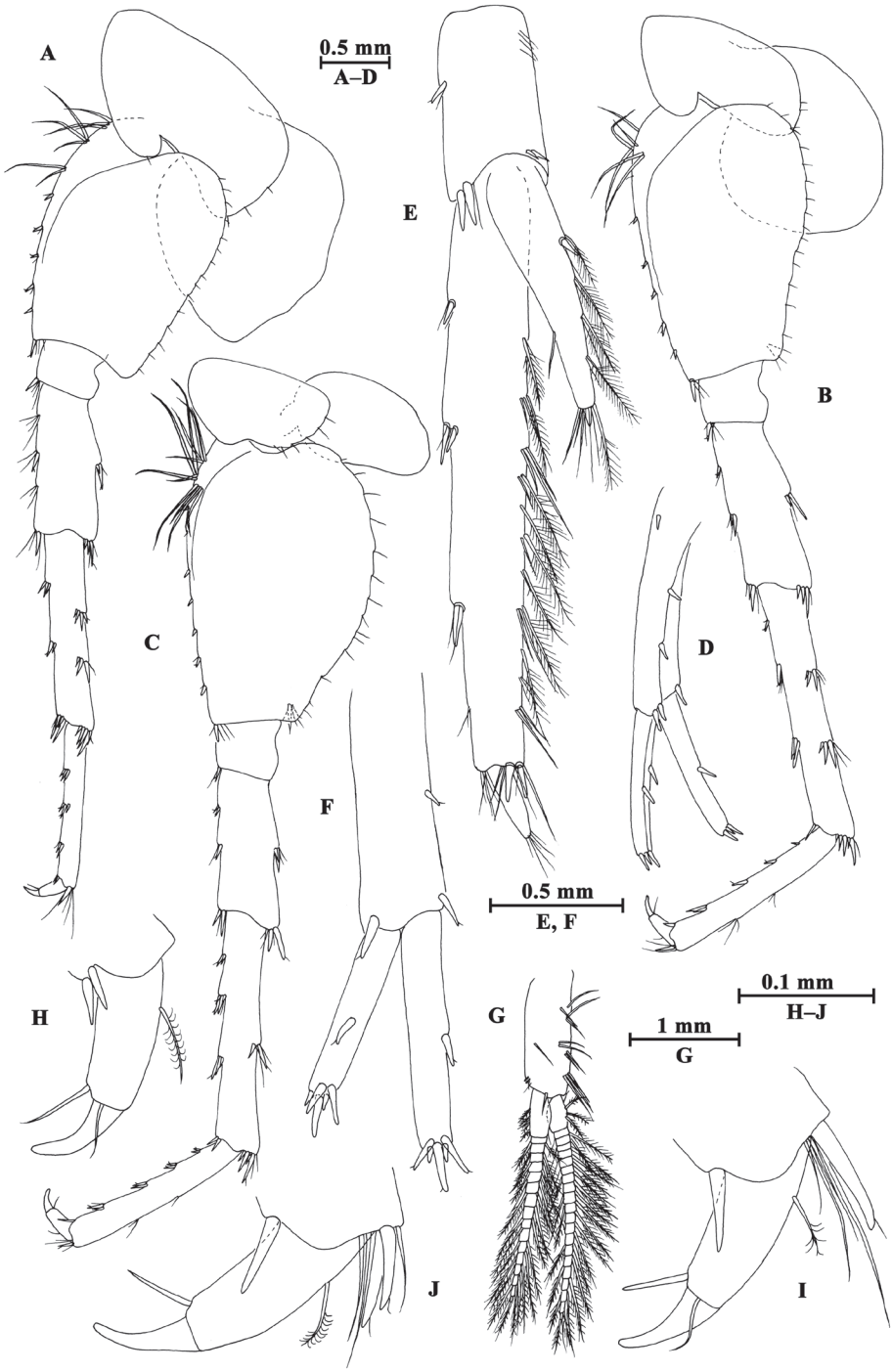

Figure 10. *Gammarus kangdingensis* sp. n., male holotype. **A** pereopod V **B** pereopod VI **C** pereopod VII **D** uropod I **E** uropod III **F** uropod II **G** pleopod III **H** dactylus of pereopod V **I** dactylus of pereopod VI **J** dactylus of pereopod VII.

Coxal gills (Figs 9A–C, 10A–C): present on gnathopod II and pereopods III–VII ovate, gill of pereopod VII smallest.

Pleon. Epimeral plates (Fig. 7D): plate I ventrally rounded, with nine setae on anteroventral margin and two setae on posterior margin; plate II with three spines on ventral margin and three setae on posterior margin, posterodistal corner blunt; plate III with four spines on ventral margin, posterodistal corner weakly acute.

Pleopods I–III (Figs 8B, C, 10G): subequal, peduncle with several marginal setae and two retinacula accompanied by two or three setae; inner and outer rami with approximately 23 articles, fringed with plumose setae.

Urosome. Urosomites I–III (Fig. 7C, E): non-humped, urosomites I–II with four groups of spines accompanied by setae; urosomite III with two dorsal setae and one spine accompanied by setae on each side.

Uropod I (Fig. 10D): peduncle with one basofacial spine, two spines on outer margin, two spines on outer distal corner, one spine on inner distal corner; outer ramus with one spine on each side; inner ramus with one mid-lateral spine on outer margin.

Uropod II (Fig. 10F): peduncle with one spine on inner margin, one spine on inner and outer distal corners each; outer ramus a little shorter than inner ramus, with one spine on outer margin; inner ramus with one spine on inner margin, both rami with five distal spines.

Uropod III (Fig. 10E), peduncle with one marginal spine and four distal spines; inner ramus 0.4 times as long as outer ramus, with one lateral and one distal spines, inner margin with four plumose setae; proximal article of outer ramus only with three pairs of spines on outer margin, inner margin with ten plumose setae, terminal article longer than adjacent spines, with simple setae distally.

Telson (Fig. 8F): deeply cleft, each lobe with one distal spine accompanied by some setae, and some facial short setae.

Description of paratype female. (IZCAS-I-A0059-2), 8.5 mm.

Pereon. Gnathopod I (Fig. 11A, C): carpus and propodus shorter than those of male, carpus triangular; palm of propodus not oblique as that of male, palm with seven spines on posterior margin; dactylus with one seta on outer margin.

Gnathopod II (Fig. 11B, E): carpus and propodus elongated, carpus parallel-sided; propodus subrectangular, palm with three spines on posterior corner.

Pereopods III–VII (Fig. 11G–I): similar to those of male.

Oostegites (Fig. 11F, I): present on gnathopod II and pereopods III–V, oostegite of gnathopod II broad, with marginal setae; oostegite of pereopod V smallest.

Urosome. Uropod III (Fig. 11D): inner ramus length approx. half of outer ramus length, inner margins of inner and outer rami with a few plumose setae.

Habitat. This species was collected from a small stream at the foot of mountain, with weak water flow but many detritus.

Remarks. *Gammarus kangdingensis* sp. n. resembles *G. emeiensis* Hou, Li & Koenemann, 2002 in pereopods III and IV having long setae on posterior margins; pereopods V–VII having marginal spines, but with few setae; and epimeral plates with blunt posterodistal corners. *Gammarus kangdingensis* sp. n. can be distinguished from *G. emeiensis*

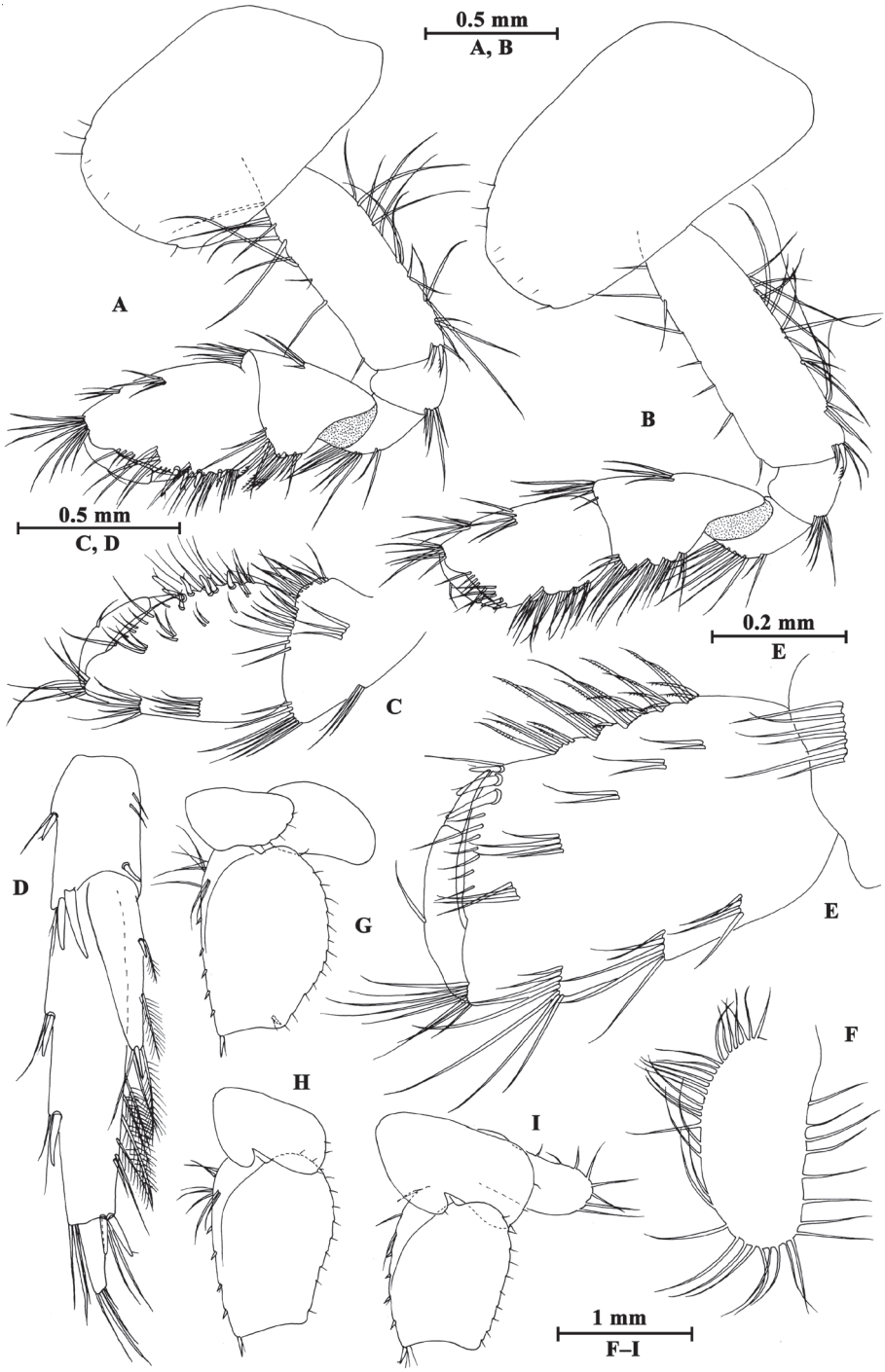

Figure 11. *Gammarus kangdingensis* sp. n., female paratype. **A** gnathopod I **B** gnathopod II **C** propodus of gnathopod I (medial view) **D** uropod III **E** propodus of gnathopod II (medial view) **F** oostegite of gnathopod II **G** basis of pereopod VII **H** basis of pereopod VI **I** basis of pereopod V.

(*G. emeiensis* in parentheses) in antenna II peduncle having short setae along anterior and posterior margins, and calceoli (peduncle with long setae on anterior and posterior margins, calceoli absent); uropod III inner ramus 0.4 times the length of outer ramus (inner ramus 0.7 times the length of outer ramus); uropod III terminal article of outer ramus longer than adjacent spines (terminal article as long as adjacent spines).

Gamamrus kangdingensis sp. n. is similar to *G. altus* sp. n. in the shape of gnathopods I and II. It differs from *G. altus* sp. n. (*G. altus* in parentheses) in having pereopods III and IV with long setae on posterior margins (with a few short setae on posterior margins); and inner ramus of uropod III 0.4 times the length of outer ramus (0.3), inner margins of inner and outer rami with a row of plumose setae (with no plumose setae).

***Gammarus gonggaensis* sp. n.**

http://zoobank.org/ED25CC10-321D-44B1-98F3-E2E30CC99286
Figs 12–16

Material examined. Holotype: male (IZCAS-I-A0065-1), 10.0 mm, Hepinggou, Baoxing County (30.3°N, 102.7°E), Gongga Mountains, altitude 2110 m, June 15, 2001, collected by Jinzhong Fu and Yuezhao Wang. Paratype: female (IZCAS-I-A0065-2) 8.6 mm; paratypes: two males (IZCAS-I-A0065-3), same data as holotype.

Etymology. The specific name is derived from the type locality; adjective.

Diagnosis. Antenna II with long setae along anterior and posterior margins of peduncle articles IV and V, calceoli absent; pereopods III and IV with long straight setae on posterior margin; inner ramus of uropod III less than half the length of outer ramus, both inner and outer rami with few marginal setae.

Description of holotype male. (IZCAS-I-A0065-1), 10.0 mm.

Head. (Fig. 12A): Eyes medium in size, oval.

Antenna I (Fig. 15B): peduncle articles I–III in length ratio 1.0 : 0.7 : 0.5, bearing distal setae; flagellum with 17 articles, aesthetascs present; accessory flagellum with five articles.

Antenna II (Fig. 15A): gland cone reaching peduncle article III, peduncle article III with distal setae, article IV a little shorter than article V, both with five to six groups of long setae along anterior and posterior margins; flagellum with 12 articles, bearing some setae, calceoli absent.

Upper lip (Fig. 12L): convex, with minute setae.

Mandible (Fig. 12G, H, K): incisor of left mandible with five teeth; lacinia mobilis with four teeth; second and third articles of palp in length ratio 1.1 : 1.0, second article with 16 setae, third article with four A-setae, four B-setae, 19 D-setae and four E-setae apically. Incisor of right mandible with four teeth; lacinia mobilis bifurcate, with several small teeth.

Lower lip (Fig. 12M): inner lobes lacking, outer lobes covered with thin setae.

Maxilla I (Fig. 12I, J): asymmetrical, left inner plate with 13 plumose setae, outer plate with eleven serrated spines, second article of left palp bearing ten slender spines; second article of right palp with five blunt spines and two stiff setae.

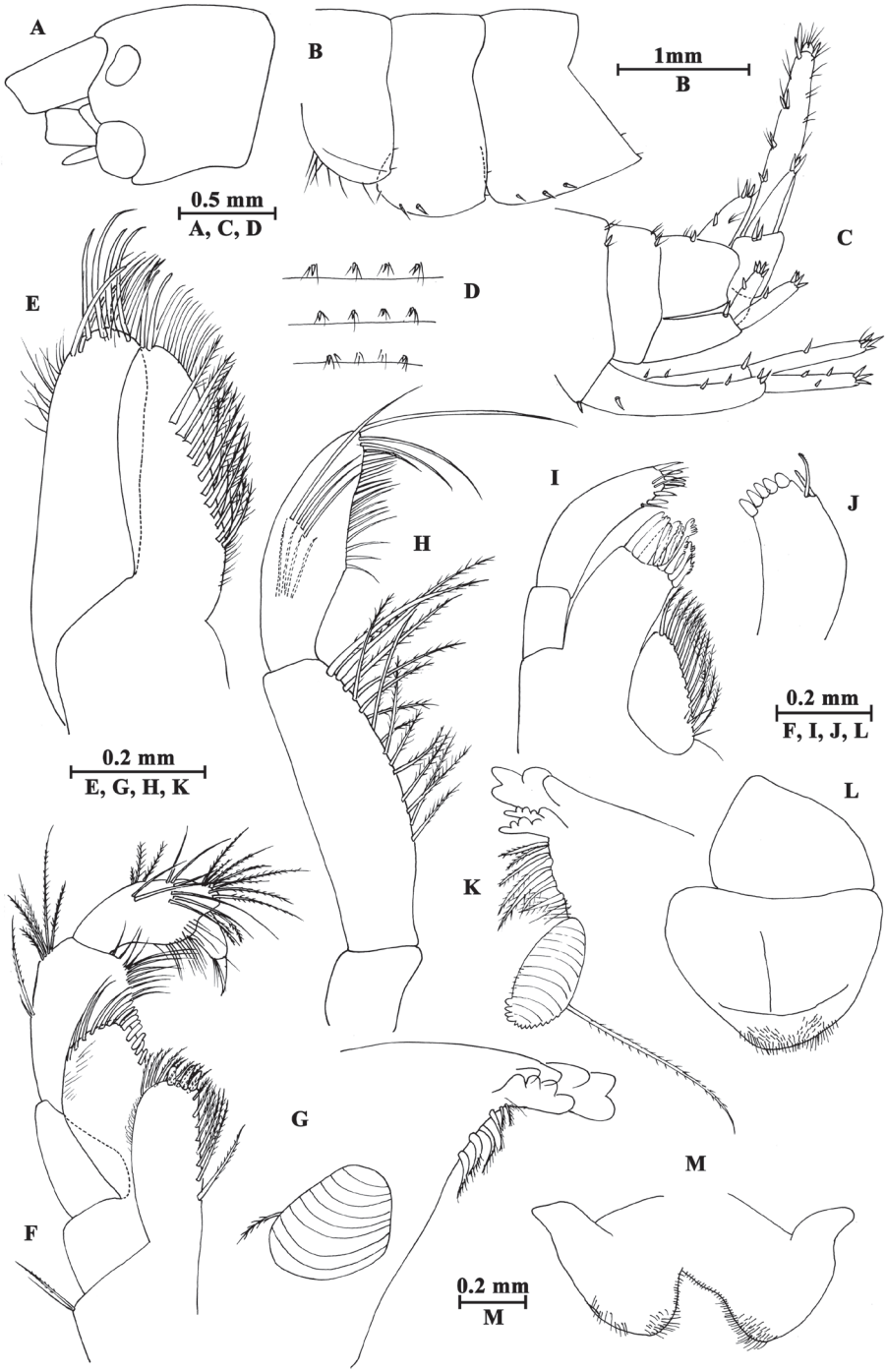

Figure 12. *Gammarus gonggaensis* sp. n., male holotype. **A** head **B** epimeral plates **C** urosomites (lateral view) **D** urosomites (dorsal view) **E** maxilla II **F** maxilliped **G** incisor of left mandible **H** palp of left mandible **I** left maxilla I **J** palp of right maxilla I **K** incisor of right mandible **L** upper lip **M** lower lip.

Maxilla II (Fig. 12E): inner plate with 12 plumose setae in an oblique row; inner and outer plates with long setae apically.

Maxilliped (Fig. 12F): inner plate with three apical spines and several plumose setae; outer plate with nine blade spines on medial margin and five long setae apically; palp with four articles.

Pereon. Gnathopod I (Fig. 13A, C): coxal plate weakly dilated distally, bearing three and one seta on anterior and posterior corners respectively; basis with setae on anterior and posterior margins; carpus and propodus in length ratio 0.6 : 1.0; palm of propodus oblique, bearing one spine on medial margin, three pairs of spines on posterior margin and three spines on inner face; dactylus more than half of posterior margin in length, with on seta one outer margin.

Gnathopod II (Fig. 13B, D): coxal plate subrectangular, with three and one seta on anterior and posterior corners respectively; carpus parallel-sided; palm of propodus truncated, bearing one medial spine, five spines on posterior corner; dactylus beyond the palm margin, with one seta on outer margin.

Pereopod III (Fig. 14A): coxal plate with three and one seta on anterior and posterior corners respectively, merus to propodus with groups of long straight setae on posterior margins; carpus and propodus accompanied by five spines on posterior margins, dactylus stout.

Pereopod IV (Fig. 14C, F): coxal plate concave, bearing two and four setae on anterior corner and posterior margin, merus with six groups of long setae on posterior margin; carpus and propodus with four groups of spines accompanied by some setae; dactylus with one seta on anterior margin and two setae at hinge of nail.

Pereopod V (Fig. 14B, G): coxal plate bearing one seta on anterior lobe and two setae on posterior lobe; basis with three setae and three spines on anterior margin, anterodistal corner with one spine accompanied by setae, posterior margin with a row of nine setae; merus with three groups of setae on anterior margin, a spine accompanied by setae on anterodistal corner, two pairs of spines on posterior margin; carpus with two groups of spines on anterior and posterior margins each, anterodistal corner with a spine, posterodistal corner with a group of six spines; propodus with three pairs of spines on anterior margin, and three clusters of setae and spines on posterior margin; dactylus with one plumose seta on posterior margin and a seta at hinge of unguis.

Pereopod VI (Fig. 14D): coxal plate with two setae on posterior margin; basis narrowing distally, with two long setae and four spines on anterior margin, anterodistal corner with one spine accompanied by setae, posterior margin with a row of 13 setae, and inner surface with two setae on posterior corner; merus with three groups of spines on anterior margin and a pair of spines on posterior margin; carpus with three or two groups of spines on anterior and posterior margins; propodus with four pairs of spines on anterior margin, posterior margin with a seta and a spine accompanied by a seta; dactylus similar to that of pereopod V.

Pereopod VII (Fig. 14E): coxal plate with three plumose setae on anterior margin and three setae on posterior margin; basis with two setae and four spines on anterior margin, posterior margin with a row of 12 setae, inner surface with one spine accom-

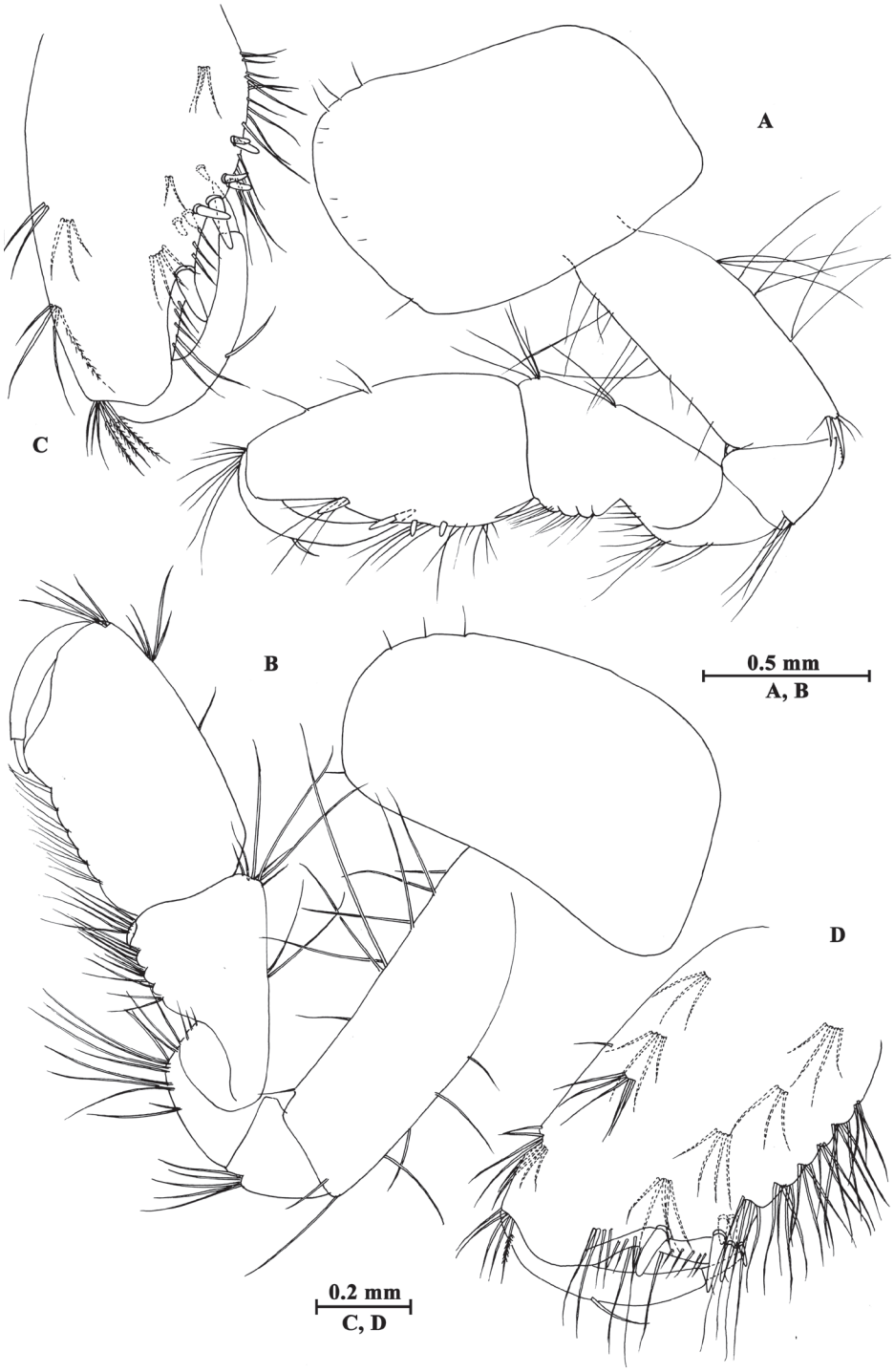

Figure 13. *Gammarus gonggaensis* sp. n., male holotype. **A** gnathopod I **B** gnathopod II **C** propodus of gnathopod I **D** propodus of gnathopod II.

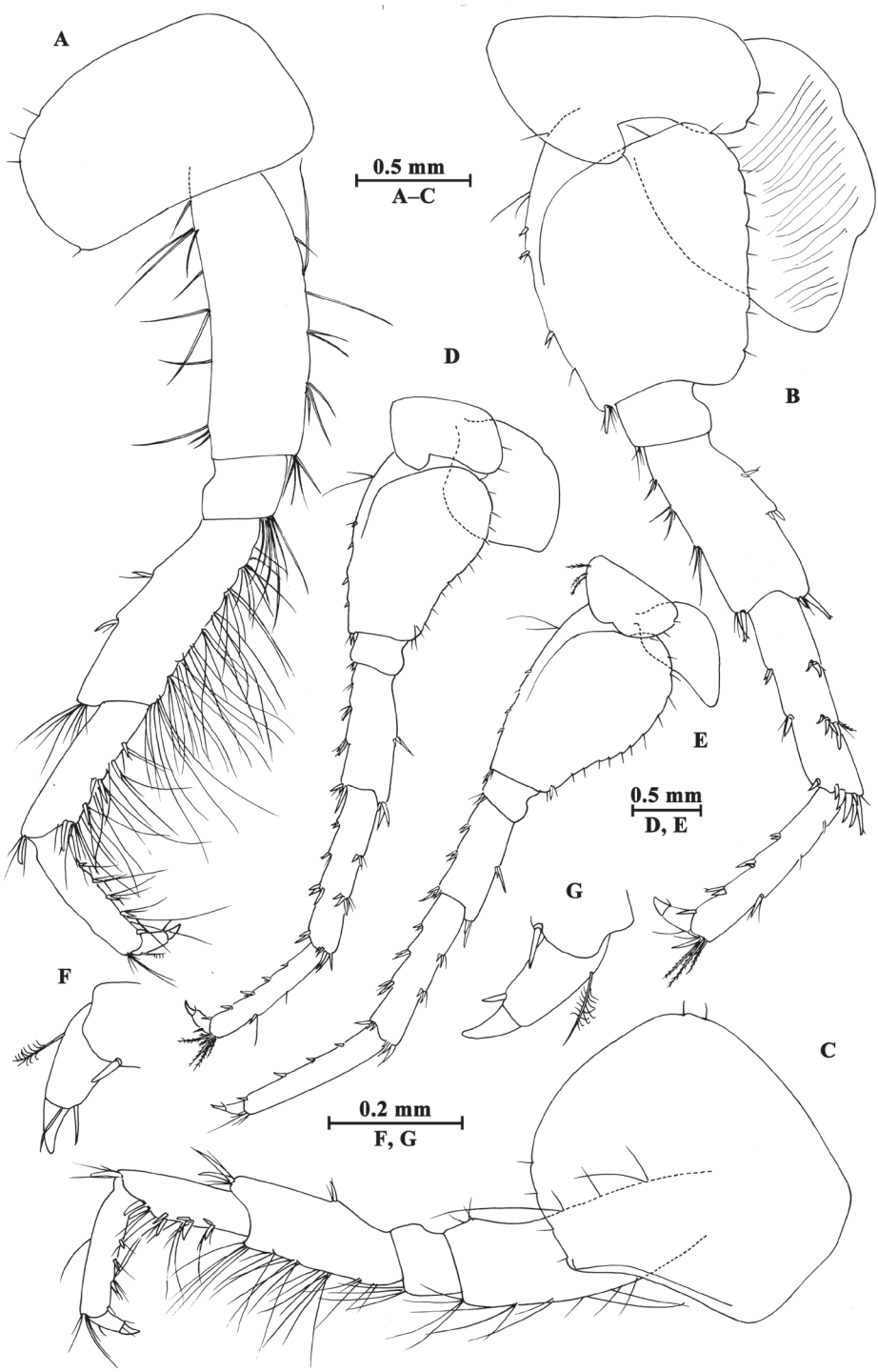

Figure 14. *Gammarus gonggaensis* sp. n., male holotype. **A** pereopod III **B** pereopod V **C** pereopod IV **D** pereopod VI **E** pereopod VII **F** dactylus of pereopod IV **G** dactylus of pereopod V.

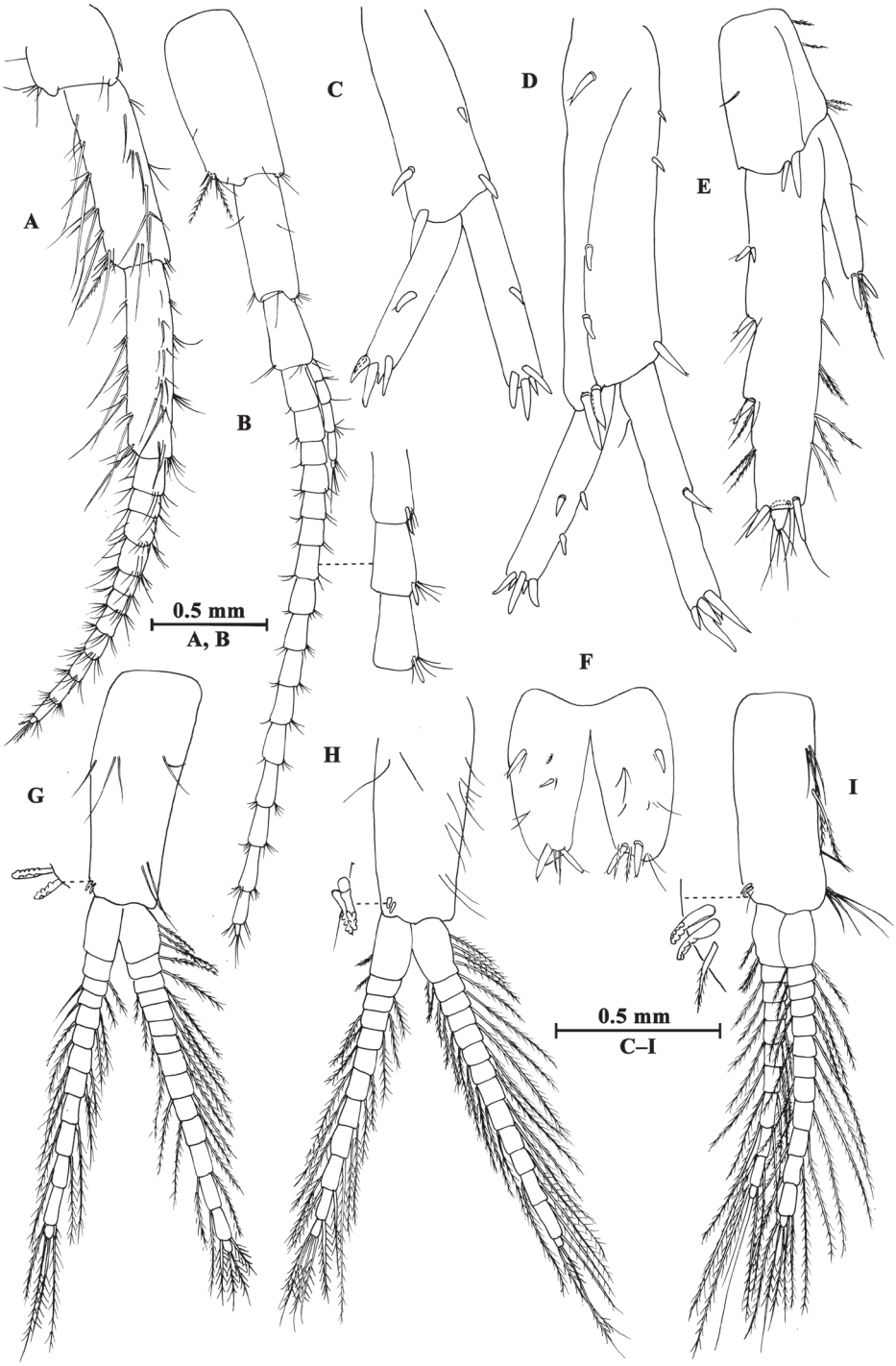

Figure 15. *Gammarus gonggaensis* sp. n., male holotype. **A** antenna II **B** antenna I **C** uropod II **D** uropod I **E** uropod III **F** telson **G** pleopod I **H** pleopod II **I** pleopod III.

panied by setae on posterior corner; merus and carpus with spines on anterior and posterior margins; propodus with three pairs of spines on anterior margin; dactylus similar to that of pereopod V.

Coxal gills (Fig. 14B, D, E): present on gnathopod II and pereopods III–VII sac-like.

Pleon. Epimeral plates (Fig. 12B): plate I ventrally rounded, with seven setae on ventral margin and two setae on posterior margin; plate II with one seta and two spines on anterior corner, two setae on posterior margin, posterodistal corner blunt; plate III with three spines on ventral margin and two setae on posterior margin.

Pleopods I–III (Fig. 15G–I): peduncle with some marginal setae, bearing two retinacula accompanied by setae; inner and outer rami nearly the same length, both rami fringed with plumose setae.

Urosome. Urosomites I–III (Fig. 12 C, D): non-humped, with four clusters of spines accompanied by setae.

Uropod I (Fig. 15D): peduncle with one basofacial spine, two spines on outer margin, two spines on outer distal corner, two spines on inner margin, and one spine on inner distal corner; outer ramus with one and two spines on outer and inner margins respectively; inner ramus with one spine on inner margin, both rami with five terminal spines.

Uropod II (Fig. 15C): peduncle with one spine on inner and outer margins each, one spine on inner and outer distal corners each; inner ramus with one spine on inner margin; outer ramus with one spine on outer margin, both rami with five terminal spines.

Uropod III (Fig. 15E): peduncle with one seta on surface, two marginal plumose setae, two distal plumose setae and two distal spines; inner ramus 0.4 times as long as outer ramus, bearing two distal spines accompanied by one long seta; proximal article of outer ramus with two-one-two spines on outer margin and two distal spines, inner margin with a few plumose setae, terminal article shorter than adjacent spines, with distal setae.

Telson (Fig. 15F): cleft, with two distal spines and one facial spine.

Description of paratype female. (IZCAS-I-A0065-2), 8.6 mm.

Pereon. Gnathopod I (Fig. 16A, B): propodus pyriform, palm slant, bearing four spines on posterior corner.

Gnathopod II (Fig. 16C, D): palm of propodus transverse, with four spines on posterior corner.

Oostegites (Fig. 16F): present on gnathopod II and pereopods III–V, broad, with many long setae.

Urosome. Uropod III (Fig. 16E): peduncle with one marginal spine accompanied by setae, and three pairs of distal spines; inner ramus around half the length of outer ramus, bearing one marginal and three distal spines; proximal article of outer ramus with two groups of spines on outer margin, one spine on inner margin and three spines on distal margin, terminal article shorter than adjacent spines.

Habitat. This species was collected from a small brook flowing under a large stone, forming a pool with an area of one square meter.

Remarks. The new species of *Gammarus gonggaensis* sp. n. is similar to *G. kangdingensis* sp. n. in pereopods III and IV having long setae on posterior margins; and inner

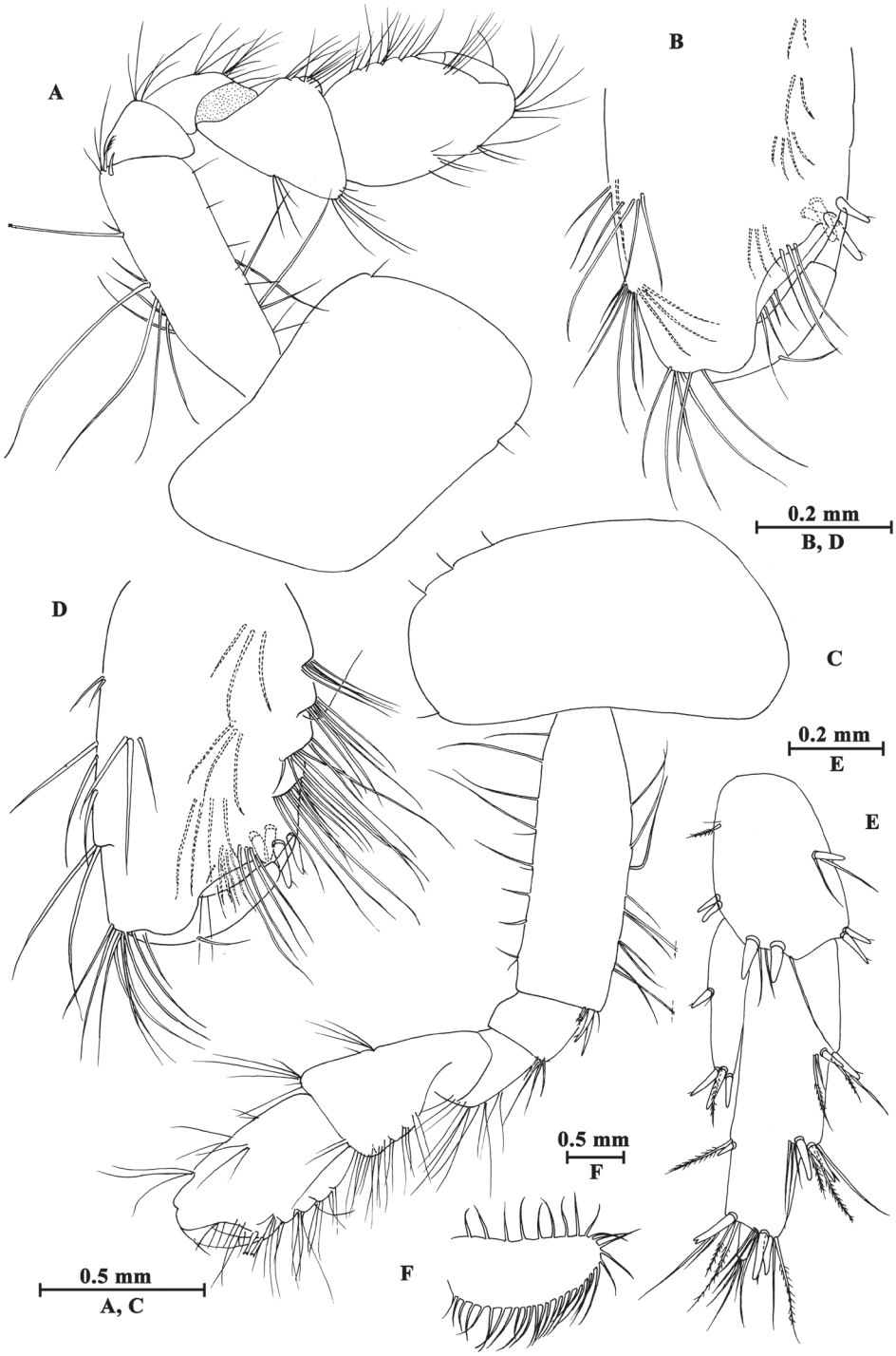

Figure 16. *Gammarus gonggaensis* sp. n., female paratype. **A** gnathopod I **B** propodus of gnathopod I **C** gnathopod II **D** propodus of gnathopod II **E** uropod III **F** oostegite of gnathopod II.

ramus of uropod III 0.4 times the length of outer ramus. *Gammarus gonggaensis* sp. n. can be distinguished from *G. kangdingensis* sp. n. (*G. kangdingensis* in parentheses) by antenna II peduncle having long setae along anterior and posterior margins, calceoli absent (peduncle with short setae, calceoli present); outer ramus of uropod III with a few plumose setae on inner margin, inner ramus with no plumose marginal setae (with a row of plumose setae on inner margins of inner and outer rami); terminal article of uropod III shorter than adjacent spines (longer than adjacent spines).

Gammarus gonggaensis sp. n. is similar to *G. emeiensis* Hou, Li & Koenemann, 2002 in antenna II peduncle with long setae along anterior and posterior margins, calceoli absent, and pereopods III and IV with long setae on posterior margins. It differs from *G. emeiensis* Hou et al., 2002 by uropod III inner ramus 0.4 times the length of outer ramus, while reaching 0.7 times in *G. emeiensis*.

Gammarus gonggaensis sp. n. differs from *G. altus* sp. n. (*G. altus* in parentheses) by anternna II peduncle with long setae, calceoli absent (with short setae, calceoli present); pereopods III and IV with long setae on posterior margin (with a few short setae); uropod III with plumose setae on inner margin of inner ramus (with no plumose setae), terminal article shorter than adjacent spines (longer than adjacent spines).

***Gammarus limosus* sp. n.**

http://zoobank.org/9ACD4C39-16EC-47AF-A3B0-C32C3BA8EAC3
Figs 17–22

Material examined. Holotype: male (IZCAS-I-A0063-1), 8.6 mm, Baxoi County (30.2°N, 97.2°E), Tibet, altitude 4400 m, August 21, 2001, collected by Xianjin Peng. Paratype: female (IZCAS-I-A0063-2), 5.5 mm; paratypes: five males and five females (IZCAS-I-A0063-3), same data as holotype.

Etymology. This specific name alludes to its living environment, living silt beside a polluted river; adjective.

Diagnosis. Antenna I accessory flagellum with three articles; antenna II calceoli present; pereopods III and IV with few setae on posterior margin; inner ramus of uropod III reaching 0.6 times the length of outer ramus, terminal article of outer ramus longer than adjacent spines, both inner and outer rami with few marginal setae.

Description of holotype male. (IZCAS-I-A0063-1), 8.6 mm.

Head. (Fig. 17A): cephalic lateral lobe truncated, inferior antennal sinus deep, eyes ovate.

Antenna I (Fig. 18A): peduncle articles I–III in length ratio 1.0 : 0.7: 0.4, each article with distal setae, article II with two groups of setae on inner face; primary flagellum with 21 articles, most with aesthetascs; accessory flagellum with three articles, the distal article tiny.

Antenna II (Fig. 19A): gland cone shorter than peduncle article III, article IV approximately as long as article V, both with two or three groups of short setae along anterior and posterior margins; flagellum with 12 articles, proximal six articles with calceoli.

Upper lip (Fig. 17E): convex, with minute setae.

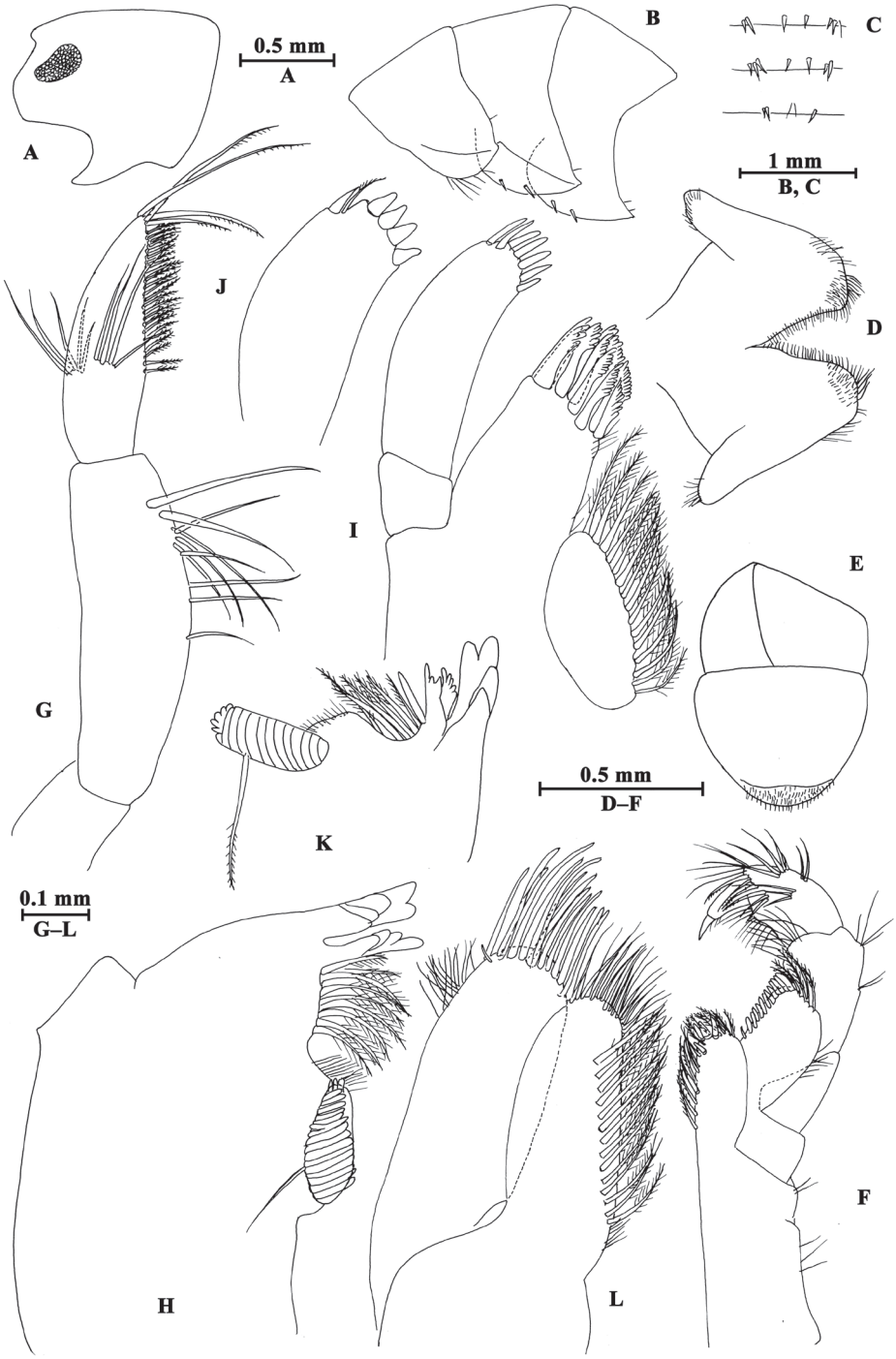

Figure 17. *Gammarus limosus* sp. n., male holotype. **A** head **B** epimeral plates I–III **C** urosomites I–III (dorsal view) **D** lower lip **E** upper lip **F** maxilliped **G** palp of left mandible **H** incisor of left mandible **I** left maxilla I **J** palp of right maxilla I **K** incisor of right mandible **L** maxilla II.

Mandible (Fig. 17G, H, K): asymmetrical, left incisor with five teeth; lacinia mobilis with four teeth; spine row with nine plumose setae; second article of palp with ten setae on medial margin, third article 0.7 times the length of second article, with four A-setae on outer face, five B-setae on inner face, a row of 22 D-setae and four E-setae. Incisor of right mandible with four teeth; lacinia molibis bifurcate, with small teeth; molar with one long seta.

Lower lip (Fig. 17D): inner lobes lacking, outer lobes covered with thin setae.

Maxilla I (Fig. 17I, J): asymmetrical, left inner plate with 15 plumose setae on medial margin; outer plate with eleven serrated spines; second article of palp with seven slender spines. Second article of right palp broad, with five blunt spines and one stiff seta.

Maxilla II (Fig. 17L): inner plate with 14 plumose setae on inner face; inner and outer plates with apical setae.

Maxilliped (Fig. 17F): inner plate with three apical and one subapical spines, and 17 plumose setae; outer plate with 13 blade spines on medial margin and five apical plumose setae; palp with four articles, terminal article unguis-form.

Pereon. Gnathopod I (Fig. 18C, D): coxal plate weakly dilated distally, lower margin with short setae; basis with long setae on anterior and posterior margins; carpus triangular, posterior margin with setae; propodus oval, palm oblique, with one median spine, seven spines on posterior margin and seven spines on inner face; dactylus longer than half of posterior margin, with one seta on outer margin.

Gnathopod II (Fig. 18B, E): coxal plate slightly narrowing distally, with short setae on lower margin; basis with long setae on anterior and posterior margins; carpus a little shorter than propodus, with sub-parallel margins, bearing setae on posterior margin; propodus subrectangular, palm transverse, with one median spine and four spines on posterior corner; dactylus beyond the palm margin, with one seta on outer margin.

Pereopod III (Fig. 19B, G): coxal plate with one seta on anterodistal and posterodistal corners each; basis with long setae on anterior and posterior margins; merus to propodus with few setae on posterior margin; merus with two spines on anterior margin and three clusters of setae on posterior margins; carpus and propodus with three groups of spines accompanied by setae on posterior margins; dactylus with one plumose seta on anterior margin and one simple and one stiff setae at hinge of unguis.

Pereopod IV (Fig. 19C, H): coxal plate concave, with one seta on anterior corner and five setae on posterior margin; basis with long setae on posterior margin; merus with one spine on anterior margin, posterior margin with two pairs of setae; carpus and propodus with two to four groups of spines accompanied by setae on posterior margins; dactylus with one plumose seta on anterior margin and a seta at hinge of unguis.

Pereopod V (Fig. 19D, I): coxal plate with one seta on anterior lobe and three setae on posterior lobe; basis nearly straight on posterior margin, with three setae and four spines on anterior margin, anterodistal corner with two spines accompanied by setae; posterior margin with a row of nine setae; merus and carpus with two groups of spines accompanied with few setae on anterior margins and one group of spines on posterior margins; propo-

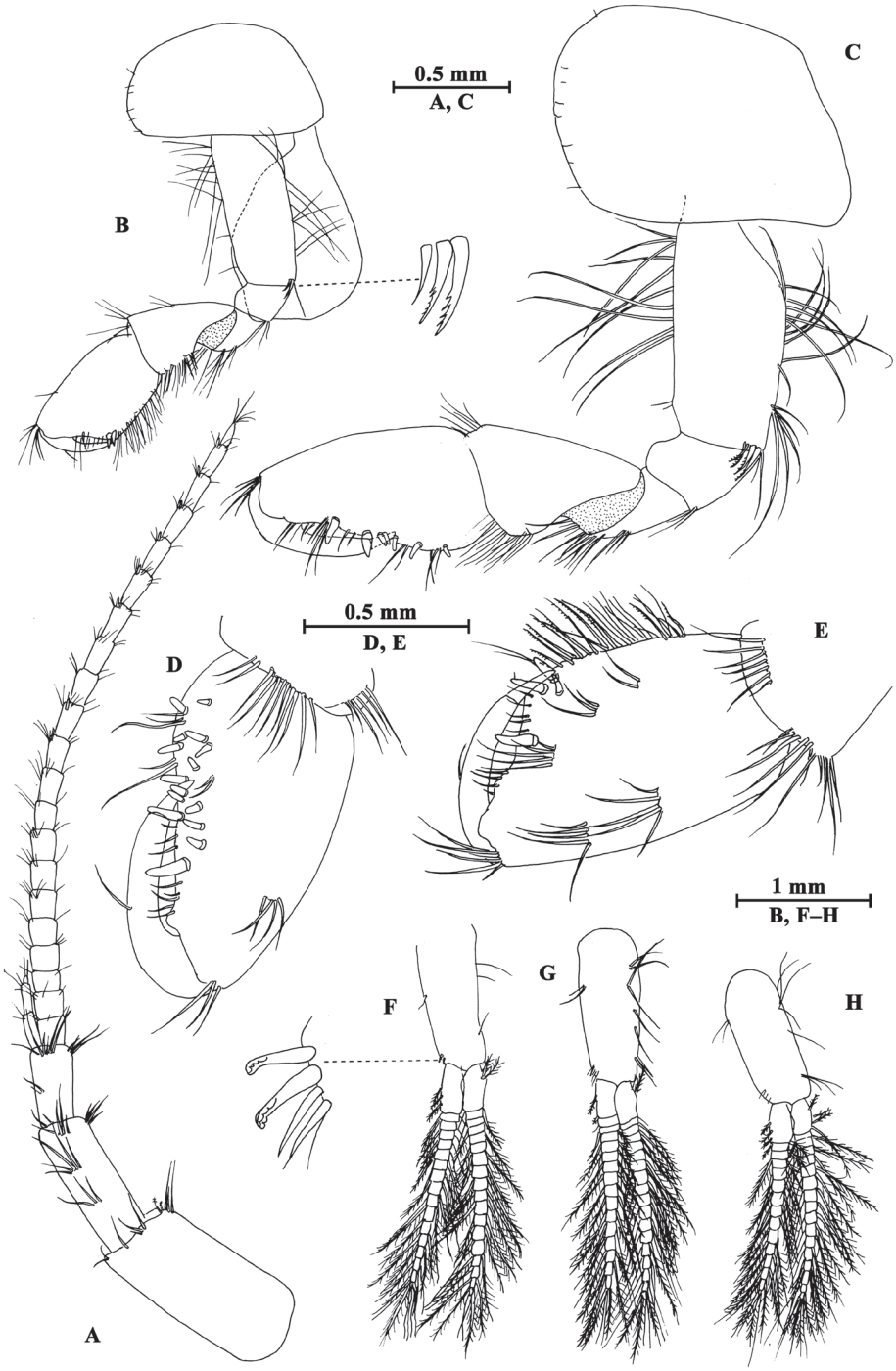

Figure 18. *Gammarus limosus* sp. n., male holotype. **A** antenna I **B** gnathopod II **C** gnathopod I **D** propodus of gnathopod I (medial view) **E** propodus of gnathopod II (medial view) **F** pleopod I **G** pleopod II **H** pleopod III.

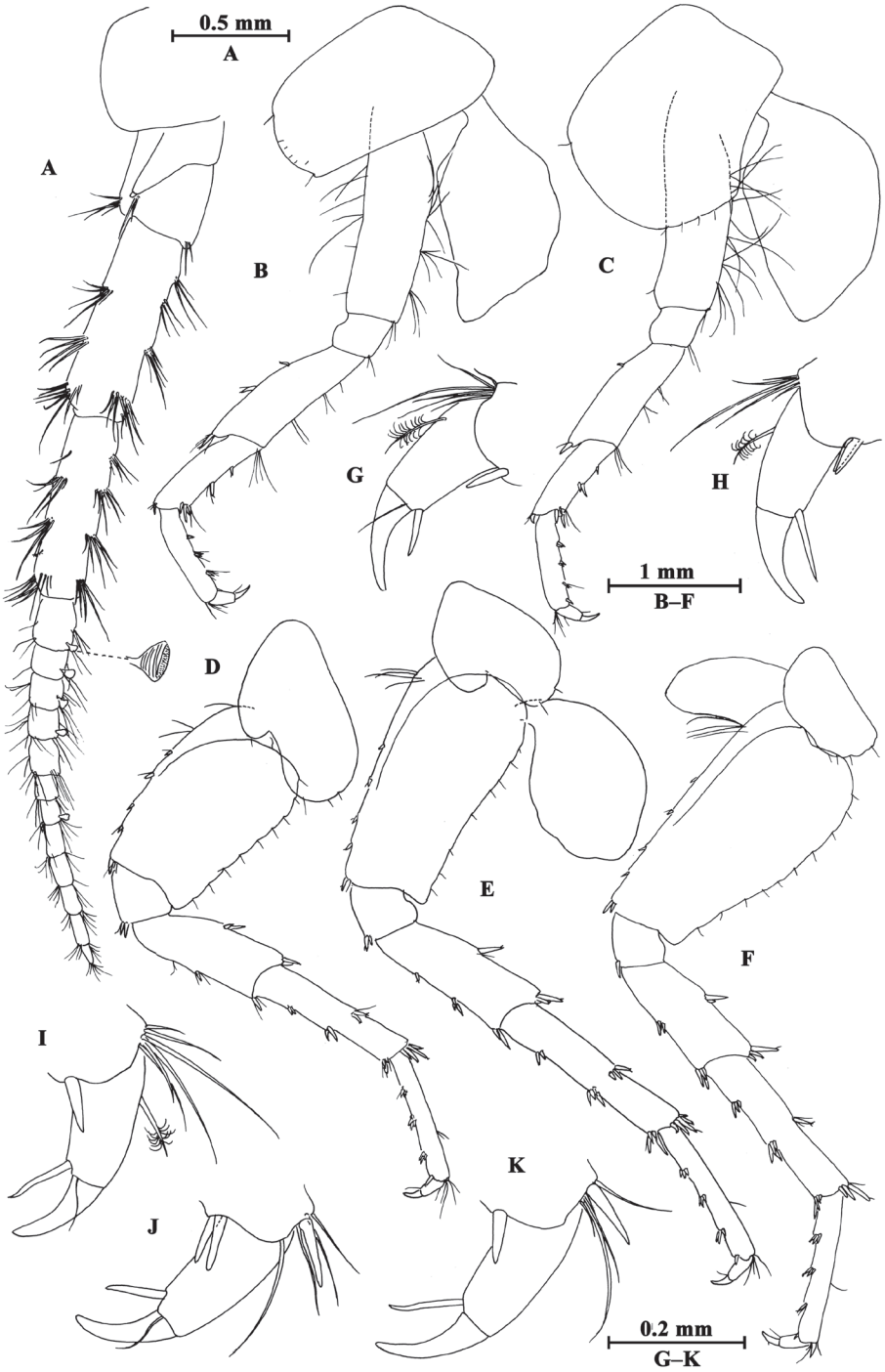

Figure 19. *Gammarus limosus* sp. n., male holotype. **A** antenna II **B** pereopod III **C** pereopod IV **D** pereopod V **E** pereopod VI **F** pereopod VII **G** dactylus of pereopod III **H** dactylus of pereopod IV **I** dactylus of pereopod V **J** dactylus of pereopod VI **K** dactylus of pereopod VII.

dus with three groups of spines on anterior margin and a pair of setae on posterior margin; dactylus with one plumose seta on posterior margin and two setae at hinge of unguis.

Pereopod VI (Fig. 19E, J): coxal plate with two setae on posterior margin; basis elongated, anterior margin with four setae and four spines on anterior margin, anterodistal corner with one spine, posterior margin with a row of eight setae; merus and carpus with two groups of spines on anterior margins and a group of spines on posterior margins; propodus with three groups of spines on anterior margin and a seta on posterior margin; dactylus with two setae at hinge of unguis.

Pereopod VII (Fig. 19F, K): coxal plate with four setae on posterior margin; basis elongated, with five setae and four spines on anterior margin, anterodistal corner with two spines; posterior margin with a row of ten setae; merus and carpus with one or two groups of spines on anterior margins, and two or one spine on posterior margins; propodus with three groups of spines on anterior margin and a seta on posterior margin; dactylus with one seta at hinge of unguis.

Coxal gills (Figs 18B, 19B, C, E, F): present on gnathopod II and pereopods III–VII, sac-like.

Pleon. Epimeral plates (Fig. 17B): plate I ventrally rounded, with six setae on anteroventral margin and two setae on posterior margin; plate II with two spines on ventral margin, posterior margin blunt, with one seta; plate III with two spines on ventral margin, posterior margin acute, with two setae.

Pleopods (Fig. 18F–H): subequal, peduncle with some long setae, bearing two retinacula accompanied by two setae; rami with approximately 18 segments, fringed with plumose setae.

Urosome. Urosomites (Fig. 17C): non-humped, urosomite I with two-one-one-two spines on dorsal margin; urosomite II with three-one-one-two spines on dorsal margin; urosomite III with two and one spine on lateral margins respectively, and two setae on dorsal margin.

Uropod I (Fig. 20D): peduncle with one basofacial spine, outer margin with one spine on outer margin, two spines on outer distal corner, one spine on inner margin, and one spine on inner distal corner; outer ramus with one spine on inner and outer margins each; inner ramus with one mid-lateral spine, both inner and outer rami with five distal spines.

Uropod II (Fig. 20E): peduncle with one spine on outer margin, and one spine on outer and inner corners each; outer ramus with one spine on outer margin; inner ramus with one spine on inner margin, both rami with five distal spines.

Uropod III (Fig. 20G): peduncle with one marginal spine and three distal spines; inner ramus 0.6 times the length of outer ramus, with two marginal and two distal spines; proximal article of outer ramus with three pairs of spines on outer margin, one spine on inner margin and four distal spines; terminal article of outer ramus longer than adjacent spines; both rami with few marginal setae.

Telson (Fig. 20F): cleft, each with three or four distal spines accompanied by few short setae.

Description of paratype female. (IZCAS-I-A0063-2), 5.5 mm.

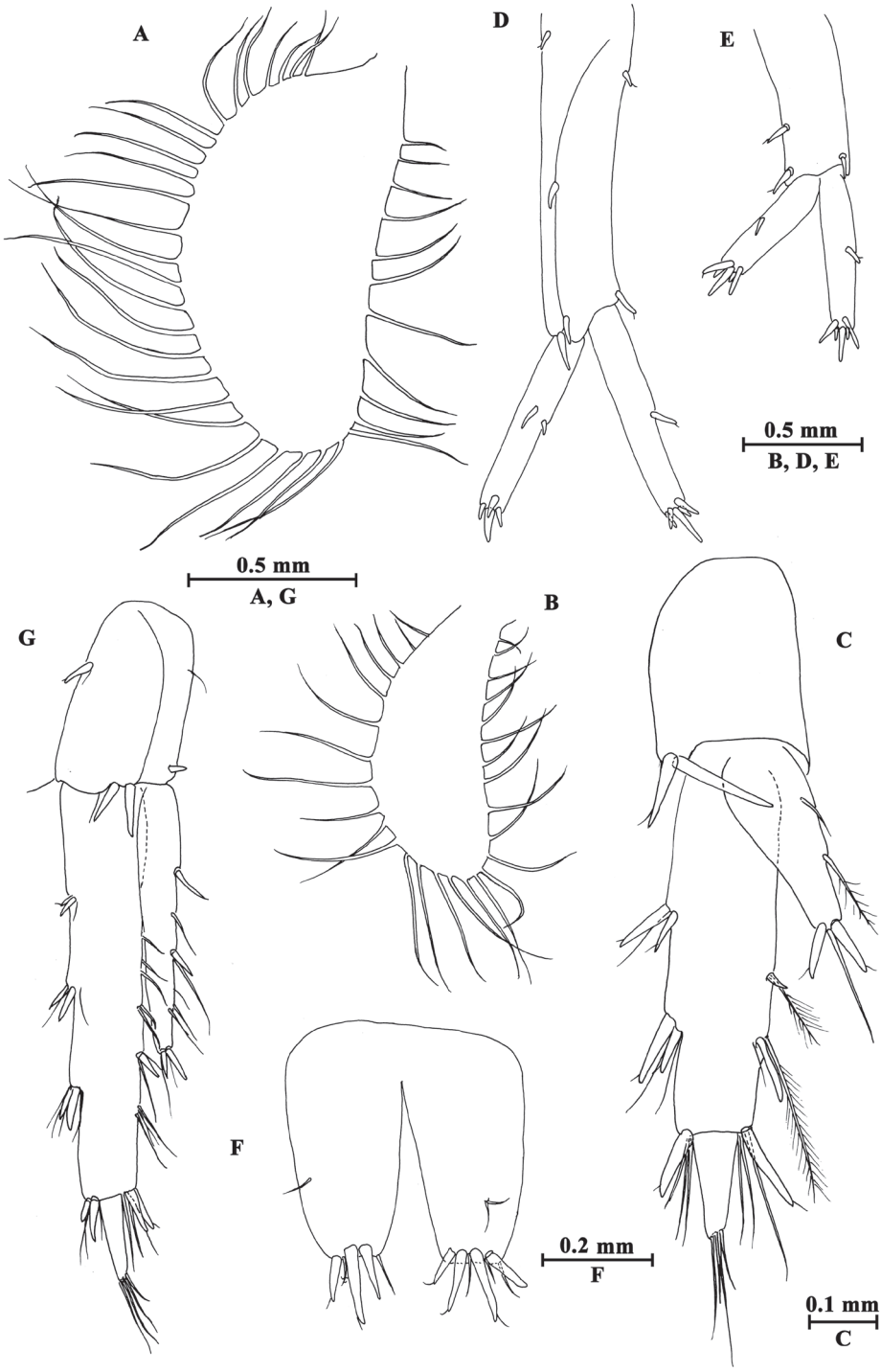

Figure 20. *Gammarus limosus* sp. n., **D–G** male, holotype; **A–C** female, paratype. **A** oostegite of gnathopod II **B** oostegite of pereopod III **C** uropod III **D** uropod I **E** uropod II **F** telson **G** uropod III.

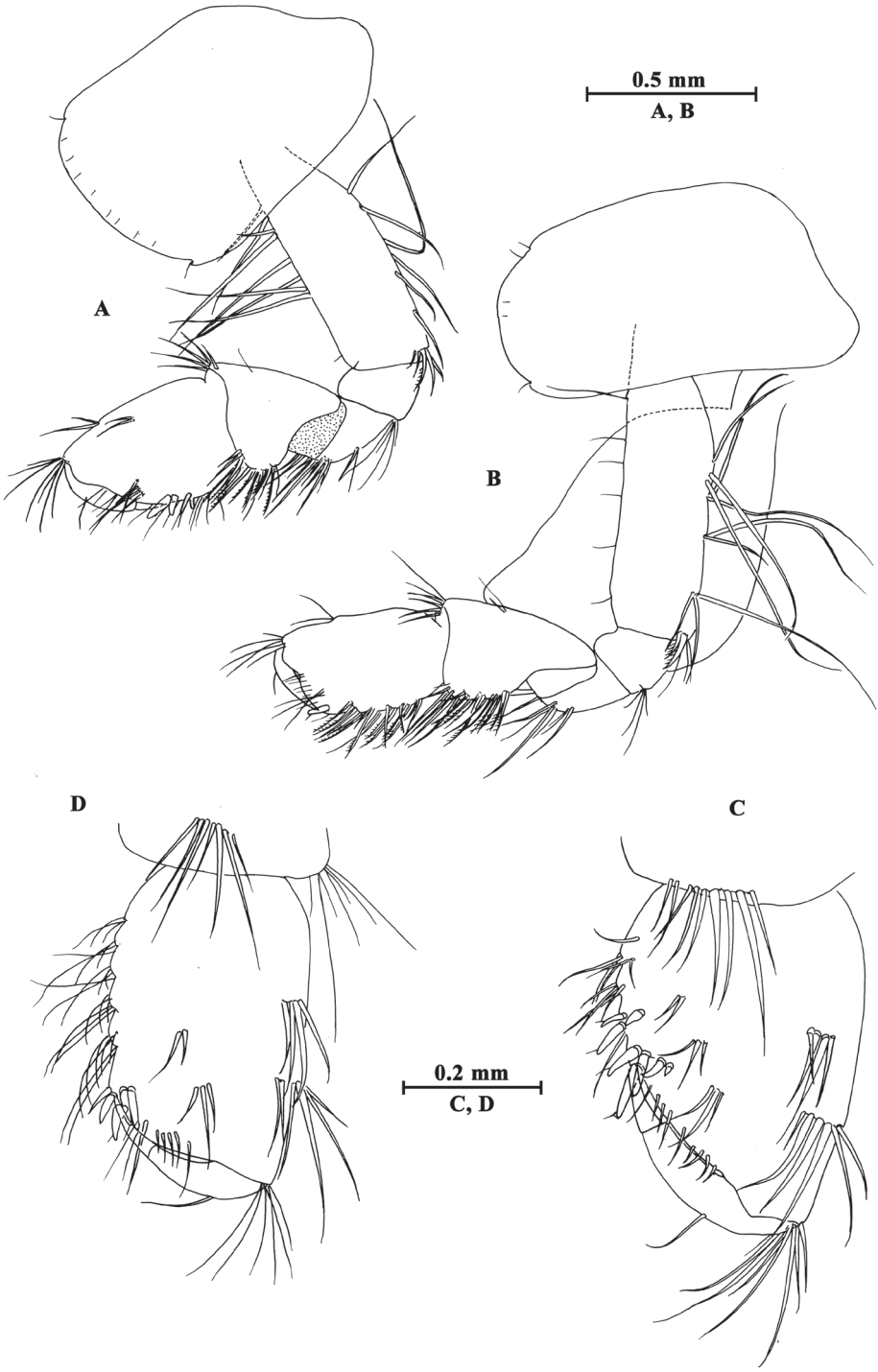

Figure 21. *Gammarus limosus* sp. n., female paratype. **A** gnathopod I **B** gnathopod II **C** propodus of gnathopod I (medial view) **D** propodus of gnathopod II (medial view).

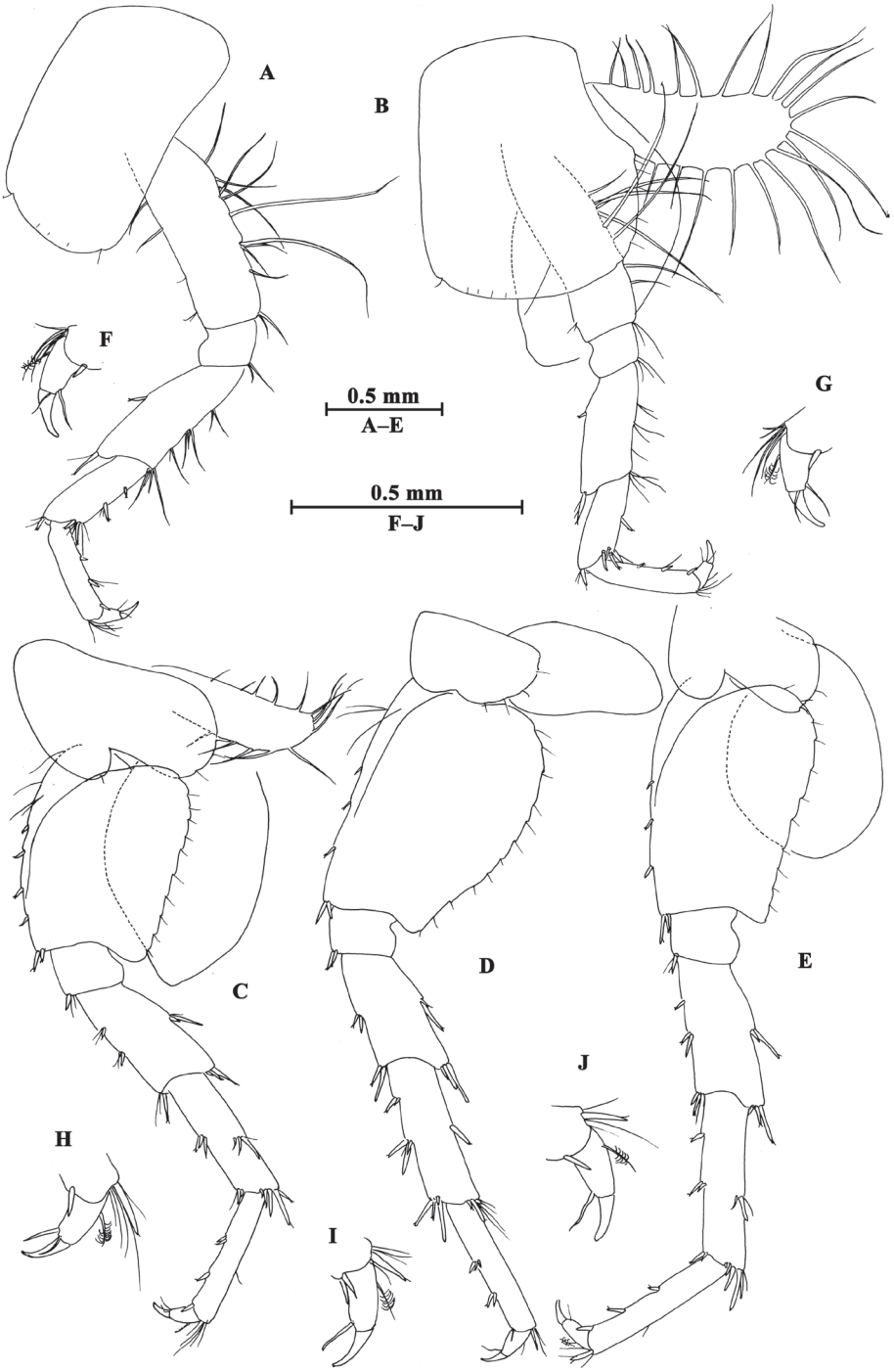

Figure 22. *Gammarus limosus* sp. n., female paratype. **A** pereopod III **B** pereopod IV **C** pereopod V **D** pereopod VII **E** pereopod VI **F** dactylus of pereopod III **G** dactylus of pereopod IV **H** dactylus of pereopod V **I** dactylus of pereopod VII **J** dactylus of pereopod VI.

Pereon. Gnathopod I (Fig. 21A, C): palm of propodus not oblique as that of male, with eight spines on posterior corner.

Gnathopod II (Fig. 21B, D): carpus approx. as long as propodus, propodus subrectangular, palm truncated, with four spines on posterior corner.

Pereopods III–VII (Fig. 22A–J): similar to those of male. Pereopods III and IV with more setae on posterior margins; pereopods V–VII stouter, basis broader than those of male.

Oostegites (Figs 20A, B, 22B, C): progressively decreasing in size, with long marginal setae.

Urosome. Uropod III (Fig. 20C): stouter than that of male, inner ramus less than half the length of outer ramus; both rami with few setae.

Habitat. This species was collected along a riverside with altitude 4400 m, water polluted.

Remarks. *Gammarus limosus* sp. n. is similar to *G. altus* sp. n. in antenna II having calceoli; pereopod V having few setae on posterior margin; and bases of pereopods V–VII elongated. *Gammarus limosus* sp. n. can be distinguished from *G. altus* (*G. altus* in parentheses) by pereopod III with few setae on posterior margin (merus with four groups of setae on posterior margin); epimeral plate III acute on posterodistal corner (blunt); and uropod III inner ramus longer than half of outer ramus length (inner ramus 0.3 times the length of outer ramus).

Gammarus limosus sp. n. is very similar to *G. balcanicus* Schäferna, 1922 (widespread in Europe). It differs from the latter by pereopods III–IV and uropod III having few setae; bases of pereopods VI and VII slender.

The species of the genus *Gammarus* recorded from the Tibetan Plateau can be classified into four groups based on morphological comparison: (1) *G. lacustris* group, is characterized by uropod III inner ramus longer than half of outer ramus length, both rami fringed with plumose setae, and includes five species: *G. lacustris* Sars, 1863, *G. lasaensis* Barnard & Dai, 1988, *G. hongyuanensis* Barnard & Dai, 1988, *G. frigidus* Hou & Li, 2004, and *G. jaspidus* Hou & Li, 2004; (2) cave species with no eyes, including *G. abstrusus* Hou, Platvoet & Li, 2006, and *G. praecipuus* Li, Hou & An, 2013; (3) *G. sinuolatus* Hou & Li, 2004 with long simple setae on uropod III; and (4) *G. kangdingensis* group is characterized by uropod III having a few simple or plumose setae, and includes *G. emeiensis* Hou, Li & Koenemann, 2002, *G. sichuanensis* Hou, Li & Zheng, 2002, *G. glaber* Hou, 2017, *Gammarus altus* sp. n., *G. kangdingensis* sp. n., *G. gonggaensis* sp. n., and *G. limosus* sp. n. A key to these species is presented as follows.

Key to the species of *Gammarus* from the Tibetan Plateau

1 Eyes absent **2**
– Eyes presen **3**
2 Pereopod III with long curled setae on posterior margin ..... ***G. abstrusus***
– Pereopod III with short setae on posterior margin..... ***G. praecipuus***

3 Uropod III inner ramus longer than half of outer ramus, both rami with dense plumose setae **4**
– Uropod III with some simple or plumose setae **8**
4 Epimeral plates II and III very acute on posterodistal corners **5**
– Epimeral plate II and III moderate on posterodistal corners **6**
5 Gnathopod II propodus palm with three medial spines ..... ***G. lasaensis***
– Gnathopod II propodus palm with one medial spine ..... ***G. lacustris***
6 Urosomites dorsally elevated ..... ***G. jaspidus***
– Urosomites dorsally non-humped **7**
7 Uropod III inner ramus reaching 0.8 times the length of outer ramus ..... ***G. frigidus***
– Uropod III inner ramus reaching 0.6 times the length of outer ramus ..... ***G. hongyuanensis***
8 Uropod III only armed with long simple setae ..... ***G. sinuolatus***
– Uropod III with simple or plumose setae **9**
9 Pereopods III and IV merus and carpus with long setae on posterior margins... **10**
– Pereopods III and IV merus and carpus with a few short setae on posterior margins **12**
10 Antenna II peduncle with long setae, calceoli absent **11**
– Antenna II peduncle with short setae, calceoli present ..... ***G. kangdingensis* sp. n.**
11 Uropod III inner ramus reaching 0.4 times the length of outer ramus ..... ***G. gonggaensis* sp. n.**
– Uropod III inner ramus reaching 0.7 times the length of outer ramus ..... ***G. emeiensis***
12 Uropod III inner ramus reaching 0.6 times the length of outer ramus, both rami with plumose setae ..... ***G. sichuanensis***
– Uropod III with few plumose setae **13**
13 Pereopods V–VII bases elongated **14**
– Pereopods V–VII bases broad ..... ***G. glaber***
14 Uropod III inner ramus longer than half of outer ramus .... ***G. limosus* sp. n.**
– Uropod III inner ramus 0.3 times the length of outer ramus..... ***G. altus* sp. n.**

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RESEARCH ARTICLE

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Tubuca alcocki, a new pseudocryptic species of fiddler crab from the Indian Ocean, sister to the southeastern African *T. urvillei* (H. Milne Edwards, 1852) (Crustacea, Decapoda, Brachyura, Ocypodidae)

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Abstract

A new pseudocryptic species of fiddler crab, *Tubuca alcocki* **sp. n.**, is described from the northern Indian Ocean. The new species was previously identified with *T. urvillei* (H. Milne Edwards, 1852), but can be distinguished by the structures of the anterolateral angle of the carapace and male first gonopod. The molecular data of the mitochondrial cytochrome oxidase subunit I gene shows that both are sister taxa and the divergence time is estimated at 2.2 million years ago, around the beginning of the Pleistocene. While the new species is widely distributed in the northern part of Indian Ocean, occurring from the Red Sea to India and the Andaman Sea; *T. urvillei* sensu stricto has a more restricted range, and is known only from southeastern Africa.

Keywords

mitochondrial cytochrome oxidase subunit I, molecular clock, morphology, new species, *Tubuca alcocki*, *Tubuca urvillei*

Introduction

In recent years, various genetic and morphological studies on fiddler crabs (Ocypodidae) from the Indian Ocean have shown that there are a number of species endemic to the region: *Austruca albimana* (Kossmann, 1877), *A. bengali* (Crane, 1975), *A. iranica* (Pretzmann, 1971), *A. occidentalis* (Naderloo, Schubart & Shih, 2016), *A. sindensis* (Alcock, 1900), *Cranuca inversa* (Hoffmann, 1874), *Paraleptuca chlorophthalmus* (H. Milne Edwards, 1837), *Gelasimus hesperiae* (Crane, 1975), and *Tubuca urvillei* (H. Milne Edwards, 1852) (Shih et al. 2009, 2010, 2012, 2013a,b, 2015, 2016; Naderloo et al. 2016). The genetics suggest that the cladogenesis of these taxa have their origins in the Indian Ocean.

Of these taxa, *Tubuca urvillei* is a large-sized species, which has been widely reported from throughout the Indian Ocean and is the only *Tubuca* Bott, 1973 species known in the western Indian Ocean (Crane 1975; Shih et al. 2016). Aspects of its biology has also been investigated in southeastern Africa (e.g., Macnae 1963; Hartnoll 1975; Litulo 2005; Peer et al. 2015), Thailand (e.g., Jaroensutasinee et al. 2003; Jaroensutasinee and Jaroensutasinee 2004), and Pakistan (Ghory and Siddiqui 2006).

In this study, specimens from the range of *Tubuca urvillei*, including the type specimens, were examined. There are two clades, with small but consistent morphological differences supported by DNA evidence from cytochrome oxidase subunit I (COI). The material from the northern and eastern parts of the Indian Ocean is herein described as a new pseudocryptic species, *T. alcocki*.

Materials and methods

Specimens of *Tubuca urvillei* sensu lato collected from southeastern Africa, India and western Thailand examined (including the types) are deposited in the Muséum national d'Histoire naturelle, Paris, France (**MNHN**); Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (**NCHUZOOL**); Senckenberg Museum, Frankfurt am Main, Germany (**SMF**); and Zoological Reference Collection of the Lee Kong Chian Natural History Museum (formerly Raffles Museum of Biodiversity Research), National University of Singapore, Singapore (**ZRC**). The abbreviation G1 is used for male first gonopod. Measurements, all in millimeters (mm), are of the maximum carapace width (**CW**), carapace length (**CL**) and pollex length (**PL**). The terminology used essentially follows Crane (1975) and Davie et al. (2015).

Sequences of COI were obtained following the method described by Shih et al. (2016), after verification with the complimentary strand. Sequences of the different haplotypes have been deposited in the DNA Data Bank of Japan (**DDBJ**) (accession numbers in Table 1). According to Shih et al. (2016), *T. urvillei* is sister to the clade composed of *T. dussumieri* (H. Milne Edwards, 1852), *T. paradussumieri* (Bott, 1973) and *T. capricornis* (Crane, 1975). As a result, the sequences of these three species, as published in Shih et al. (2016) (LC150436, LC053373 and LC150430), are used as outgroups in this paper.

Table 1. The haplotypes of COI gene of *Tubuca alcocki* sp. n. and *T. urvillei* from the Indian Ocean. Abbreviations of museums or universities see Material and methods.

Species	Locality	Catalogue no.	Sample size	Access. no. of COI
Tubuca alcocki sp. n.	India: Mumbai	NCHUZOOL 14899, 14925, 14901, 14902	4	LC150445
		NCHUZOOL 14903	2	LC150445
	Thailand: Ranong	ZRC (paratype)	2	LC369625
		NCHUZOOL 14896 (paratype)	1	LC369625
		ZRC 2017.1278 (holotype)	1	LC369625
	Thailand: Phuket	ZRC 1999.1131	1	LC369625
		ZRC 1999.1131	1	LC369626
Tubuca urvillei	Mayotte: Poroani	ZRC 1999.1107	1	LC053375
	Kenya: Shimo la Tewa	SMF 19985	1	LC053375
	Kenya: Mida Creek, Malindi	NCHUZOOL 14895	1	LC053375

The phylogenetic tree was reconstructed by the maximum likelihood (**ML**) analysis by using RAxML (vers. 7.2.6, Stamatakis 2006), with the model GTR + G (i.e. GTRGAMMA) was used with 100 runs, and found the best ML tree by comparing the likelihood scores. The robustness of the ML tree was evaluated by 1000 bootstrap pseudoreplicates under the model GTRGAMMA. Basepair (bp) difference, as well as the pairwise estimates of Kimura 2-parameter (**K2P**) distance (Kimura 1980) and the uncorrected p-distance for genetic diversities between haplotypes were also calculated by MEGA (vers. 7.0, Kumar et al. 2016).

Systematic account

Family Ocypodidae Rafinesque, 1815
Subfamily Gelasiminae Miers, 1886 (*sensu* Shih et al. 2016)
Genus *Tubuca* Bott, 1973

***Tubuca urvillei* (H. Milne Edwards, 1852)**
Figures 1, 2, 4B, 5E–H, 7B, D, F, H

Gelasimus arcuatus – Krauss 1843: 39 [Natal Bay, South Africa] (not *Ocypode* (*Gelasimus*) *arcuata* De Haan, 1835).

Gelasimus urvillei H. Milne Edwards, 1852: 148, pl. 3(10) [type locality: "Vanikoro"]; Kingsley 1880: 145 [list]; De Man 1891: 21, 34 [Nossy Faly, Madagascar]; Ortmann 1894: 59 [Dar es Salaam, Tanzania].

Gelasimus dussumieri – A. Milne-Edwards 1868: 71 [list; Zanzibar]; Hilgendorf 1869: 84, pl. 4(1) [Zanzibar]; Hoffmann 1874: 17–18, pl. 3(19–22) [part; Nossy Faly, Madagascar]; De Man 1880: 68 [part; Madagascar]; Kingsley 1880: 145 [list;

part]; Lenz and Richters 1881: 423 [Madagascar]; Pfeffer 1889: 30 [Zanzibar]; De Man 1891: 20, 26 [part; Nossy Faly, Madagascar]; Lenz 1910: 559 [Zanzibar; Pemba] (not *Gelasimus dussumieri* H. Milne Edwards, 1852).

Uca arcuata – Stebbing 1905: 40 [South Africa]; Stebbing 1910: 327 [list] (not *Ocypode* (*Gelasimus*) *arcuata* De Haan, 1835).

Uca arcuatus – Stebbing 1917: 15 [Natal, South Africa] (not *Ocypode* (*Gelasimus*) *arcuata* De Haan, 1835).

Uca dussumieri – Maccagno 1928: 17–19 [part; Giumbo, Somalia] (not *Gelasimus dussumieri* H. Milne Edwards, 1852).

Uca urvillei – Barnard 1950: 93–94, figs 18d–f, 19a–b; Fourmanoir 1954: 3 [Madagascar]; Macnae 1963: 23 [Inhaca I., Mozambique to Cape Province, South Africa]; Richmond 1997: 226, 2 unnumbered figs on p. 227 [eastern Africa]; Crosnier 1965: 110–112, figs 186, 191–193, 195–196; Kensley 1981: 49 [list]; Rosenberg 2001: 860, 868 [South Africa]; Serbino 2008: 62–72, fig. 1 [Mozambique].

Tubuca urvillei – Bott 1973: fig. 11; Shih et al. 2016: 159 [list; part].

Uca (*Uca*) *urvillei* – Hartnoll 1975: 308, 310, 322, 324, fig. 8 [Tanzania].

Uca (*Uca*) *dussumieri* – Hartnoll 1975: 308, 310 [list; Tanzania] (not *Gelasimus dussumieri* H. Milne Edwards, 1852).

Uca (*Deltuca*) [*coarctata*] *urvillei* – Crane 1975: 58–61, figs 7, 8D, 9D, 27G–H, 38U–X, 62E, 75, pl. 9A–B, E–H [part, southeastern Africa].

Uca (*Deltuca*) *urvillei* – Vannini and Valmori 1981: 212–213, figs 5F1, F2, 6F [Giumbo, Somalia].

Uca (*Tubuca*) *urvillei* – Bouchard et al. 2013: 46, fig. 40 (Mayotte); Peer et al. 2014: 60, fig. 15; 2015: 190, 198, fig. 4c, d (upper figure) [South Africa].

Material examined. Lectotype ♂ (CW 18.5 mm, CL 11.0 mm, PL 17.0 mm) (MNHN B.12073), "Vanikoro", coll. J. R. C. Quoy and J. P. Gaimard (Fig. 1A–E). Paralectotypes: 2 ♀♀ (MNHN B. 3208), same data as lectotype (Fig. 1F–G).

Other material. 1 ♂ (CW 28.5 mm), 1 ♀ (CW 22.9 mm) (SMF 19985), Shimo la Tewa, ca. 20 km N Mombasa, ca. 2 km von Küste entfernt, Schlickmangrove, Kenya, coll. H. Langer, 11 Aug. 1990; 1 ♂ (CW 29.7 mm) (ZRC 1999.1107), Poroani, mangrove to the south, Mayotte, 23 July 1998; 2 ♂♂ (CW 27.9–34.9 mm), NCHUZOOL 14895, Mida Creek, Malindi, Kenya.

Diagnosis. Male. Carapace (Figs 1A, 2A, 4B, 7B, D, F) with anterolateral angle (= external orbital angle) broadly triangular, directed laterally; anterolateral margin short to moderately long; dorsolateral margin long, definite, strongly converging; 1 posterolateral stria. Floor of orbit with row of fewer than 17 tubercles, sometime with blunt ridge (Figs 1B, 2C, D). Major cheliped (Figs 1C, 2B) with dactylus usually longer than palm, outer surface of dactylus and pollex each with 1 long groove proximally extending beyond midlength. Fingers of minor cheliped without conspicuous tooth on either finger. G1 (Fig. 5E–H) with distal tube relatively stout, distinctly curved, gently tapering towards tip, distal part distinctly narrower than proximal part; thumb of moderate length, extending beyond base of distal tube. **Female**. Carapace with anterolateral an-

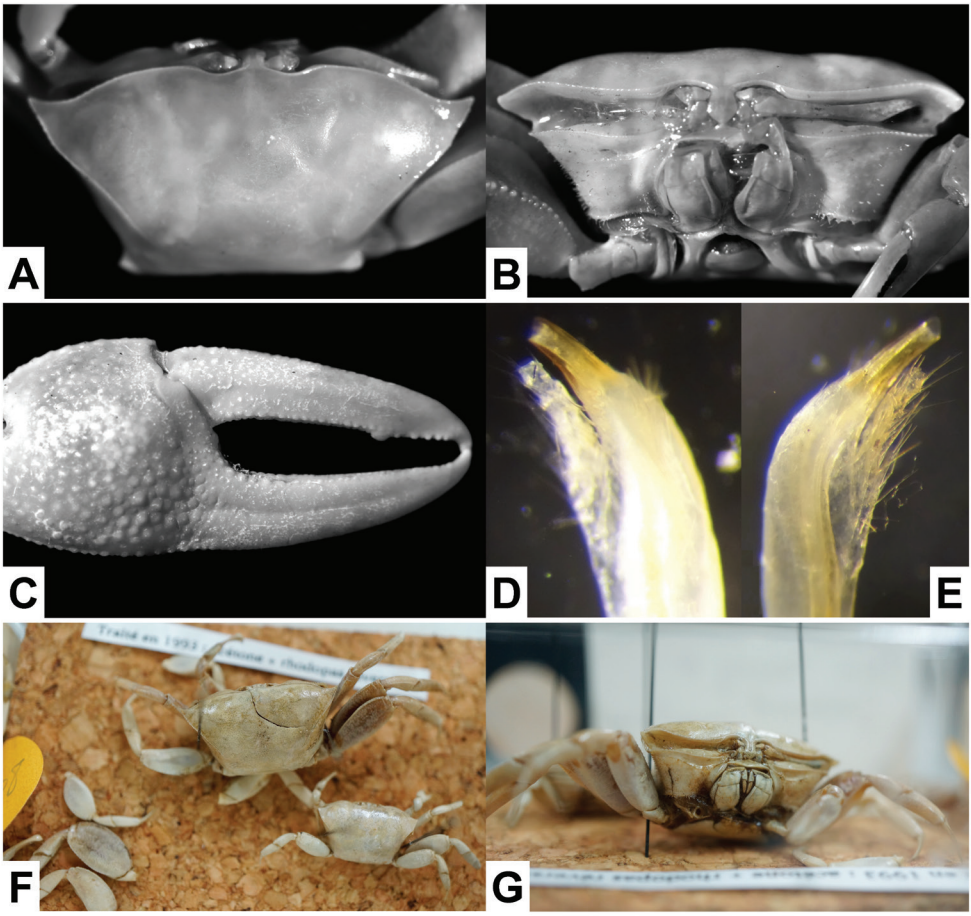

Figure 1. *Tubuca urvillei* (H. Milne Edwards, 1852). **A–E** lectotype (CW 18.5 mm, PL 17 mm, MNHN B.12073) **F–G** 2 dried female paralectotypes (MNHN B. 3208). **A** dorsal view **B** frontal view **C** major cheliped **D, E** distal part of right G1. **D** mesial view **E** lateral view.

gle acutely triangular; anterolateral margin short or absent, joining dorsolateral margin as almost straight line (Fig. 7H). Floor of orbit with row of 14–16 tubercles (Fig. 2F). Fingers of cheliped (Fig. 2F) each with conspicuous tooth on occlusal margin. (See also Remarks under *T. alcocki* sp. n. for comparisons of morphology and colouration.)

Distribution. Southeastern Africa from Giumbo (= Jumboo), southern Somalia, to Cape Province, South Africa (mouth of Umtata R.); Madagascar (Crane 1975).

Remarks. In his revision of the genera and subgenera of the fiddler crabs of the world, Bott (1973) established *Tubuca* and designated *Gelasimus urvillei* H. Milne Edwards, 1852 as the type species from the lectotype (Bott 1973: fig. 11). The type specimens of *Tubuca urvillei* were supposedly collected from "Vanikoro" (an island between Solomon and Vanuatu) in the western Pacific. Crane (1975) queried this type locality noting that the species as she understood it did not occur outside the In-

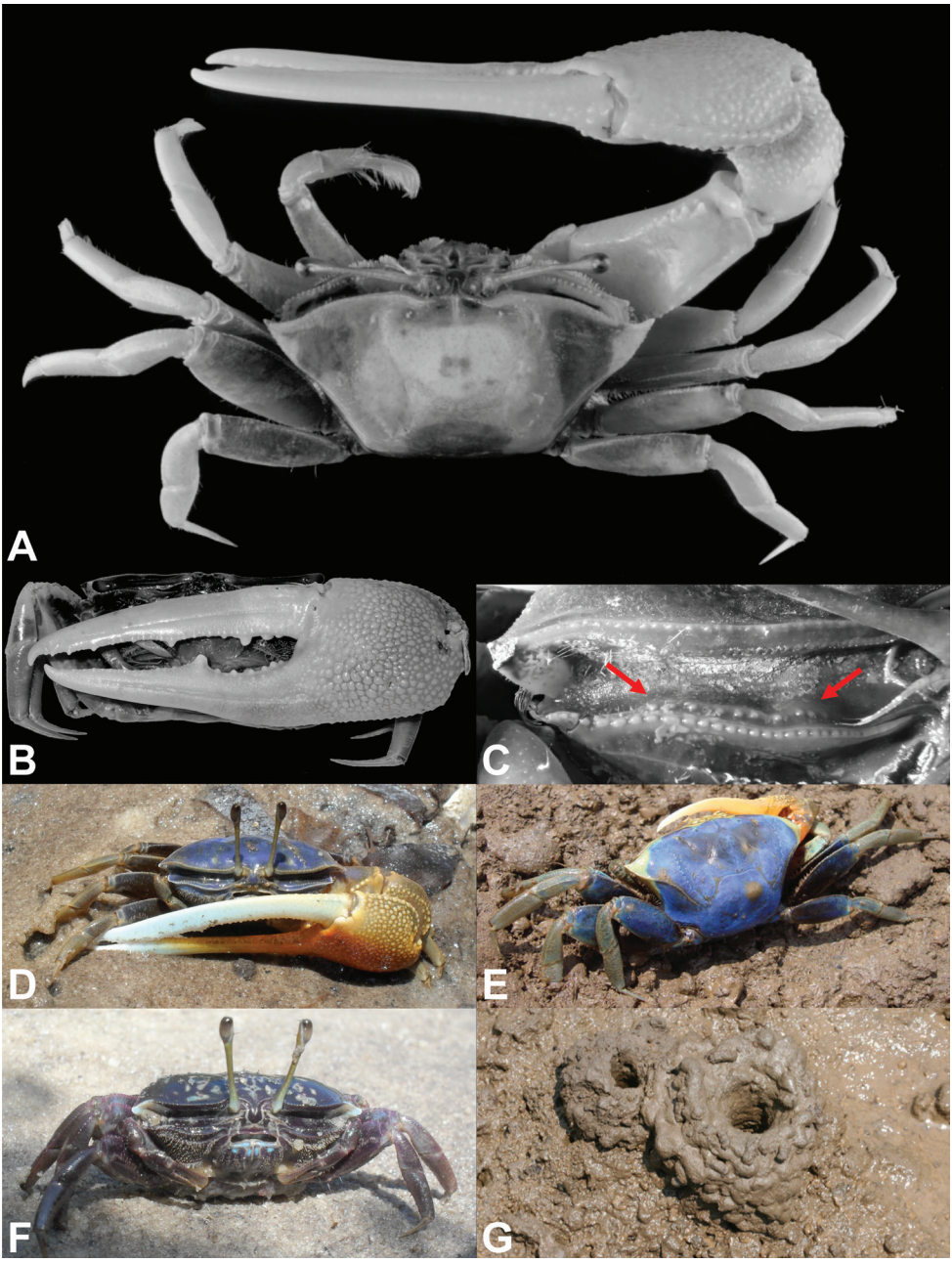

Figure 2. *Tubuca urvillei* (H. Milne Edwards, 1852) **A** male (CW 29.7 mm, ZRC 1999.1107; Mayotte) **B–C** male (CW 34.9, NCHUZOOL 14895; Kenya). **A** dorsal view **B** major cheliped **C** floor of right orbit of showing the tubercles (arrowed). **D–F** live colouration. **D** male from Kenya **E** male from Mayotte **F** female from Kenya **G** chimneys built by *T. urvillei* in Mayotte **D, F** courtesy of S. Cannicci **E, G** courtesy of J. Poupin.

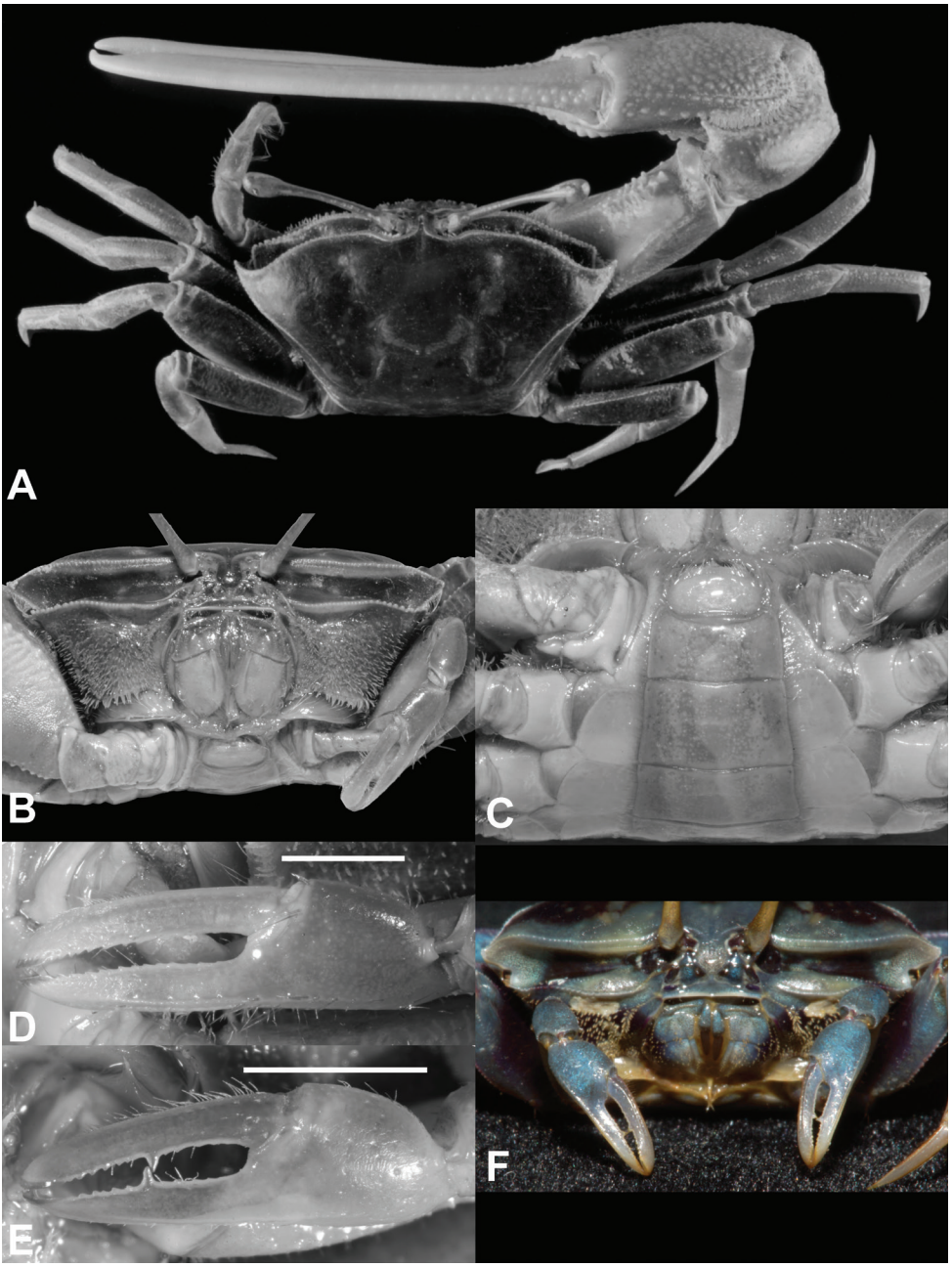

Figure 3. *Tubuca alcocki* sp. n. **A–D** holotype (CW 30.1 mm, ZRC 2017.1278) **E, F** ovigerous female (CW 19.8 mm, NCHUZOOL 14897; Thailand). **A** dorsal view **B** frontal view **C** pleon and telson **D, E** left minor cheliped **F** frontal view, with living colouration. Scale bars: 5.0 mm.

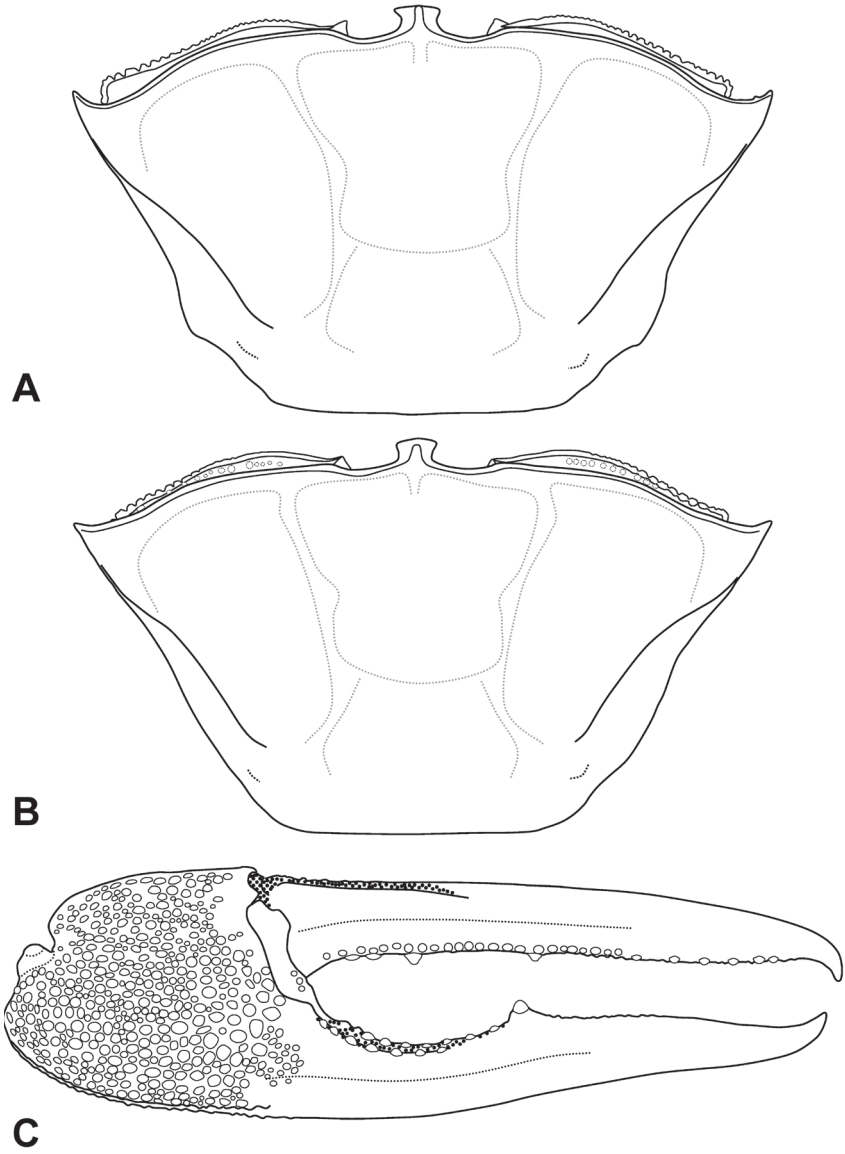

Figure 4. *Tubuca alcocki* sp. n. **A, C** holotype (CW 30.1 mm, PL 58.2 mm, ZRC 2017.1278; Thailand); *T. urvillei* (H. Milne Edwards, 1852) **B** male (CW 29.7 mm, ZRC 1999.1107; Mayotte). **A, B** dorsal view **C** major cheliped.

dian Ocean. As such, Crane (1975) considered the data on the label to be wrong. Of the three extant type specimens of *Gelasimus urvillei* H. Milne Edwards, 1852, Crane (1975) selected the male as the lectotype, the other two females becoming paralectotypes (Fig. 1F–G). Crane (1975) considered the male to be an immature specimen (CW 18.5 mm) but its G1 is actually already developed (present study). According to Litulo (2005), the smallest ovigerous female from Mozambique is only CW 10.0

mm. This suggests that the lectotype male, while small is probably already mature. In any case, the G1 of the lectotype of *T. urvillei* (Crane 1975: fig. 9D) agrees well with the species as is now understood from southeastern Africa (cf. Fig. 5E–H). They also agree in all other morphological characters.

A note on *Gelasimus dussumieri* H. Milne Edwards, 1852 (at present *Tubuca dussumieri*) is necessary. The type material of *Tubuca dussumieri* include specimens from Samarang (Java, Indonesia) and Malabar (Mumbai, India) (H. Milne Edwards, 1852), and as no holotype was originally selected, Crane (1975) designated a male from Samarang as the lectotype of *T. dussumieri*. The paralectotype male from Malabar, however, she reidentified as *T. urvillei* instead. She also found that *T. dussumieri* and *T. paradussumieri* were sympatric in the western Pacific and eastern part of Indian Ocean. She reidentified all the records (including "*T. acuta*") from western Indian Ocean as *T. urvillei*, with one exception – the record of *G. dussumieri* by Hoffmann (1874: pl. 3(22)) and De Man (1891) from Nossy Faly, northern Madagascar, which was referred to *T. paradussumieri* instead. As no other record of *T. paradussumieri* from eastern Africa has been reported since 1874 (Crosnier 1965), Crane (1975) regarded this specimen's provenance as questionable. Another record of "*T. dussumieri*" from Bombay, western India (Krishnan 1992) will also need to be confirmed in the future as well. In summary, Crane (1975) emphasized the westernmost distribution of the genus *Tubuca* (= *Deltuca* Crane, 1975) should be *T. urvillei* from southeastern Africa (Tanzania, Madagascar and South Africa), with the species also present in Pakistan and western India. Later, the species was reported from the Red Sea by Hogarth (1986) and Price et al. (1987).

With regard to the records of *T. urvillei* and *T. acuta* in Alcock (1900), Crane (1975: 61) considered only those from Pakistan and western India as belonging to true *T. urvillei* (shown as "(part)" behind these records). That is, she did not think or was uncertain if the records from the Bay of Bengal and the Andaman Sea (e.g. Madras; Sunderbunds; Mergui; Andamans and Nicobars) by Alcock (1900) were also *T. urvillei*. Lundoer (1974) added a new record of "*U. angustifrons* (De Man, 1892)" from Phuket, Thailand, but this was later reidentified as *T. urvillei* by Frith et al. (1976) and Frith and Frith (1977a) (see also Frith and Frith 1978; Frith and Brunenmeister 1980, 1983; Jaroensutasinee et al. 2003; Jaroensutasinee and Jaroensutasinee 2004).

***Tubuca alcocki* sp. n.**

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Figures 3, 4A, C, 5A–D, 6, 7A, C, E, G

Gelasimus Dussumieri H. Milne Edwards, 1852: 148, pl. 4(12) [part; Malabar, India]; Kingsley 1880: 145 [part; list]; Chandy 1973: 402 [Gulf of Kutch, W India] (not *Gelasimus dussumieri* H. Milne Edwards, 1852 sensu stricto).

Gelasimus acutus – Alcock 1900: 360–361 [Sunderbunds, Mergui; Andamans; Karachi] (not *Gelasimus acutus* Stimpson, 1858).

Gelasimus Urvillei – Alcock 1900: 362–363 [Nicobars; Madras; Karachi] (not *Gelasimus urvillei* H. Milne Edwards, 1852).

Uca angustifrons – Lundoer 1974: 8 [Phuket, SW Thailand]; Ng and Davie 2002: 378 [list; Phuket, SW Thailand] (not *Gelasimus signatus* var. *angustifrons* De Man, 1892 = *Tubuca bellator* (White, 1847)).

Uca (*Deltuca*) [*coarctata*] *urvillei* – Crane 1975: 35, 58–61, figs 8B, 9E, pl. 9C, D [part, Pakistan to southern India]; Frith and Frith 1977a: 100–101 [Phuket, SW Thailand] (not *Gelasimus urvillei* H. Milne Edwards, 1852).

Uca urvillei – Frith et al. 1976: 14, 19, 23–24, 28 [Phuket, SW Thailand]; Tirmizi and Ghani 1996: 103–105, fig. 39 [Pakistan]; Jaroensutasinee et al. 2003: 1–3 [W Thailand]; Jaroensutasinee and Jaroensutasinee 2004: 534, 538, 540–548 [W Thailand]; Naiyanetr 2007: 133 [list; Thailand]; Saher 2008: 21–22, fig. 2.2, pl. 2.1 [Pakistan]; Dev Roy and Nandi 2012: 218 [Nicobar, India]; Hossain 2015: 203, 1 unnumbered fig. [Bangladesh]; Odhano et al. 2015: 170–171, figs 1–2 [Pakistan] (not *Gelasimus urvillei* H. Milne Edwards, 1852).

Uca (*Deltuca*) *urvillei* – Hogarth 1986: 222–223 [Red Sea]; Price et al. 1987: 456, 464 [Red Sea]; Krishnan 1992: 471–472 [Bombay, India] (not *Gelasimus urvillei* H. Milne Edwards, 1852).

Uca (*Deltuca*) *dussumieri* – Krishnan 1992: 471–472 [Bombay, India] (not *Gelasimus dussumieri* H. Milne Edwards, 1852)

Uca (*Tubuca*) *urvillei* – Beinlich and von Hagen 2006: 10, 14, 25, fig. 7f, k [Thailand; India] (not *Gelasimus urvillei* H. Milne Edwards, 1852).

Uca (*Tubuca*) *acuta* – Trivedi et al. 2015: 27 [Gujarat, India] (not *Gelasimus acutus* Stimpson, 1858).

Tubuca urvillei – Shih et al. 2016: 159, 174 [part], fig. 12A.

Material examined. Holotype: ♂ (CW 30.1 mm, CL 17.9 mm; PL 58.2 mm) (ZRC 2017.1278), Ranong mangroves, Thailand, coll. H.-T. Shih et al., 27 May 2012. Paratypes: 2 ♂♂ (CW 22.4–29.9 mm), 1 ♀ (CW 25.1 mm) (NCHUZOOL 13661), 1 ♂ (CW 29.5 mm) (NCHUZOOL 14896), 13 ♂♂ (CW 14.7–31.2 mm), 4 ♀♀ (CW 19.9–24.1 mm), 1 ovig. ♀ (CW 25.7 mm) (NCHUZOOL 14905), same data as holotype; 1 ♂ (CW 24.6 mm), 1 ovig. ♀ (CW 14.8 mm) (ZRC 2017.1279), Kamphuan mangroves, Ranong, Thailand, 9 Sep. 2000; 1 ♂ (CW 24.0 mm) (ZRC 2001.2347), Ranong, Thailand, coll. P. Clark, 7 Nov. 2001.

Other material. Thailand: 2 ♂♂ (CW 17.8–26.1 mm) (ZRC 1988.616–617), Phuket, coll. D. H. Murphy, 12 Nov. 1987; 2 ♂♂ (CW 20.3–22.4 mm) (ZRC 1999.1131), mangrove area south east of Phuket Town ca. 8 km, W. B. Jeffries and H. K. Voris, 14 June 1990; 4 ♂♂ (CW 13.0–16.9 mm), 1 ♀ (CW 18.8 mm), 1 ovig. ♀ (CW 19.8 mm) (NCHUZOOL 14897), 6 ♂♂ (CW 9.0–12.4 mm), 3 ♀♀ (CW 11.4–14.0 mm), 2 ovig. ♀♀ (CW 13.9–14.8 mm) (NCHUZOOL 14906), Chalong Bay, Phuket, coll. H.-T. Shih et al., 28 May 2012; 4 ♂♂ (CW 4.4–16.9 mm), 1 ♀ (CW 12.8 mm), 1 ovig. ♀ (CW 14.7 mm) (NCHUZOOL 14898), Laem Tukkae, Phuket, coll. H.-T. Shih et al., 29 May 2012; 1 ♂ (CW 17.2 mm), 2 ♀♀ (CW 14.0–15.6 mm) (NCHUZOOL 14907), Tha Thiap Ruea Bang Rong, Phuket, coll. H.-T. Shih et al., 30 May 2012. India: 1 ♂ (CW 17.7 mm) (NCHUZOOL 14925), 1 ♂ (CW 19.0 mm) (NCHUZOOL 14899), 1 ♂ (CW 12.6 mm) (NCHUZOOL

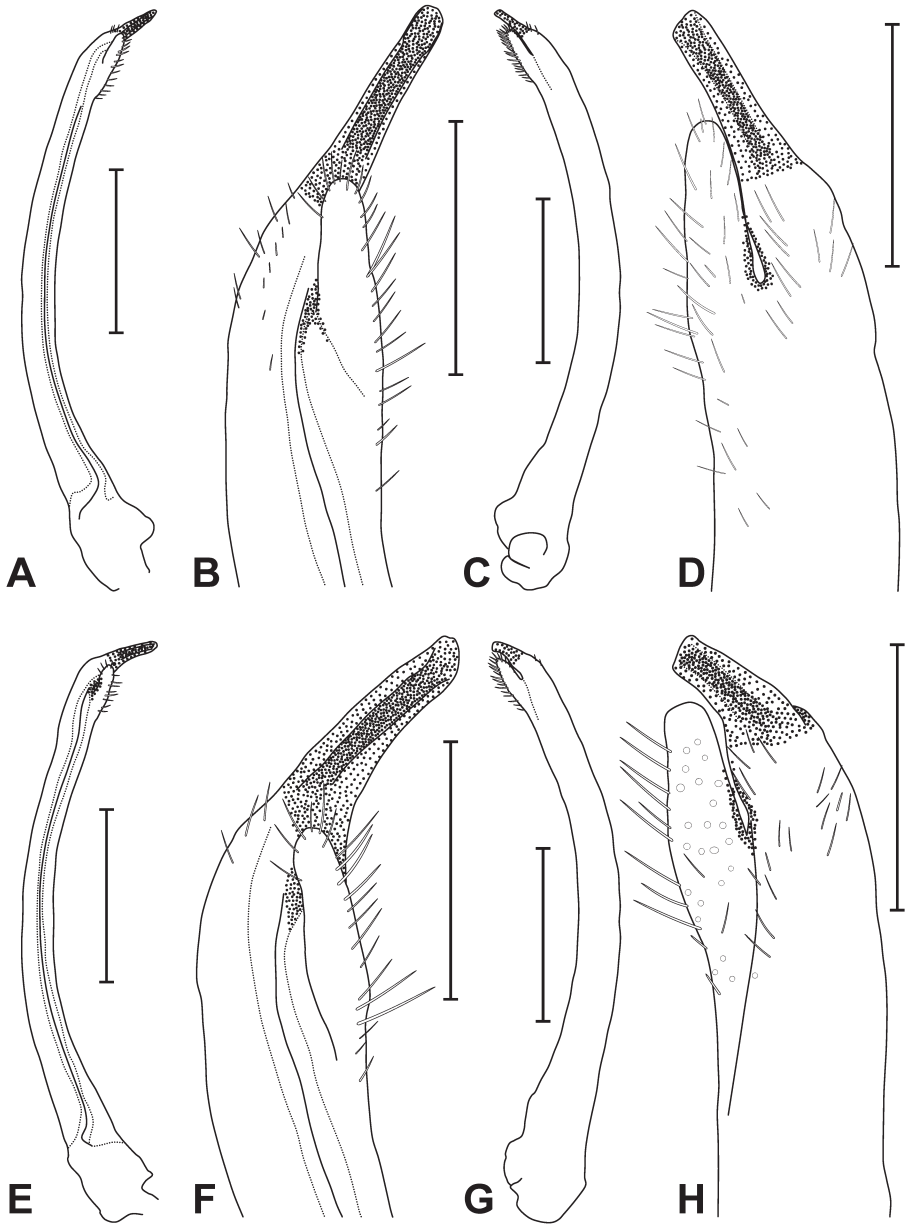

Figure 5. Right G1. *Tubuca alcocki* sp. n. **A–D** holotype (CW 30.1 mm, ZRC 2017.1278; Thailand) **E–H** *T. urvillei* (H. Milne Edwards, 1852), male (CW 29.7 mm, ZRC 1999.1107; Mayotte). **A, E** mesial view **B, F** mesial view of distal part **C, G** lateral view **D, H** lateral view of distal part. Scale bars: **A, C, E, G** 5.0 mm **B, D, F, H** 1.0 mm.

14901), 1 ♀ (CW 17.5 mm) (NCHUZOOL 14902), 13 ♂♂ (CW 9.9–18.2 mm), 3 ♀♀ (CW 11.4–17.9 mm), 1 ovig. ♀ (CW 19.9 mm) (NCHUZOOL 14903), Mumbai, coll. H.-N. Chen et al., 17 Mar. 2010; 1 ♀ (CW 22.6 mm) (NCHUZOOL 14900), Diu mangroves, coll. K. Wong, 20 Mar. 2010.

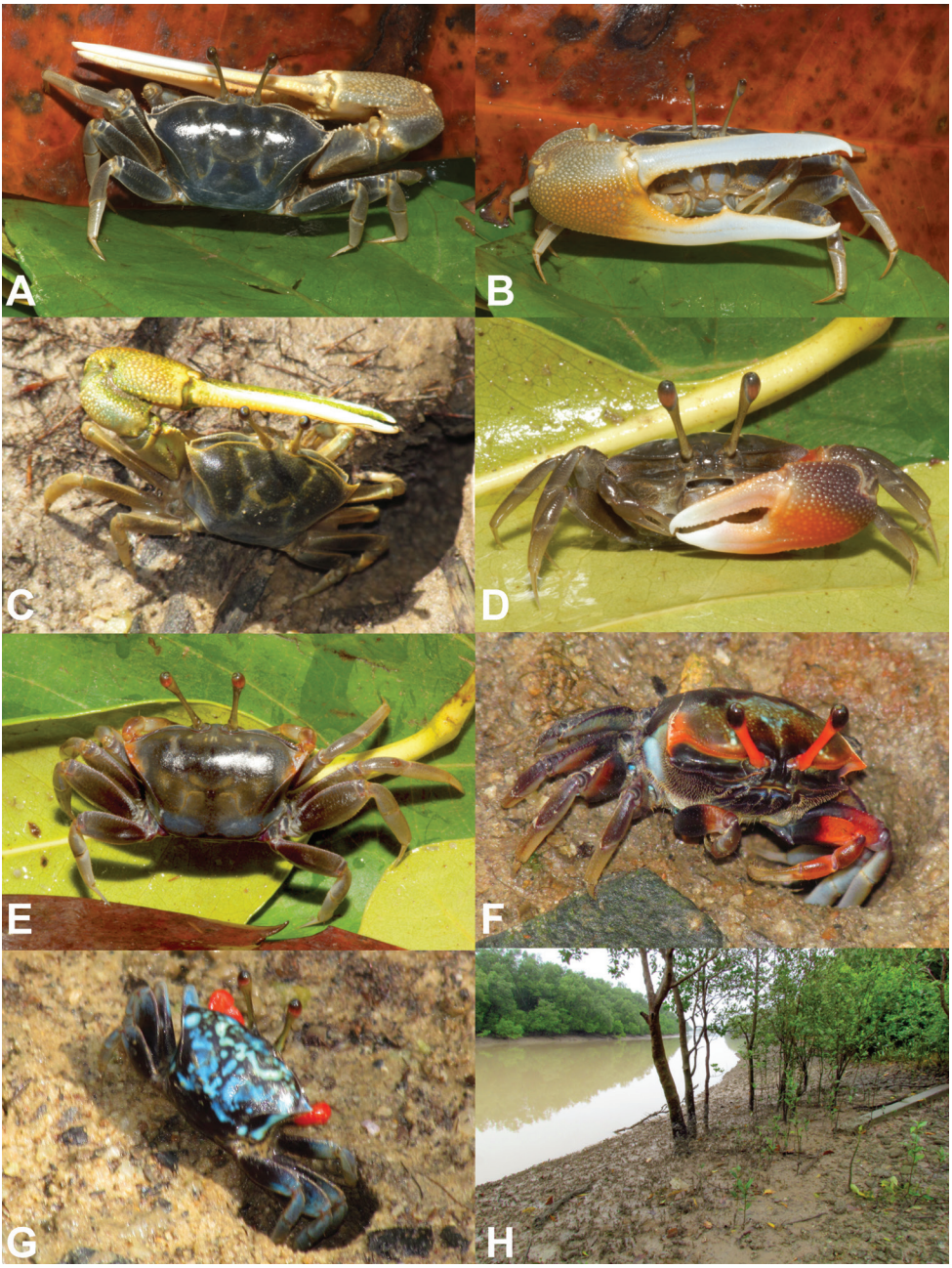

Figure 6. *Tubuca alcocki* sp. n. **A–G** variation of the live colouration. **A, B** holotype (CW 30.1 mm, ZRC 2017.1278; Thailand) **C** adult male (not collected; Phuket, Thailand) **D** young male (CW 13.0 mm, NCHUZOOL 14897; Thailand) **E** ovigerous female (CW 19.8 mm, NCHUZOOL 14897, Thailand) **F, G** females in the field (not captured; Phuket, Thailand) **H** habitat in Ranong, Thailand.

Diagnosis. Male. Carapace (Figs 3A, 4A, 6A, C, G, 7A, C, E) trapezoidal, smooth; front narrow, with distinct, narrow median groove; anterolateral angle acutely triangular, directed obliquely anteriorly; anterolateral margin short to moderately long; dorsolateral margin long, definite, strongly converging; one posterolateral stria. Floor of orbit with row of 5–11 tubercles, sometimes with blunt ridge. Major cheliped (Figs 4C, 6B, D) with dactylus usually longer than palm, outer surface of dactylus and pollex each with 1 long groove proximally extending beyond midlength. Fingers of minor cheliped (Figs 3B, D, 6B, D) without conspicuous tooth on either finger. G1 (Fig. 5A–D) with distal tube slender, slightly curved to almost straight, distal and proximal parts subequal in width; thumb of moderate length, extending beyond base of distal tube.

Female. Anterolateral angle more broadly triangular; anterolateral margin moderately long, joining dorsolateral margin as convex structure (Fig. 7G). Floor of orbit with row of 17–19 tubercles (Figs 3F, 6F). Fingers of cheliped (Fig. 3E, F) each with conspicuous tooth on occlusal margin.

Colouration in life. Adults with carapace and legs brown or dark brown, posterior part gray, especially in females (Fig. 6A, C, E). Some females with anterolateral angles orange (Fig. 6E, F) or with dark blotches on blue carapace (Fig. 6G). Major cheliped with fingers white; lower palm deep yellow in large individuals, orange in young individuals; upper palm brown (Fig. 6B–D). Females sometimes with minor chelipeds orange, sometimes with tint of blue (Figs 3F, 6F, G).

Ecological notes. In western Thailand, this species inhabits muddy banks of mangroves (Fig. 6H) and is sympatric with several species of fiddler crabs, including *Austruca annulipes* (H. Milne Edwards, 1837), *A. bengali*, *Tubuca forcipata* (Adams & White, 1849) and *T. paradussumieri* (cf. Frith and Frith 1977a, 1978; this study). In Pakistan, this species is sympatric with *Austruca iranica* (cf. Saher et al. 2014).

Etymology. This species is named after Alfred William Alcock, who first recorded this species from India and Pakistan as "*Uca urvillei*" (cf. Alcock 1900).

Distribution. Western Thailand, India, Pakistan, and the Red Sea (see Remarks).

Remarks. Although the number of tubercles on the floor of orbit and thumb morphology of G1 are sometimes useful for distinguishing species of fiddler crabs, they are too variable in *Tubuca alcocki* sp. n. and *T. urvillei* (Crane 1975: 58–59; this study) to be used. The two species are similar, but can be morphologically distinguished by the characters of the anterolateral angle of the carapace and G1. The anterolateral angle in male *T. alcocki* is acutely triangular and directed obliquely anteriorly (Fig. 7A, C, E) (vs. relatively broadly triangular in shape and directed more laterally in position in *T. urvillei*; Fig. 7B, D, F). In female *T. alcocki*, the anterolateral angle is broadly triangular in shape and the anterolateral margin is relatively longer and curves gently to join the dorsolateral margin (Fig. 7G) (vs. anterolateral angle acutely triangular in shape with the anterolateral margin short and merging with the dorsolateral margin in an almost straight line in *T. urvillei*; Fig. 7H). The G1 structure is also different. The distal tube of the G1 of *T. alcocki* is proportionately more slender, being slightly curved to almost straight, with the widths of the distal and proximal

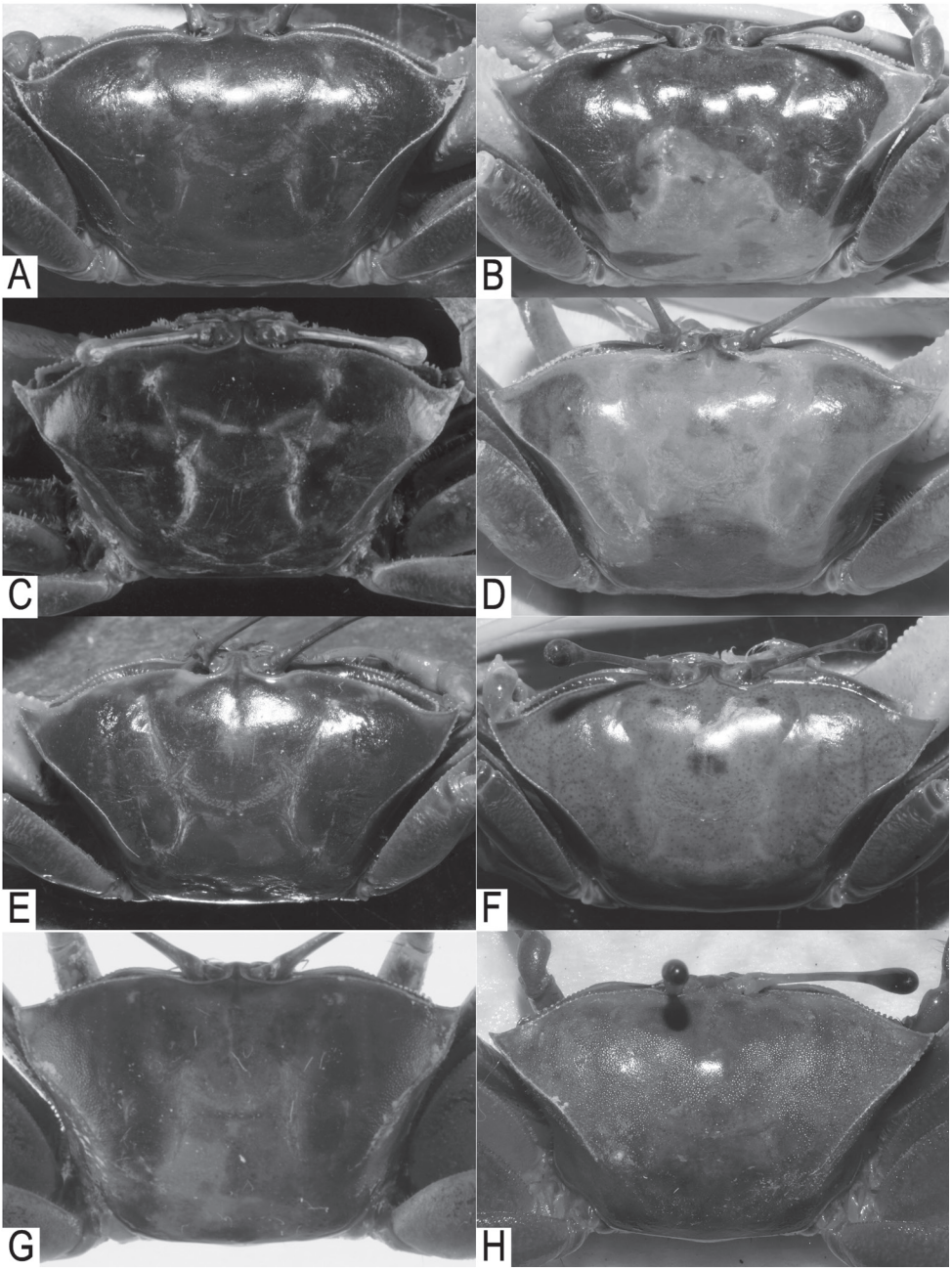

Figure 7. Carapace morphology. **A, C, E, G** *Tubuca alcocki* sp. n., **B, D, F, H** *T. urvillei* (H. Milne Edwards, 1852). **A** holotype male (CW 30.1 mm, ZRC 2017.1278; Thailand) **B** male (CW 34.9 mm, NCHUZOOL 14895; Kenya) **C** male (CW 29.5 mm, NCHUZOOL 14896; Ranong, Thailand) **D** male (CW 29.7 mm, ZRC 1999.1107; Mayotte) **E** male (CW 27.8 mm, NCHUZOOL 14905; Thailand) **F** male (CW 27.9 mm, NCHUZOOL 14895; Kenya) **G** female (CW 22.6 mm, NCHUZOOL 14900; India) **H** female (CW 22.9 mm, SMF 19985; Kenya).

parts subequal (Fig. 5A–D) (vs. distal tube relatively stouter, more distinctly curved and gently tapering towards the tip, with the distal part distinctly narrower than the proximal part in *T. urvillei*; Fig. 5E–H).

Crane (1975) figured specimens of what she referred to as *T. urvillei* from southeastern Africa and western India, and they agree with the characters of *T. urvillei* and *T. alcocki*, respectively. The anterolateral angles of the male lectotype of *T. urvillei* (Fig. 1A; Crane 1975: pl. 9E) and the male specimen from Tanzania (Crane 1975: fig. 7A) are both broadly triangular. In addition, the G1 distal tubes of the lectotype of *T. urvillei* as well as those from Somalia and Madagascar figured by Vannini and Valmori (1981: fig. 6F) and Crosnier (1965: figs 195–196) are all relatively stout, curved and tapering towards the tip. As such the material from Tanzania, Somalia and Madagascar should all be referred to *T. urvillei* sensu stricto.

The specimen from Malabar, western India, and one of the paralectotypes of *Gelasimus dussumieri* (see discussion earlier), have the G1 distal tube relatively more slender, almost straight, with the distal and proximal parts subequal in width (Crane 1975: fig. 9E) and are thus is clearly referable to *T. alcocki*. The G1 structures of specimens from Pakistan (Saher 2008: fig. 2.2; Tirmizi and Ghani 1996: fig. 39) also match that of *T. alcocki*. Interestingly, Hogarth (1986) reported "*Uca* (*Deltuca*) *urvillei*" from the Red Sea, which was a new record of this species for this region, but without any figure or description. The first author has examined specimens from the Red Sea and they are clearly *T. alcocki* as well (H-T Shih and BA Kumar, in preparation). The distribution of *T. alcocki* thus stretches from the northern part of the Indian Ocean (Red Sea) to the Arabian Sea and Andaman Sea.

There are also colour differences between *T. urvillei* and *T. alcocki*. While the colouration of females, young males, and juveniles are variable in *Tubuca* species, the colouration of the adult male carapace is generally more useful (Crane 1975; von Hagen and Jones 1989; Beinlich and von Hagen 2006). Adult male *T. urvillei* sensu stricto have various degrees of blue on the carapace and ambulatory legs (Fig. 2D, E), with the palm of the major cheliped ochraceous to apricot brown (Fig. 2D); while young and females sometimes have pale and dark blotches on a blue background (Fig. 2F). In adult male *T. alcocki*, the dorsal surface of the carapace is always dark brown (Fig. 6A, C) whereas in *T. urvillei*, it is always blue (Fig. 2D, E).

DNA analyses and discussion

The molecular analyses include 12 specimens of *Tubuca alcocki* sp. n. from western Thailand and western India; and three specimens of *T. urvillei* from southeastern Africa (Table 1). The phylogenetic tree (Fig. 8) based on COI shows that specimens from southeastern Africa form a distinct clade, sister to another clade with material from western India and western Thailand. The genetics therefore supports the recognition of two species. Only one haplotype is found from *T. urvillei* from southeastern Africa, with two haplotypes from *T. alcocki*.

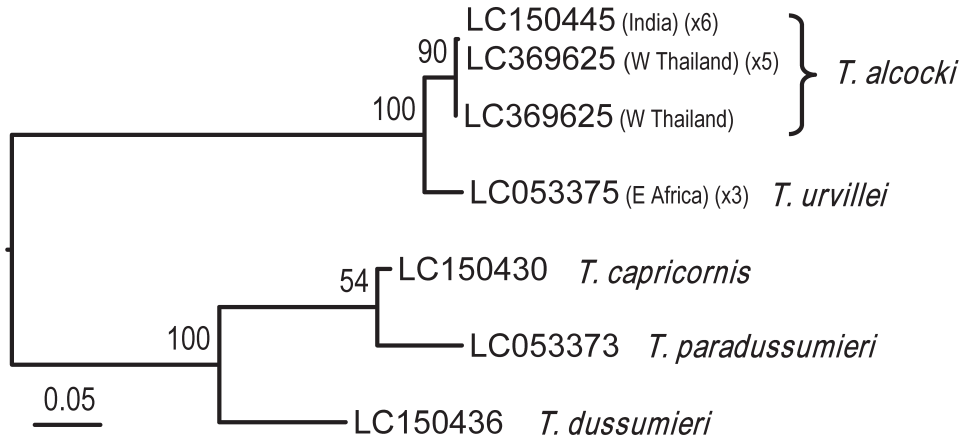

Figure 8. A maximum likelihood (ML) tree for *Tubuca urvillei* (H. Milne Edwards, 1852) and *T. alcocki* sp. n. from the Indian Ocean, and outgroups, based on COI gene. Bootstrap proportions are shown at the nodes. For accession numbers, see Table 1 and Materials and methods.

The genetic distance between these two sister species is 3.78 % (K2P distance) or 3.65 % (p-distance), and the total bp difference is 24 bp. The value is higher than some species within the Ocypodoidea, e.g., the minimum genetic distance of K2P between two species is 2.79 % between *Paraleptuca crassipes* (White, 1847) and *P. splendida* (Stimpson, 1858); 3.62 % between *Gelasimus hesperiae* (Crane, 1975) and "Clade U"; and 3.62 % between *Mictyris brevidactylus* Stimpson, 1858 and *M. guinotae* Davie, Shih & Chan, 2010, but still smaller than 6.25 % between *Ocypode stimpsoni* Ortmann, 1897 and *O. mortoni* George, 1982; and 4.43 % between *Scopimera globosa* (De Haan, 1835) and *S. ryukyuensis* Wong, Chan & Shih, 2010 (see Davie et al. 2010; Shih et al. 2010, 2012; Wong et al. 2010, 2012; Chu et al. 2015).

Tubuca alcocki and *T. urvillei* are quite similar in general morphology, but can be still distinguished by characters of the carapace and G1 (see Remarks under *T. alcocki*), which is supported by molecular evidence (Fig. 8). As a result, *T. alcocki* can be considered a pseudocryptic species (i.e., minor morphological difference, only after other methods have unveiled their existence), which is not uncommon in marine organisms (Knowlton 1993, 2000), including brachyuran crabs (Ragionieri et al. 2009, 2012; Shih et al. 2013a; Ng and Shih 2014; Lai et al. 2017).

According to Shih et al. (2016) and this study, the clade of *T. urvillei* and *T. alcocki* is sister to the clade composed of *T. dussumieri*, *T. paradussumieri* and *T. capricornis*. From the distributional patterns of these two main clades, while *T. urvillei* and *T. alcocki* are found only in the Indian Ocean, another main clade, composed of *T. dussumieri*, *T. paradussumieri* and *T. capricornis* (Shih et al. 2016), is primarily western Pacific, although *T. alcocki* and *T. paradussumieri* are sympatric in the eastern Indian Ocean (Frith and Frith 1977a, 1978; present study). Because *T. dussumieri* has been recorded from Surin Islands, Phang Nga Province, Thailand (Frith and Frith 1977a, b, 1978), *T. alcocki* is probably also sympatric with it.

Hogarth (1986) has emphasized that the Red Sea population of "*T. urvillei*" is discontinuous with other populations and represents a significant extension of the known range. His Red Sea material is now recognized as *T. alcocki* (unpublished data; see Remarks under *T. alcocki*), and the northernmost distribution of *T. urvillei* sensu stricto is in southern Somalia (Crane 1975; Hogarth 1986). *Tubuca alcocki* thus has a wider range, which includes most of the northern Indian Ocean, from western Thailand (facing the Andaman Sea), through the Bay of Bengal and India, to the Red Sea. *Tubuca urvillei*, on the other hand, is known with certainty only from southeastern Africa. This distributional pattern is probably caused by the major oceanographic circulation systems at around 10°S, which limit the dispersal of larvae to the southeastern African coastline (Tsang et al. 2012).

Based on the pairwise divergence rates of 1.66 % per million years for COI of marine coastal crabs (Schubart et al. 1998), *T. urvillei* and *T. alcocki* diverged 2.2±0.4 million years ago (mya) (with uncorrected p-distance divergences of 3.65 % ± 0.71 %) around the beginning of the Pleistocene. The divergence between them is probably caused by the change of larval dispersal routes through ocean currents (e.g., the Equatorial Counter Current for a biogeographic barrier of barnacles; Tsang et al. 2012), which was likely influenced by the extreme climate during the glaciation periods in the Pleistocene (Shih et al. 2013a).

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RESEARCH ARTICLE

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A new species of the genus *Gonatopus* Ljungh from the USA (Hymenoptera, Dryinidae)

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Abstract

A new species of *Gonatopus* Ljungh, 1810 is described from the USA, Florida: *G. jacki* **sp. n**. Morphologically, the new species is similar to *G. ashmeadi* Kieffer, 1905 and *G. agropyrus* Fenton, 1921, but it is distinguished by the different shape of the mesoscutum (very slender in *G. jacki*; broader in *G.ashmeadi* and *G.agropyrus*). Published identification keys to the Nearctic species of *Gonatopus* are modified to include the new species.

Keywords

Chrysidoidea, Florida, Gonatopodinae, key, Nearctic region, taxonomy

Introduction

Based on all known host records, Dryinidae (Hymenoptera, Chrysidoidea) are parasitoids of Auchenorrhyncha (Hemiptera) (Guglielmino et al. 2013). However, the biology of this group of small wasps is still poorly known (Guglielmino et al. 2006, 2008, 2015). *Gonatopus* Ljungh, 1810 is a genus that is present in all zoogeographical regions (Olmi 1984; Guglielmino and Virla 1998; Guglielmino and Bückle 2003, 2010; Xu

et al. 2013; Olmi and Virla 2014; Olmi and Xu 2015). In total 441 species have been described from all continents (Guglielmino and Olmi 2014; Olmi and Xu 2015) and the genus was revised at world level by Olmi (1984, 1991), and more recently in the Oriental, Neotropical and Eastern Palaearctic regions by Xu et al. (2013), Olmi and Virla (2014) and Olmi and Xu (2015),

The species of *Gonatopus* inhabiting the Nearctic region were studied by Olmi (1984, 1987, 1992, 1993a, 1993b, 1995, 2003). More recently, Olmi and Guglielmino (2013) described one further new species from the USA, Arkansas (*Gonatopus rileyi* Olmi & Guglielmino). In total, 51 *Gonatopus* species have been described from the Nearctic region (Olmi 1984, 1987, 1992, 1993a, 1993b, 1995, 2003; Olmi and Guglielmino 2013).

Gonatopus species are parasitoids of leafhoppers and planthoppers belonging to the Acanaloniidae, Cicadellidae, Delphacidae, Dictyopharidae, Flatidae, Issidae, Lophopidae, Meenoplidae, Tropiduchidae (Guglielmino et al. 2013). As in almost all dryinids, females of *Gonatopus* have a chelate protarsus. Chelae are used to capture and restrain the host during ovipositions and hostfeeding (Olmi 1984, 1994).

In 2015, additional specimens of *Gonatopus* from the USA were examined and the new species found is described herein.

Materials and methods

The descriptions follow the terminology used by Olmi (1984), Olmi and Guglielmino (2010), and Olmi and Virla (2014). The measurements reported are relative, except for the total length (head, except antennae, to abdominal tip), which is expressed in millimeters. In the descriptions, **POL** is the distance between the inner edges of the two lateral ocelli; **OL** is the distance between the inner edges of a lateral ocellus and the median ocellus; **OOL** is the distance from the outer edge of a lateral ocellus to the compound eye; **OPL** is the distance from the posterior edge of a lateral ocellus to the occipital carina; and **TL** is the distance from the posterior edge of an eye to the occipital carina. The term "metapectal-propodeal complex" is here used in the sense of Kawada et al. (2015). It corresponds to the term "propodeum" *sensu* Olmi (1984, 1994), Xu et al. (2013), Olmi and Virla (2014), and Olmi and Xu (2015).

The types of all Nearctic and Neotropical species of *Gonatopus* have been previously examined by the authors.

The material studied in this paper is deposited in the Department of Agriculture and Forestry Sciences, University of Tuscia, Viterbo, Italy (**MOLC**).

The description of the new species is based on the study of a single specimen. The authors are aware that descriptions of new taxa should normally be based on more individuals. However, Dryinidae are so rare that it is uncommon to collect more than one specimen of each species. In addition, on the basis of the experience and knowledge of the authors, the new species is sufficiently delimited by unique characters to justify its description.

Taxonomy

Genus *Gonatopus* Ljungh, 1810

Gonatopus Ljungh, 1810: 161. Type species: *Gonatopus formicarius* Ljungh, 1810, by monotypy.

Diagnosis. Female: Apterous or macropterous; palpal formula 3/2, 4/2, 4/3, 5/2, 5/3, or 6/3; pronotum crossed or not by transverse furrow; enlarged claw with distal apex pointed and with one large or small subapical tooth (occasionally subapical tooth absent, then enlarged claw with distal group of lamellae); in macropterous forms, protarsomere V with more than 20 lamellae; tibial spurs 1/0/1. Male: Fully winged; occipital carina absent or incomplete (in this last case, present behind and shortly on sides of posterior ocelli); occiput concave; temple present; palpal formula 3/2, 4/2, 4/3, 5/2, 5/3, or 6/3; tibial spurs 1/1/2.

Gonatopus jacki sp. n.

http://zoobank.org/58D11919-7B91-4A07-87CA-E94B23BCE001

Diagnosis. Female apterous (Fig. 1A, B); palpal formula 5/2; pronotum crossed by deep transverse furrow (Fig. 1B); mesoscutum without lateral pointed apophyses (Fig. 1A); metanotum not hollow behind mesoscutellum (Fig. 1B); meso-metapleural suture obsolete; first abdominal tergum strongly transversely striate (Fig. 1A); enlarged claw with peg-like hairs and one small subapical tooth (Fig. 2A).

Description. ***Female.*** Apterous (Fig. 1A, B); length 3.4 mm. Head brown, except mandible, clypeus, region of face between antennal toruli and two short frontal stripes along orbits yellow-whitish; antenna brown, except antennomere 10 whitish; mesosoma and metasoma black; legs brown, except metatrochanter testaceous. Antenna clavate; antennomeres in following proportions: 9:6:14:10:10:9:8:8:7:10. Head excavated, shiny, not sculptured; frontal line complete; occipital carina absent; POL = 1; OL = 2; OOL = 8; greatest breadth of posterior ocellus about as long as POL. Palpal formula 5/2. Mesosoma with long sparse setae. Pronotum shiny, unsculptured, crossed by deep transverse impression. Mesoscutum slender (Fig. 1A), dull, granulated, laterally without pointed apophyses (Fig. 1A). Mesoscutellum very small, flat, not sculptured. Metanotum flat, transversely striate, not hollow behind mesoscutellum (Fig. 1B). Metapectal-propodeal complex shiny, with metapostonotum not sculptured; first abdominal tergum transversely striate. Mesopleuron and metapleuron granulated and transversely striate. Meso-metapleural suture obsolete. Protarsomeres in following proportions: 13:2:4:17:26. Protarsomere III produced into hook. Enlarged claw (Fig. 2A) with one small subapical tooth and nine peg-like hairs + one bristle. Protarsomere V (Fig. 2A) with two rows of 4 + 22 lamellae situated in distal half; distal apex with approximately eleven lamellae. Tibial spurs 1/0/1.

Male. Unknown.

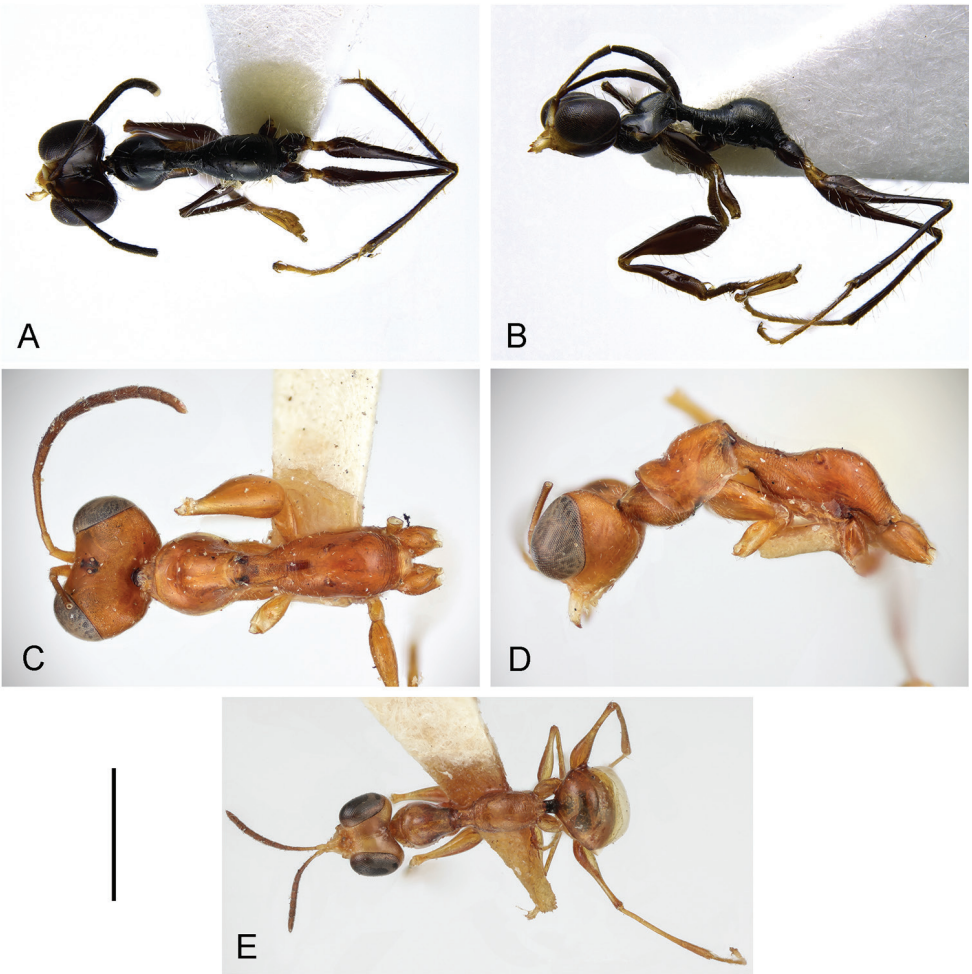

Figure 1. A, B *Gonatopus jacki* sp. n., holotype: head and mesosoma in dorsal (**A**) and lateral (**B**) view. *Gonatopus ashmeadi* holotype: head and mesosoma in dorsal (**C**) and lateral (**D**) view; *Gonatopus agropyrus* holotype in dorsal view (**E**). Scale bars: 1.38 mm (**A**);1.54 mm (**B**); 0.51 mm (**C, D**); 1.09 mm (**E**).

Material examined. Holotype: a female from the USA, Florida, Sarasota Co., Turtle Beach, 27.217°N 82.517°W ± 2 km, 5 m, 30.xii.1989, beach margin, No 2601-S, John T. Longino leg. (MOLC).

Distribution. USA.

Hosts. Unknown.

Etymology. The species is named after the collector, John T. (Jack) Longino.

Remarks. The new species is similar to *G. ashmeadi* Kieffer in Kieffer & Marshall, 1905 and *G. agropyrus* Fenton, 1921, by having head mostly brown, labial palpus bisegmented, mesoscum with no lateral pointed apophyses, meso-metapleural suture obsolete, first abdominal tergum transversely striate, protarsomere I shorter than IV, protarsomere V with lamellae situated in distal half. The main difference among *G. jacki*

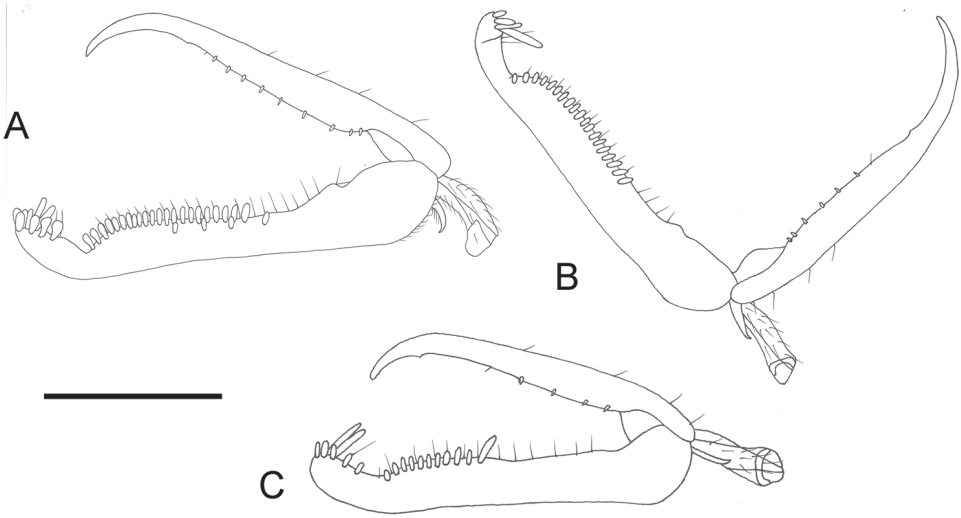

Figure 2. A *Gonatopus jacki* sp. n., chela of holotype. **B** *Gonatopus ashmeadi* Kieffer: chela of female from USA, Georgia, Spring Creek **C** *Gonatopus agropyrus* Fenton: chela of female from USA, Kentucky, Lexington. Scale bars: 0.16 mm (**A**); 0.13 mm (**B, C**).

and the other two species is in the mesoscutum shape: very slender in *G. jacki* (Fig. 1A); broader in *G.ashmeadi* (Fig. 1C) and *G. agropyrus* (Fig. 1E). The comparison of the holotypes of the above three species shows also a difference regarding the colour: mostly black in *G. jacki* (Fig. 1A, B), yellow-testaceous in *G. agropyrus* (Fig. 1E) and testaceous-ferruginous in *G. ashmeadi* (Fig. 1C, D). However, these differences are not significant, because the colour can be very variable, so that mostly black specimens are known in both *G. agropyrus* and *G. ashmeadi*. Following the description of *G. jacki*, the key to the females of the Nearctic species of *Gonatopus* group 7 published by Olmi (1993b) can be modified by replacing couplet 14 as follows:

14 Scutum very slender (Fig. 1A)..... ***G. jacki* sp. n.**
– Scutum broader (Fig. 1C, E)..... **14***

14* Protarsomere V with lamellae of approximately same length (Fig. 2B) .....
..... ***G. ashmeadi* Kieffer**
– Protarsomere V with lamellae much longer near base (Fig. 2C).....
.....***G. agropyrus* Fenton**

Conclusions

Olmi (1984, 1987, 1992, 1993a, 1993b, 1995, 2003) and Olmi and Guglielmino (2013) listed 51 *Gonatopus* from the Nearctic region. With the description of the above new species the number of species now known in the USA is 52. In comparison with the

135 species listed in Mexico (Moya Raygoza and Olmi 2010), the dryinid fauna of the USA is poorly known, as is that of Canada (18 listed species). A similar situation exists also regarding the hosts: they are known only in 26 species (Guglielmino et al. 2013).

Acknowledgments

Many thanks to John T. (Jack) Longino, University of Utah, Salt Lake City, for sending the specimen of *Gonatopus* described in the present paper. We are also grateful to Sean Brady and Karolyn Darrow for sending multifocal photos of holotypes deposited in the Smithsonian Institution, Washington, DC, USA. Many thanks to Robert S. Copeland (ICIPE, Nairobi, Kenya) for checking the English language of this paper.

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Two new species of *Ateuchus* with remarks on ecology, distributions, and evolutionary relationships (Coleoptera, Scarabaeidae, Scarabaeinae)

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Abstract

Two new species of the genus *Ateuchus* Weber are described from the region of Los Chimalapas, Oaxaca, Mexico: *A. benitojuarezi* **sp. n.** and *A. colossus* **sp. n.** A diagnosis for distinguishing these new species from the other species of this genus in North America is included. This paper is illustrated with pictures of the dorsal habitus and the male genitalia of the new species. The evolutionary relationships of the species are discussed, as well as their distribution and ecology. It is considered that the species of the genus *Ateuchus* present in North and Central America correspond to the Typical Neotropical and Mountain Mesoamerican distribution patterns.

Resumen

Describimos dos especies nuevas del género *Ateuchus* Weber, de la región de Los Chimalapas, Oaxaca, México: *A. benitojuarezi* **sp. n.** y *A. colossus* **sp. n.** Incluimos diagnosis para distinguir a estas especies nuevas del resto de especies del género presentes en Norteamérica. Presentamos ilustraciones del hábito dorsal y la genitalia masculina de las nuevas especies. Discutimos las relaciones evolutivas de las especies, así como también su distribución y ecología. Consideramos que las especies del género *Ateuchus* corresponden con los patrones de distribución Neotropical Típico y Mesoamericano de Montaña.

Keywords

Ateuchini, distribution patterns, dung beetles, Los Chimalapas, Mexican Transition Zone, Mountain Mesoamerican

Palabras clave
Ateuchini, escarabajos del estiércol, Los Chimalapas, Mesoamericano de Montaña, patrones de distribución, Zona de Transición Mexicana

Introduction

Ateuchus Weber is a dung beetle genus found in the New World. *Ateuchus* includes species of small to moderate size, oval and very convex in shape. These species normally have a bidentate clypeus, concealed scutellum, elytra with eight striae, mesosternon largely exposed, and protibia possessing three or four teeth. Most of the species present a certain degree of sexual dimorphism, since the males can present an expanded protibial spur and differences in the clypeal shape (Kohlmann 2003).

The greatest diversity of *Ateuchus* is concentrated in South America, where more than one hundred species are estimated to occur. However, the taxonomic status of several species that conform this genus is confusing and a review is required. Mexico is one of the countries where the species of the genus *Ateuchus* are best known: 14 are recorded from the country, *A. candezei* (Harold), *A. carolinae* Kohlmann, *A. chrysopyge* (Bates), *A. gershensoni* Kohlmann, *A. guatemalensis* (Bates), *A. halffteri* Kohlmann, *A. hornai* (Balthasar), *A. illaesum* (Harold), *A. klugi* (Harold), *A. laetitiae* Kohlmann, *A. perezvelai* Kohlmann, *A. rodriguezi* (Predhomme de Borre), *A. texanus* Robinson and *A. tuza* Kohlmann and Vaz-de-Mello (Kohlmann and Vaz-de-Mello in press). The objective of this article is to describe two new species of *Ateuchus* from Mexico and to discuss their possible evolutionary relationships, distributions, and ecology.

Materials and methods

Abbreviations for the collections used in this work are as follows:

CEMT Seção de Entomologia da Coleção Zoológica, Departamento de Biologia e Zoologia, Universidade Federal de Mato Grosso, Cuiabá, Brazil
CMNC Canadian Museum of Nature, Gatineau, Quebec, Canada
CNIN Colección Nacional de Insectos, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico
FSCA Florida State Collection of Arthropods, Gainesville, FL, USA
IEXA Sección G Halffter, Colección Entomológica Miguel Ángel Morón Ríos, Instituto de Ecología, A. C., Xalapa, Veracruz, Mexico
JLSHC JL Sánchez-Huerta Collection, Xalapa, Veracruz, Mexico
TAMU Texas A&M University Insect Collection, TX, USA
VMC V Moctezuma Collection, Xalapa, Mexico

For this study, the phylogenetic species concept was used. The phylogenetic species concept is classified in two distinct versions according to Zachos (2016): the monophyly version and the diagnosability version. We follow the diagnosability version (Wheeler and Platnick 2000), which defines species as the smallest aggregation of populations or lineages that is diagnosable by a unique combination of character states. All type specimens bear determination labels printed on red acid-free paper. The internal sacs and aedeagi were prepared as outlined by Moctezuma et al. (2016) and we followed the sclerite nomenclature proposed by Marchisio and Zunino (2012). Male genitalia were stored in microvials with glycerol. Measurements and pictures were taken using a Leica Z16APOA stereomicroscope and the software of the manufacturer (z-stack image capture method).

Taxonomy

***Ateuchus benitojuarezi* sp. n.**
http://zoobank.org/AAE3B380-C535-4C1D-A3D0-6EDC82170386
Figs 1, 2

Type material (**100** ♂♂, **161** ♀♀). Holotype: 1 ♂, labeled "MEXICO, Oaxaca, San Miguel Chimalapa, San Antonio, 14-X-2015, coprotrap; 16°39'39.3"N, 94°13'23.6"W, cloud forest, 1605 m, V. Moctezuma col.". Paratypes: 1 ♂, 1 ♀, same data as holotype; 1 ♂, 1 ♀, same data except "16°39'40.9"N, 94°13'25.1"W, 1611 m"; 1 ♂, same data except "16°3'38.3"N, 94°13'39.8"W, 1702 m"; 5 ♂♂, 7 ♀♀, same data except "16°39'42.5"N, 94°13'15.1"W, 1553 m"; 4 ♂♂, 8 ♀♀, same data except "16°39'41.2"N, 94°13'15.6"W, 1562 m"; 6 ♀♀, same data except "16°39'40.7"N, 94°13'19.7"W, 1593 m"; 3 ♂♂, 1 ♀, same data except "16°39'40.2"N, 94°13'21"W, 1595 m"; 1 ♂, 2 ♀♀, same data except "16°39'41.8"N, 94°13'13.9"W, 1548 m"; 1 ♀, same data except "16°39'37.5"N, 94°13'27.1"W, 1621 m"; 2 ♂♂, 3 ♀♀, same data except "16°39'41.1"N, 94°13'16.9"W, 1573 m"; 1 ♂, 1 ♀, same data except "16°39'42.5"N, 94°13'15.1"W, 1553 m"; 1 ♂, same data except "16°39'36.8"N, 94°13'29.8"W, 1636 m"; 1 ♂, same data except "16°39'36.7"N, 94°13'13.1"W, 1647 m"; 2 ♂♂, 1 ♀, same data except "03-VII-2017, 16°39'44.5"N, 94°13'14.6"W, light trap UV and metallic additives, 1550 m", J.L. Sánchez-Huerta and V. Moctezuma cols."; 1 ♀, labeled "MEXICO, Oaxaca, San Miguel Chimalapa, Benito Juárez, 8-X-2015, coprotrap, 16°43'58.4"N, 94°12'17"W, cloud forest, 1356 m, V. Moctezuma col."; 1 ♀, same data except "16°44'6.2"N, 94°12'20.6"O, 1374 m"; 5 ♂♂, 7 ♀♀, same data except "16°44'10.9"N, 94°12'17.5"W, 1389 m"; 5 ♀♀, same data except "16°44'5.9"N, 94°12'20.5"W, 1384 m"; 5 ♀♀, same data except "16°43'58.6"N, 94°12'22.8"W, 1341 m"; 3 ♀♀, same data except "16°44'12.3"N, 94°12'17.7"W, 1400 m"; 1 ♂, 3 ♀♀, same data except "16°44'10.9"N, 94°12'17.5"W, 1389 m"; 1 ♂, 3 ♀♀, same data except "16°44'7.1"N, 94°12'20.4"W, 1373 m"; 1 ♀, same data except "16°44'12.3"N, 94°12'17.7"W, 1400 m"; 1 ♂, 1 ♀, same data except "16°44'2.4"N,

Figure 1. *Ateuchus benitojuarezi*, dorsal habitus.

94°12'20.4"W, 1372 m"; 3 ♂♂, 11 ♀♀, same data except "16°43'53.9"N, 94°12'21"W, 1338 m"; 1 ♂, 1 ♀, same data except "16°44'13.6"N, 94°12'18.1"W, 1405 m"; 2 ♀♀, same data except "16°43'54"N, 94°12'18.4"W, 1347 m"; 1 ♀, same data except "16°43'57.3"N, 94°12'23"W, 1344 m"; 1 ♀, same data except "16°44'23.3"N, 94°12'19.3"W, 1275 m";

2 ♂♂, 4 ♀♀, same data except "16°43'59.4"N, 94°12'22.3"W, 1342 m"; 19 ♂♂, 16 ♀♀, same data except "16°44'30.6"N, 94°12'20"W, 1269 m"; 1 ♂ same data except "16°44'22.1"N, 94°12'19.9"W, 1293 m"; 2 ♀♀, same data except "16°44'0.5"N, 94°12'22.1"W, 1360 m"; 3 ♀♀, same data except "16°44'4.8"N, 94°12'19.9"W, 1382 m"; 19 ♂♂, 34 ♀♀, same data except "16°44'29.3"N, 94°12'20.1"W, 1275 m"; 9 ♂♂, 8 ♀♀, same data except "16°44'28.1"N, 94°12'20.9"W, 1292 m"; 1 ♀, same data except "9-X-2015, 16°44'22.5"N, 94°13'4.8"W, 1173 m"; 1 ♂, same data except "16°44'21.9"N, 94°13'1.9"W, 1140 m"; 2 ♂♂, 2 ♀♀, same data except "16°44'35.6"N, 94°13'17.5"W, 1113 m"; 3 ♀♀, same data except "16°44'17.1"N, 94°13'4.5"W, 1175 m"; 2 ♂♂, 1 ♀, same data except "16°44'15.8"N, 94°13'4.1"W, 1180 m"; 1 ♂, same data except "16°44'40.7"N, 94°13'17.4"W, 1110 m"; 2 ♂♂, same data except "16°44'26.9"N, 94°13'9"W, 1130 m"; 1 ♀, same data except "16°39'40.1"N, 94°13'22.4"W, 1599 m"; 1 ♂, 1 ♀, same data except "16°44'36.9"N, 94°13'17.3"W, 1112 m"; 1 ♂, 2 ♀♀, same data except "16°44'22"N, 94°13'3.3"W, 1152 m"; 1 ♀, same data except "16°44'14.6"N, 94°13'4.7"W, 1190 m"; 2 ♂♂, 4 ♀♀, same data except "16°44'11.5"N, 94°13'6.5"W, 1204 m"; 1 ♂, 1 ♀, same data except "16°44'16.3"N, 94°13'16.3"W, 1112 m"; 1 ♂, 2 ♀♀, same data except "16°44'27.1"N, 94°13'11.1"W, 1137 m"; 1 ♂, 1 ♀, same data except "16°44'27.3"N, 94°13'12.5"W, 1133 m"; 1 ♀, labeled "MEXICO, Oaxaca, Santa María Chimalapa, Cerro Azul, 19-X-2015, coprotrap, 16°51'37.9"N, 94°43'32.5"W, subtropical rainforest, 382 m, V. Moctezuma col."; 1 ♀, same data except "16°51'32.8"N, 94°43'30.8"W, 392 m".

Type deposition. Holotype and 10 ♂♂, 10 ♀♀ paratypes will be deposited in IEXA. Paratypes will be deposited in the following collections: CEMT (10 ♂♂, 10 ♀♀), CMNC (10 ♂♂, 10 ♀♀), CNIN (10 ♂♂, 10 ♀♀), FSCA (10 ♂♂, 10 ♀♀), JLSHC (10 ♂, 10 ♀), TAMU (10 ♂♂, 10 ♀♀), VMC (rest of paratypes).

Description. Holotype male, total length 7.9 mm, maximum elytral width 4.5 mm. Body elongate-oval and convex, dorsum and venter glossy black with cupreous red and green sheen, clypeal margin dark reddish brown. Clypeal margin slightly V-shaped, with rounded teeth, lateral margin of head arcuate. Clypeal surface with coarse and well-spaced punctures, frons surface finely punctate with punctures of regular size, well-impressed clypeogenal suture, genae finely punctate. Pronotum strongly punctate, with coarse punctures of regular size, midline impressed on posterior half of pronotum, anterior pronotal margin incomplete. Pronotal lateral angles acute. Center of pronotal posterior margin with a line of coarse and large punctures. Proepisternum and proepimeron coarsely wrinkled. Elytral surface smooth, shiny, and punctate. Striae well-impressed, becoming deeply impressed on elytral apex. Well-impressed strial punctures, slightly wider than striae. Interstriae flat. Pygidium strongly convex and finely punctate. Pygidium dark reddish brown with green metallic sheen on apex. Protibia tridentate, apical spur expanded into a rectangular shape. Mesotibia with two apical spiniform spurs. Metatibia with apical spur small and spiniform. Ventral apical half of profemur finely punctate, but punctures becoming coarse along posterior margin of profemur. Ventral surface of meso- and metafemur minutely punctate. Internal sac of the aedeagus with two hook-shaped and one filiform copulatrix lamellae; three accessory sclerites (one large canoe-shaped, one small and flat, and one bispiniform); welldeveloped raspule.

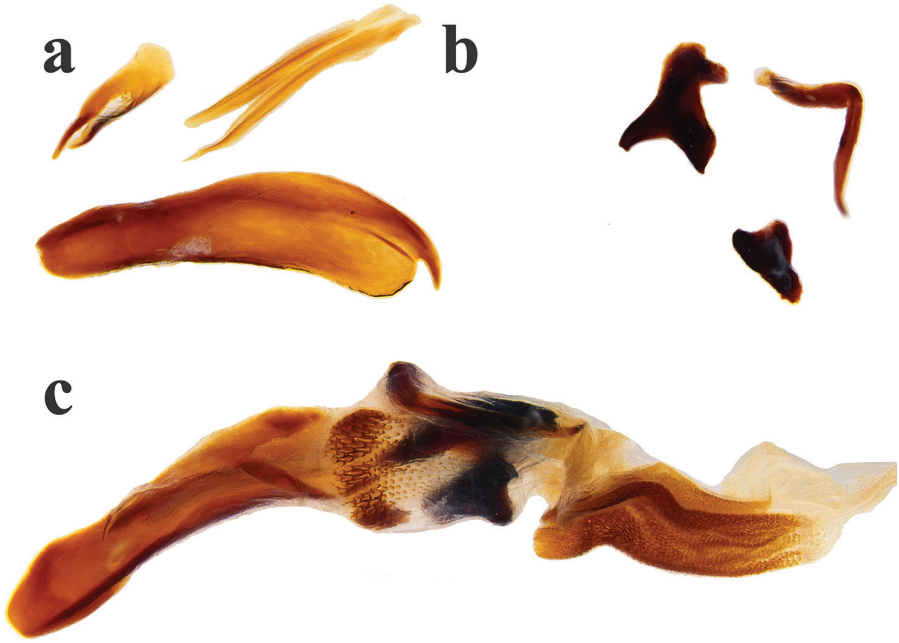

Figure 2. *Ateuchus benitojuarezi*: **a** dissected accessory lamellae **b** dissected copulatrix lamellae and raspule **c** "intact" internal sac of the aedeagus.

Female. Differs from the male by protibia with apical spur expanded into a slightly irregular oval shape, clypeal teeth less rounded and more acute, last abdominal sternite broader and pygidium less convex.

Variation (among 30 randomly selected paratypes). Mean total length 8.1 mm (7.5–8.7 mm). Mean elytral width 4.5 mm (4.2–4.9 mm). Type series color is uniform.

Etymology. We dedicate this species to Benito Juárez, the first indigenous president of Mexico. The name also refers to one of the localities where the type series was collected.

Geographical distribution. The type series was collected in three sites of the region of Los Chimalapas, in the east of the state of Oaxaca: San Antonio, Benito Juárez, and Cerro Azul (Fig. 3).

Ecology. *Ateuchus benitojuarezi* inhabits the cloud forest and the subtropical rainforest, within an elevational range of 380 to 1700 m asl. This species was collected using pitfall traps baited with human dung and with a light trap (mercury vapor and UV light).

Diagnosis. *Ateuchus benitojuarezi* is distinguished from other *Ateuchus* present in Mexico by the following combination of characters: dorsum glossy black with red and green cast, pronotum strongly punctate, anterior margin of pronotum incomplete, posterior pronotal margin with a line of coarse and large punctures, elytral surface smooth and the male genitalia includes one large canoe-shaped lamellae with an apical claw (Fig. 2a).

Remarks. *Ateuchus benitojuarezi* seems to be closely related to *A. guatemalensis* (Fig. 4), but the clypeal margin is slightly V-shaped in *benitojuarezi* males (broadly V-shaped in *guatemalensis* males) and the large canoe-shaped accessory lamellae of *benitojuarezi* shows an apical claw (this apical claw is missing in *guatemalensis*; Fig. 5a).

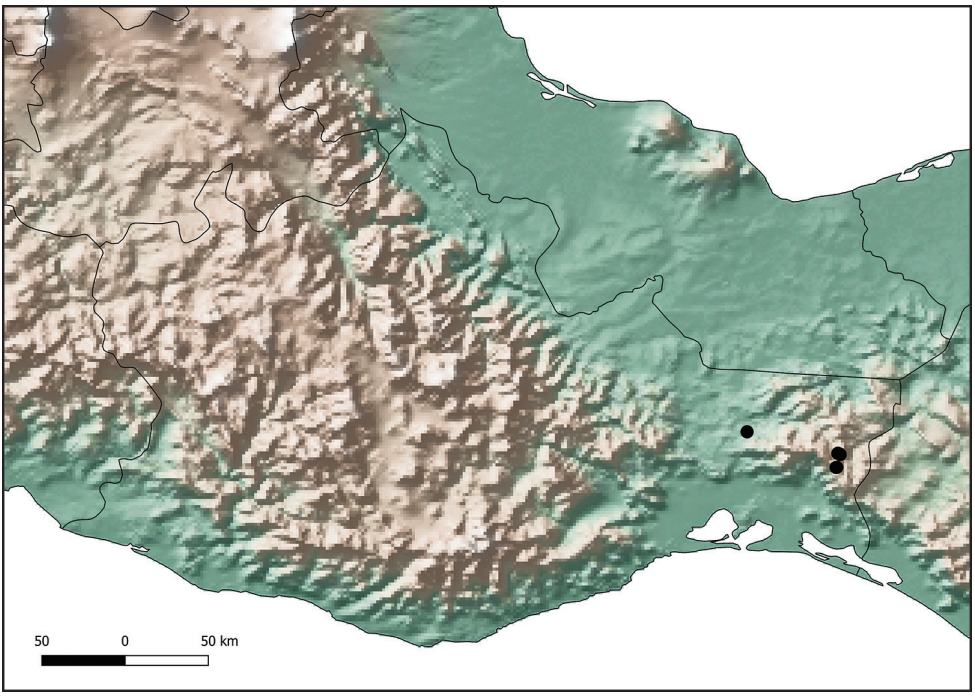

Figure 3. Distribution of *Ateuchus benitojuarezi* (black dots).

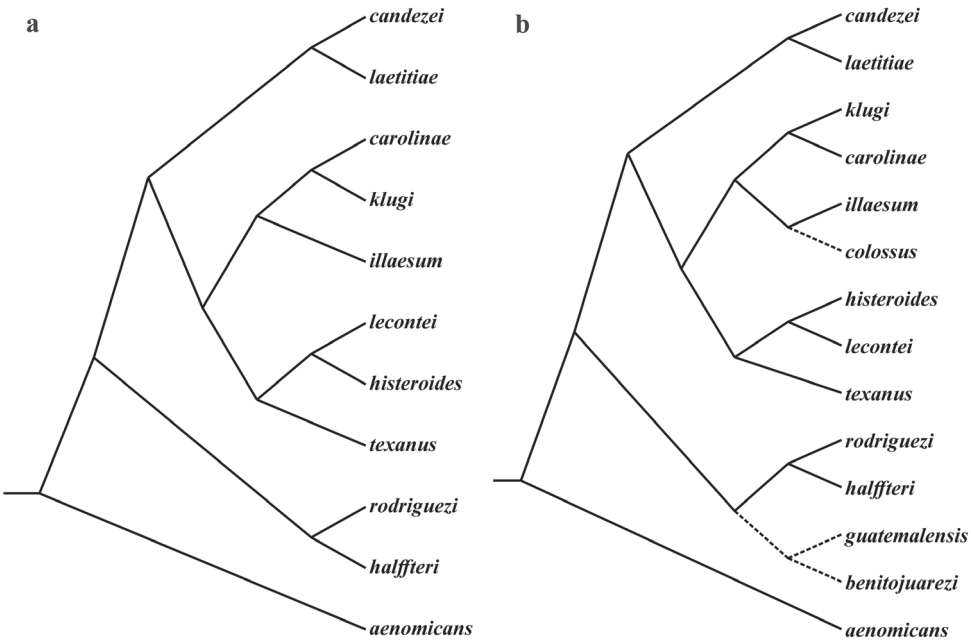

Figure 4. a Wagner (cladistic) analysis for *Ateuchus* of North America, based on morphological characters (redrawn from Kohlmann 1984, Kohlmann and Halffter 1988) **b** Same cladogram modified to include putative relationships of *A. benitojuarezi, A. colossus and A. guatemalensis* (dotted lines).

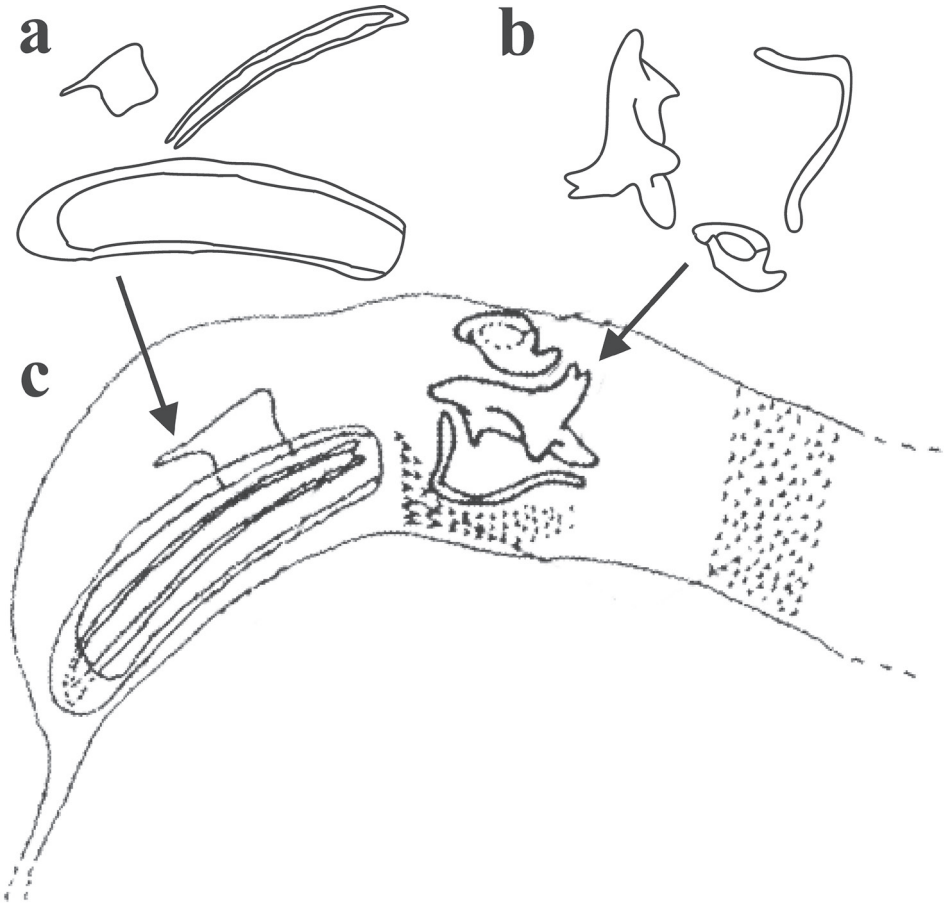

Figure 5. *Ateuchus guatemalensis* (redrawn from Kohlmann 2000, in order to allow comparison with those of *A. benitojuarezi*): **a** dissected accessory lamellae **b** dissected copulatrix lamellae **c** "intact" internal sac of the aedeagus.

***Ateuchus colossus* sp. n.**
http://zoobank.org/FB4A95B3-55E9-449C-A274-050AC7460511
Figs 6, 7

Type material (20 ♂♂, 21 ♀♀). Holotype: 1 ♂ labeled "MEXICO, Oaxaca, San Miguel Chimalapa, San Antonio, 14-X-2015, coprotrap, 16°39'39.3"N, 94°13'23.6"W, cloud forest, 1605 m, V. Moctezuma col.". Paratypes: 1 ♂, same data as holotype; 3 ♀♀ same data except "16°39'40.9"N, 94°13'25.1"W, 1611 m"; 6 ♂♂, 3 ♀♀, same data except "16°39'41.8"N, 94°13'13.9"W, 1548 m"; 1 ♂ same data except "16°39'42.5"N, 94°13'15.1"W, 1553 m"; 5 ♂♂, 5 ♀♀, same data except "16°39'41.2"N, 94°13'15.6"W, 1562 m"; 2 ♂♂, same data except "16°39'36.5"N, 94°13'35.1"W, 1665 m"; 1 ♀, same data except "16°39'40.1"N, 94°13'22.4"W, 1599 m"; 1 ♂, 2 ♀♀, same data except "16°39'40.2" N, 94°13'21"W, 1595 m"; 1 ♀, same data except "16°39'40.7" N, 94°13'19.7"W, 1593

Figure 6. *Ateuchus colossus*, dorsal habitus.

m"; 1 ♂, same data except "16°39'36.8"N, 94°13'29.8"W, 1636 m"; 2 ♂♂, same data except "16°39'42.5"N, 94°13'15.1"W, 1553 m"; 1 ♀, same data except "16°39'37.5"N, 94°13'27.1"W, 1621 m"; 2 ♀♀, same data except "16°39'41.1"N, 94°13'16.9"W,

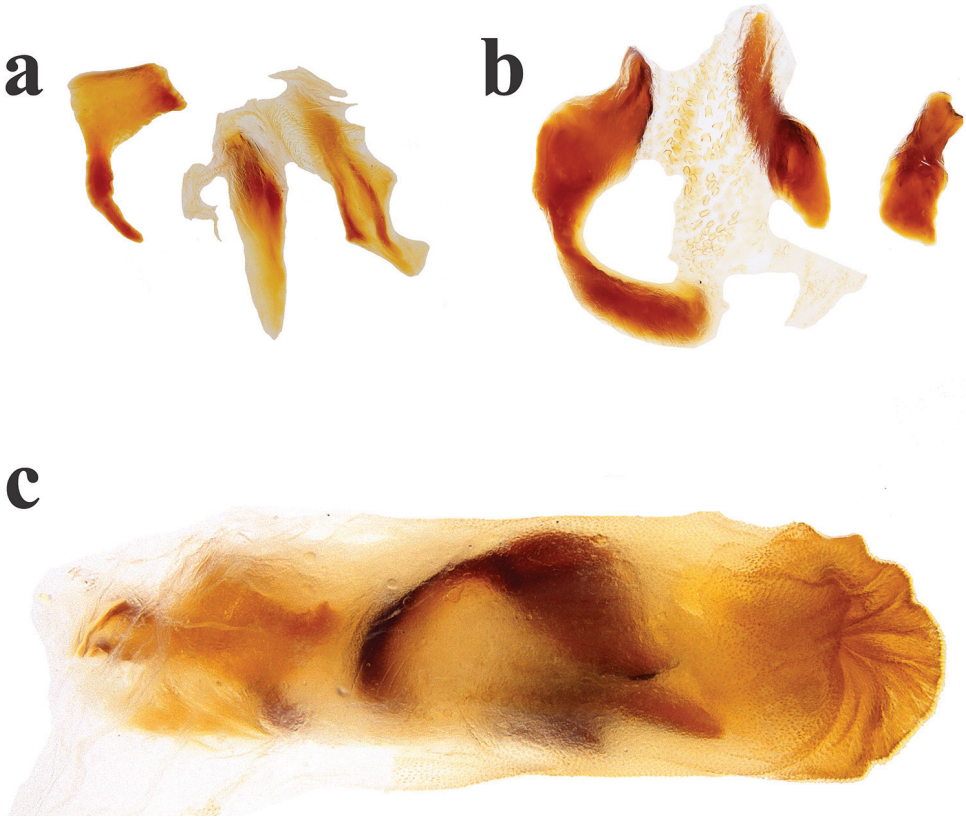

Figure 7. *Ateuchus colossus*: **a** dissected accessory lamellae **b** dissected copulatrix lamellae and raspule **c** intact internal sac of the aedeagus.

1573 m"; 2 ♀♀, labeled "MEXICO, Oaxaca, San Miguel Chimalapa, Benito Juárez, 24-IX-2015, coprotrap, 16°42'38.2"N, 94°6'40.6"W, pine-oak, 1271 m, V. Moctezuma col."; 1 ♀, labeled "MEXICO, Oaxaca, Santa María Chimalapa, López Portillo, 25-IX-2015, coprotrap, 16°40'28.6"N, 94°3'56.6"W, pine forest, 1219 m, V. Moctezuma col.".

Type deposition. Holotype and 2 ♂♂, 2 ♀♀ paratypes will be deposited in IEXA. Paratypes will be deposited in the following collections: CEMT (2 ♂♂, 2 ♀♀), CMNC (2 ♂♂, 2 ♀♀), CNIN (2 ♂♂, 2 ♀♀), FSCA (2 ♂♂, 2 ♀♀) JLSHC (2 ♂♂, 2 ♀♀), TAMU (2 ♂♂, 2 ♀♀), VMC (rest of paratypes).

Description. Holotype male, total length 10.7 mm, maximum elytral width 5.6 mm. Body elongate-oval and convex, dorsum and venter glossy black without metallic sheen, clypeal margin dark reddish brown. Clypeal margin slightly V-shaped, with rounded tooth, lateral margin of head arcuate. Clypeal surface with coarse punctures separated by ≈1-2 diameters, frons surface finely punctate with punctures becoming almost unapparent near frons center, well-impressed clypeogenal suture, genae finely punctate. Pronotum smooth but minutely punctate, midline weakly impressed on posterior half of pronotum, anterior pronotal margin complete and well impressed. Ante-

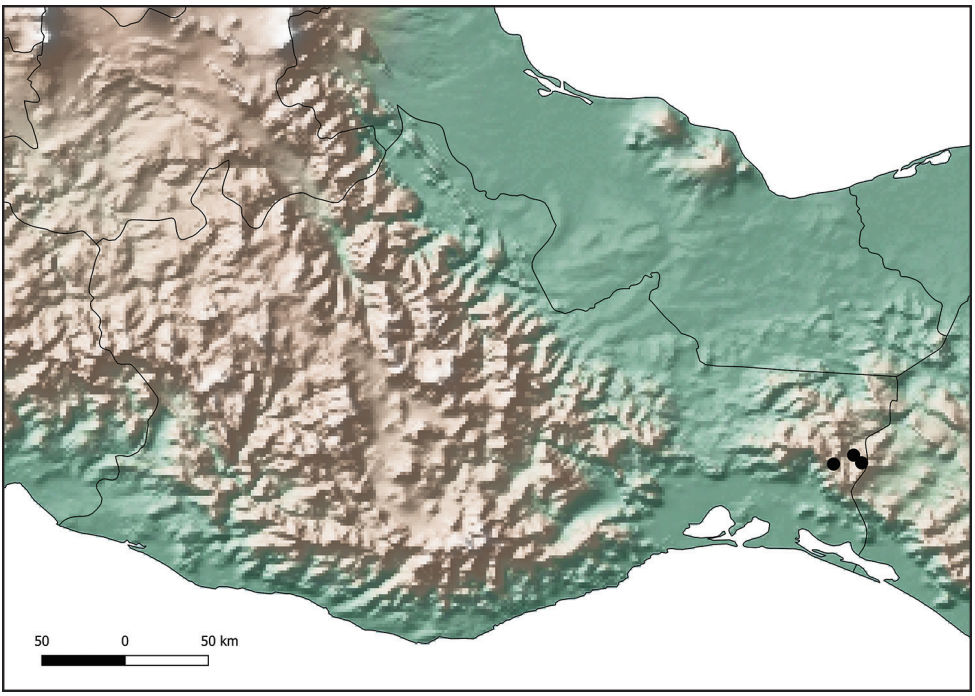

Figure 8. Distribution of *Ateuchus colossus* (black dots).

rior pronotal angles very acute and projecting anteriorly. Center of pronotal posterior margin with a line of coarse and well-impressed punctures. Proepisternum coarsely wrinkled, proepimeron finely wrinkled. Elytral surface smooth, shiny, and minutely punctate. Striae well-impressed, becoming deeply impressed on elytral apex. Well-impressed strial punctures, slightly wider than striae. Interstriae flat. Pygidium strongly convex and finely punctate. Pygidium dark reddish brown with green metallic sheen on apex. Protibia tridentate, apical spur expanded into a slightly irregular oval shape. Mesotibia with two apical spiniform spurs. Metatibia with apical spur large and spiniform. Ventral apical half of profemur finely and scarcely punctate, but punctures becoming coarse along posterior margin of profemur. Ventral surface of meso- and metafemur minutely punctate. Internal sac of the aedeagus with three hook-shaped copulatrix lamellae, two small and one large; three accessory lamellae; raspule not well developed.

Female. Differs from the male by coarsely punctate head, protibia with acute and slender spur that bends apically, last abdominal sternite broader and pygidium less convex.

Variation (among 30 randomly selected paratypes). Mean total length 9.9 mm (8.9–10.7 mm). Mean elytral with 5.5 mm (5.2–5.9 mm). Type series color is uniform.

Etymology. From the Latin adjective *colossus* that derives from the Greek noun *κολοσσός* (kolossos = gigantic statue), referring to the fact that this is the largest species of the genus *Ateuchus* in North America known to date.

Distribution. The type series was collected in the region of Los Chimalapas, in the east of the state of Oaxaca (Fig. 8).

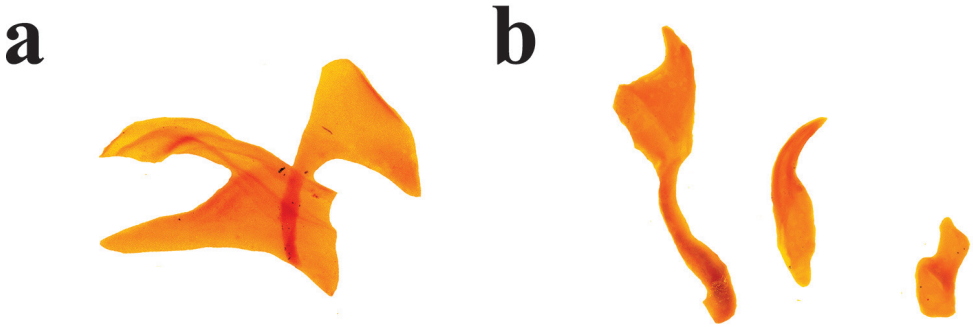

Figure 9. *Ateuchus illaesum*: **a** dissected accessory lamellae **b** dissected copulatrix lamellae.

Ecology. This species inhabits cloud and temperate forests (pine and pine-oak), within the elevational range 1219 to 1665 m a.s.l. This species was collected using pitfall traps baited with human excrements.

Diagnosis. This species is distinguished from other North American species by its large body size (at 8.9–10.7 mm, it is the largest *Ateuchus* species in the region), anterior pronotal angles very acute and produced anteriorly, anterior pronotal margin complete, pronotal posterior margin with a line of coarse punctures, and male genitalia with three hook-shaped copulatrix lamellae, three accessory lamellae and ill-developed raspule.

Remarks. *Ateuchus colossus* seems to be closely related to *A. illaesum* (Fig. 4), but they can be distinguished by differences in size (*colossus* is larger), the shape of the anterior pronotal angles (very acute and produced anteriorly on *colossus*), accessory and copulatrix lamellae (Figs 7, 9).

Discussion

The most recent key for identification of *Ateuchus* species of North America was presented by Kohlmann (1984). We decided not to include a key for identification, since a new key for identification is currently in press (Kohlmann and Vaz-de-Mello in press).

We hypothesized that *A. benitojuarezi* is closely related to *A. guatemalensis* and that they represent an evolutionary lineage, since both species present similarities in the general morphology of the sclerites of the internal sac: two hook-shaped and one filiform copulatrix lamellae, and a large canoe-shaped accessory lamella. This combination of shared characters is unique among the known species of North and Central America. Other shared characters of the external morphology are dorsal green sheen, midline impressed on posterior half of pronotum and anterior pronotal margin incomplete. Despite these similarities, *A. benitojuarezi* can be easily distinguished from its sister species by body size (smaller in *guatemalensis,* 5.2–6.7 mm), pronotum punctures, clypeal margin and differences in the sclerites of the internal sac of the aedeagus (Kohlmann 2000).

It has not been possible for us to hypothesize about the evolutionary relationships of *A. colossus* by studying its external morphology. The species of this genus present

great morphological homogeneity (Kohlmann 1984). However, the sclerites of the internal sac of the aedeagus of *A. colossus* present similarities to those of *A. illaesum* and therefore these two species could be closely related and form part of an evolutionary lineage. *Ateuchus colossus* possesses notable diagnostic characters that make its identification relatively easy, since it is the largest species of North America and has very acute and apically projected anterior pronotal angles.

In order to determine the evolutionary relationships of the *Ateuchus* species present in North and Central America, it is necessary to conduct new phylogenetic studies. The most recent study that presents a hypothesis of evolutionary relationships is based on a cladistic analysis using morphological characters (Kohlmann 1984, Kohlmann and Halffter 1988). However, the number of species described in the region has since increased. As a consequence of the morphological homogeneity presented by the genus *Ateuchus*, future implementation of molecular phylogenetic analysis would be of great interest.

The genus *Ateuchus* is Neotropical in origin, and is thought to have extended northwards from South America, following the low tropical areas, at the time at which the Panama land bridge was reestablished (Kohlmann and Halffter 1988, Morrone and Halffter 2017). However, the exact period during which the closing of Central America permitted the migration of *Ateuchus* (Pliocene *vs*. Middle Miocene), as well as other groups of organisms, is still the subject of debate (Montes et al. 2015, O'Dea et al. 2016). On entering the Mexican Transition Zone, *Ateuchus* derived in at least four evolutionary lines that coincide with distinct geographic zones: The Pacific slope (*halffteri-rodriguezi*), Mesoamerica (*candezei-laetitiae*), the mountains of central Mexico (*carolinae-illaesum-klugi*) and the Gulf of Mexico coastal plain (*histeroides-leconteitexanus*; Kohlmann 1984, Kohlmann and Halffter 1988).

Ateuchus guatemalensis was not included in the cladistic analysis of the *Ateuchus* species of Mexico (Kohlmann 1984). Kohlmann (1984) states that this species corresponds to the phyletic line of the Pacific. Due to the fact that the lineage of the Pacific lacks the putative synapomorphies of *benitojuarezi-guatemalensis* (a filiform copulatrix lamellae and a large canoe-shaped accessory lamellae), we hypothesized that they correspond to distinct but closely related lineages.

Ateuchus benitojuarezi (Los Chimalapas, cloud forest and subtropical rainforest) and *A. guatemalensis* (Sierra Madre de Chiapas and Central American Mountain Nucleus, cloud forest) fit with the Mountain Mesoamerican distribution pattern (Kohlmann 2000, Halffter and Morrone 2017). This distribution pattern corresponds to typical taxa of the mountain forests of Central America and the south of Mexico (cloud and pine-oak forests), which evolved in the Central American Mountain Nucleus and have ancient South American affinities (Halffter and Morrone 2017). Taking its geographic distribution and ecological affinities as a reference, *A. colossus* also fits with the Mountain Mesoamerican distribution pattern.

Kohlmann and Halffter (1988) state that the distribution of the genus *Ateuchus* corresponds to the Typical Neotropical distribution pattern, although they recognize a similarity with the distribution of various species with the Mountain Mesoamerican distribution pattern. In that study, these authors argue that the penetration of *Ateuchus*

into the Central American Mountain Nucleus corresponds to the Pliocene-Pleistocene period. It is not possible to temporally calibrate the cladistic analysis on which they base their conclusions, for which reason this assumption has not been corroborated. It is therefore necessary to conduct molecular phylogenetic or phylogeographic analyses in order to estimate the geologic time in which the penetration and radiation of *Ateuchus* took place in the Mexican Transition Zone, and thus adequately determine the biogeographic affinities of the species of the genus.

In a preliminary manner, we propose the following species as members of the Mountain Mesoamerican distribution pattern (Kohlmann 1981, 1984, 1996–1997, 2000, 2003, Kohlmann and Halffter 1988): *A. carolinae* (Trans-Mexican Volcanic Belt and Sierra Madre del Sur; oak forest and tropical dry forest), *A. fetteri* Kohlmann (Costa Rican Pacific mountains slope, cloud forest and tropical rainforest), *A. gershensoni* (Sierra Madre de Chiapas, cloud forest), *A. ginae* Kohlmann (Central American mountains Pacific slope, cloud forest), *A. hendrichsi* Kohlmann (Costa Rican Pacific mountains, cloud forest and subtropical rainforest), *A. illaesum* (Sierra Madre Oriental and Gulf of Mexico slope; cloud forest, tropical forest, temperate pine-oak and oak forest), *A. klugi* (Trans-Mexican Volcanic Belt and Gulf of Mexico slope; tropical forest, temperate pine-oak and oak forest), and *A. zoebischi* (Costa Rican Atlantic Volcanic slopes, cloud forest and subtropical rainforest).

Little information is available regarding the geographic area of distribution of *A. benitojuarezi* and *A. colossus*. To date, these species have only been collected in the region of Los Chimalapas, in the east of the state of Oaxaca. However, given the habitat preferences of these two new species, they may also be distributed in the states of Chiapas and Veracruz. The two new species are found in sympatry with *A. candezei*, *A. rodriguezi* and an unidentified species of *Ateuchus* (unpublished data).

Little information is available regarding the natural history of *Ateuchus*. They are insects of apparently nocturnal habit, with a broad ecological spectrum. Adults of the genus feed mainly on different types of dung and, to a lesser extent, on carrion, fungi and decomposing plants. Some species present a degree of association with vertebrate burrows and detritus of ants of the genus *Atta* (Navarrete-Heredia 2001, Kohlmann 2003, Génier 2015). To date, we have only suggested the coprophagous habit of *A. benitojuarezi* and *A. colossus*, and a certain degree of attraction to light in *A. benitojuarezi*, since no collections have been made with carrion-baited traps in the region of origin of the two new species. It is unknown whether these species may also be associated with ant detritus. We have not recorded interactions between these species and the burrows of vertebrates; however, in the region of study, pocket gopher burrows are inhabited by *Ateuchus* sp.

Finally, we recommend the use of multifocal pictures in order to illustrate the genitalia and external morphology of the species in future descriptions or redescriptions. We consider it important to illustrate the internal sac of the aedeagus, presenting its components dissected and separated, since this allows greater clarity for comparisons and species identifications. As exemplified in this and previous studies (Moctezuma and Halffter 2017, Génier 2015, Génier and Moretto 2017), this technology allows detailed visualization of the structures of the internal sac of the aedeagus as well as the aedeagus itself, facilitating the identification of taxa of great morphological homogeneity, as is the case of *Ateuchus*.

Acknowledgments

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RESEARCH ARTICLE

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Revision of the Afrotropical genus *Ivondrovia* Shenefelt & Marsh, 1976 with description of a new species (Hymenoptera: Braconidae: Doryctinae)

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Abstract

A revision of the small Afrotropical holcobraconine genus *Ivondrovia* Shenefelt & Marsh, 1976 (Doryctinae) is provided. A new species from Kenya, *Ivondrovia grangeri* **sp. n.**, is described and illustrated. The illustrated redescriptions of the genus *Ivondrovia* and its type species *Lophogaster seyrigi* Granger, 1949 are given. The two known species of this genus are keyed.

Keywords

Descriptions, Doryctinae, Holcobraconini, key to species, *Lophogaster*, parasitoid

Introduction

The doryctine genus *Ivondrovia* Shenefelt & Marsh, 1976 was originally described from Madagascar by Granger (1949) as *Lophogaster* Granger, 1949 (a primary homonym for *Lophogaster* Sars, 1857 of Crustacea) only containing its type species, *L. seyrigi*

Granger, 1949. In the World Catalogue of Braconidae, Shenefelt and Marsh (1976) subsequently changed this preoccupied name to *Ivondrovia*. This taxon was originally included by Granger (1949) in the subfamily Odontobraconinae which is now regarded as the tribe Holcobraconini within the braconid subfamily Doryctinae (Belokobylskij 1992; Belokobylskij et al. 2004; Zaldívar-Riverón et al. 2008).

For the reclassification of subfamily Doryctinae, Belokobylskij (1992) examined the holotype of *Ivondrovia* type species, *L. seyrigi*, and classified *Ivondrovia* within the monotypic subtribe Ivondroviina belonging to the tribe Holcobraconini. The Ivondroviina was characterized by the following combination of characters: hind coxa simple (without dorsal projections); occipital carina and frons keel absent; propodeum with distinct medio-posterior areola and basal carinae but without total foveolate sculpture; first flagellar segment of antenna not longer than second one; recurrent vein (1m-cu) of fore wing postfurcal in comparison with the first radiomedial vein (2RS); radial vein (RS) of hind wing arising from basal vein (1r-m) and rather far from costal vein (SC+R); second metasomal tergite long medially and laterally and very short sublaterally.

The biology of *Ivondrovia* is still unknown. However, since the majority of the Doryctinae are known as ectoparasitoids of bark boring and xylophagous beetle larvae, and several holcobraconine species belonging to the genera *Zombrus* Marshall, 1897 and *Odontobracon* Cameron, 1887 were reared from large Capricorn beetle larvae, it is likely that species of *Ivondrovia* also infest larvae of the beetle family Cerambycidae for their development.

During ongoing work on the molecular phylogeny of the tribe Holcobraconini, the authors discovered a second new species of *Ivondrovia* from Kenya. Here we describe this new species and provide a key for determination of the two known species of *Ivondrovia*.

Materials and methods

The terminology employed for morphological features and measurements follows Belokobylskij and Maetô (2009). The wing venation nomenclature follows Belokobylskij and Maetô (2009), with Sharkey and Wharton (1993) terminology shown in parentheses. Specimens were examined using a MC–2 stereomicroscope. Photographs were taken with a Leica IC 3D digital camera mounted on a Leica MZ16 microscope and using the Leica Application Suite imaging system at the Museum and Institute of Zoology, Warsaw, Poland. The photograph images were enhanced and plate was composed using Adobe Photoshop.

The specimens examined in this study are deposited in the following collections: Colección Nacional de Insectos, Instituto de Biología, Universidad Nacional Autónoma de México (**UNAM**), Muséum National d'Histoire Naturelle, Paris, France (**MNHN**), and Zoological Institute of the Russian Academy of Sciences, St Petersburg, Russia (**ZISP**).

Taxonomy

Genus *Ivondrovia* Shenefelt & Marsh, 1976

Lophogaster Granger, 1949: 93.
Ivondrovia Shenefelt & Marsh 1976: 1364; Belokobylskij 1992: 912; Yu et al. 2012.

Type species. *Lophogaster seyrigi* Granger, 1949.

Description. *Head* (Figs 3–6, 22–25), not depressed, high, transverse. Ocelli arranged in slightly obtuse triangle. Frons slightly concave, with low double longitudinal carinae in anterior third (between ocellar sockets), slightly convex medially. Eyes glabrous. Occipital carina completely absent; occiput medio-dorsally with distinct, short, and divergent postero-laterally after short base hook (Fig. 4). Malar suture absent. Clypeus slightly convex, with distinct and rather long lower flange, almost entirely delineated from face by shallow or very shallow furrow. Hypoclypeal depression medium size and subrounded. Postgenal bridge very narrow. Maxillary palpus rather long (Fig. 2), 6-segmented, its sixth (apical) segment almost as long as fifth segment, third segments slightly widened and without projection in lower margin; labial palpus (Fig. 2) short, 4-segmented, its second segment slightly thickened, third segment not shortened, 0.8 times as long as fourth segment. Antennae weakly setiform. Scape of antenna (Figs 7, 26) wide and rather short, without apical lobe or basal constriction, with deep emargination in inner upper margin, its ventral margin (lateral view) not longer than dorsal margin. First flagellar segment subcylindrical, on outer side straight, almost as long as second segment.

Mesosoma (Figs 8, 9, 28, 29) not depressed. Neck of prothorax short. Pronotum dorsally weakly convex, its anterior flange short and curved upwards; pronope absent, pronotal carina distinct and slender, placed submedially on pronotum (dorsal view). Propleural dorsoposterior flange long and partly medially wide. Mesoscutum highly and convex-roundly elevated above pronotum. Median lobe of mesoscutum without median longitudinal furrow and anterolateral corners. Notauli deep and complete. Tegula (Fig. 27) distinctly widened distally, convex along outer margin. Prescutellar depression (scutellar sulcus) long and deep, with one high median carina. Scuto-scutellar suture distinct. Scutellum almost flat, with weak lateral carinae. Metanotum without median longitudinal carina. Sternaulus (precoxal sulcus) very shallow, narrow, long, straight, smooth. Prepectal carina distinct and complete, rather wide ventrally, prolonged laterally till upper margin of sternaulus. Postpectal carina absent. Metapleural flange long, wide, subtriangular, rounded apically. Propodeum with areas distinctly delineated by carinae, mainly smooth, with high sublateral carinae; lateral tubercles indistinct, propodeal bridge absent. Propodeal spiracles rather big and bean-shape. Metapleural suture very shallow.

Wings (Figs 12, 14–16, 31–33). Pterostigma of fore wing rather narrow. Radial vein (r) arising distinctly before middle of pterostigma. Radial (marginal) cell distinctly shortened. Both radiomedial veins (2RS and r-m) present. Second radiomedial (submarginal)

cell medium length. First (r) and second (3RSa) radial abscissae forming an obtuse angle. Recurrent vein (1m-cu) slightly postfurcal or almost interstitial. Nervulus (1cu-a) postfurcal. Discoidal (first discal) cell petiolate anteriorly, petiole (1RS) not long and slightly thickened. Parallel vein (2CUb) arising from posterior 0.2 of apical margin of brachial (second subdiscal) cell. Brachial (second subdiscal) cell closed postero-apically by short, sclerotised and slightly inclivous brachial vein (2cu-a). Transverse anal veins (1a and 2a) absent. Hind wing with three hamuli (Fig. 32). First abscissa of costal vein (C+Sc+R) long, 0.8 times as long as second abscissa (SC+R); first abscissa (C+Sc+R) not divided apically on two branches. Radial vein (RS) arising from basal vein (1r-m) rather far from costal vein (SC+R). Radial (marginal) cell distinctly narrowed posteriorly, closed before apex of wing, without additional transverse vein (r). Medial (basal) cell not widened towards apex, subparallel-sided in apical half, 12.5 times longer than wide, 0.5 times as long as hind wing. Nervellus (cu-a) present, slightly sinuate. Submedial (subbasal) cell long. First abscissa of mediocubital vein (M+CU) 0.9–1.0 times as long as second abscissa (M) (till basal vein (1r-m)). Recurrent vein (m-cu) strongly antefurcal, very long, strongly curved in posterior 0.7 towards apex of wing, divergent apically with medial vein (2M).

Legs. Fore femur thick and short. Fore tibia with numerous short and thick spines arranged in wide vertical stripe (Figs 11, 30). Fore tarsus 1.5–1.6 times longer than fore tibia. Segments of middle tarsus short. Middle tibiae thick, with almost single line of thick spines. Hind coxa (Fig. 13) rather wide and short, without basoventral tooth and corner, dorsally without any processes or teeth, but distinctly convex. Fore and middle femora with low dorsal protuberances; hind femur without dorsal protuberance, thick. Hind tibia thick. Hind tibial spurs long, almost straight. Basitarsus of hind tarsus approx. half as long as second-fifth segments combined. Claws large, short, strongly curved, simple.

Metasoma (Figs 17–19, 34, 37, 38). First tergite sessile, short, and wide, strongly widened subbasally. Acrosternite of first segment short, 0.15 times as long as first tergite. Dorsope of first tergite small; basolateral lobes present, narrow and directed below; spiracular tubercles absent, spiracles situated in basal 0.3 of tergite; with distinct thick and slightly convergent posteriorly sub-lateral carinae and wide median carinae formed from two carinae curvedly fused in basal fifth of tergite. Second tergite with deep, wide, short, slightly divergent posteriorly and fused with second suture lateral furrows; these furrows and second suture medially define a large and leaf-shaped median area; additionally, second tergite in basal half with sub-triangular area and slightly separated by shallow or considerably shallow furrows. Second suture deep, rather wide, very strongly curved medially, sublaterally with very deep and sharp bends. Third tergite with shallow submedian transverse depression. Second-sixth tergites with separate laterotergites. Fourth-sixth tergites in their basal halves covered by rather sparse and long pale setae. Hypopygium medially on posterior margin with short and subpointed process. Ovipositor apically with two obtuse and weak dorsal nodes (Figs 20, 36). Ovipositor sheath longer than metasoma (Fig. 21).

Hosts. Unknown.

Distribution. Afrotropical Region.

Key to *Ivondrovia* species

1 Hind tibia entirely and most part of hind tarsus light reddish-brown. Head mainly yellow. Fore wing faintly infuscate, with yellow tint especially basally. Fore tibia with two lines of strong spines. Nervellus (cu-a) of hind wing subperpendicular to mediocubital vein (M+CU). Second tergite weakly punctate-rugulose on leaf-shaped median area. Third and fourth tergites of female sub-posteriorly without narrow transverse punctate furrows. Body length 7.2–9.7 mm. Madagascar.....***I. seyrigi* (Granger, 1949)**

– Hind tibia and hind tarsus entirely black. Head mainly light reddish-brown. Fore wing entirely strongly infuscate, without yellow tint. Fore tibia with tree lines of strong spines. Nervellus (cu-a) of hind wing distinctly oblique to mediocubital vein (M+CU). Second tergite strongly striate on leaf-shaped median area. Third and fourth tergites of female sub-posteriorly with narrow transverse punctate furrows. Body length 7.3–7.9 mm. Kenya..... .....***I. grangeri* sp. n.**

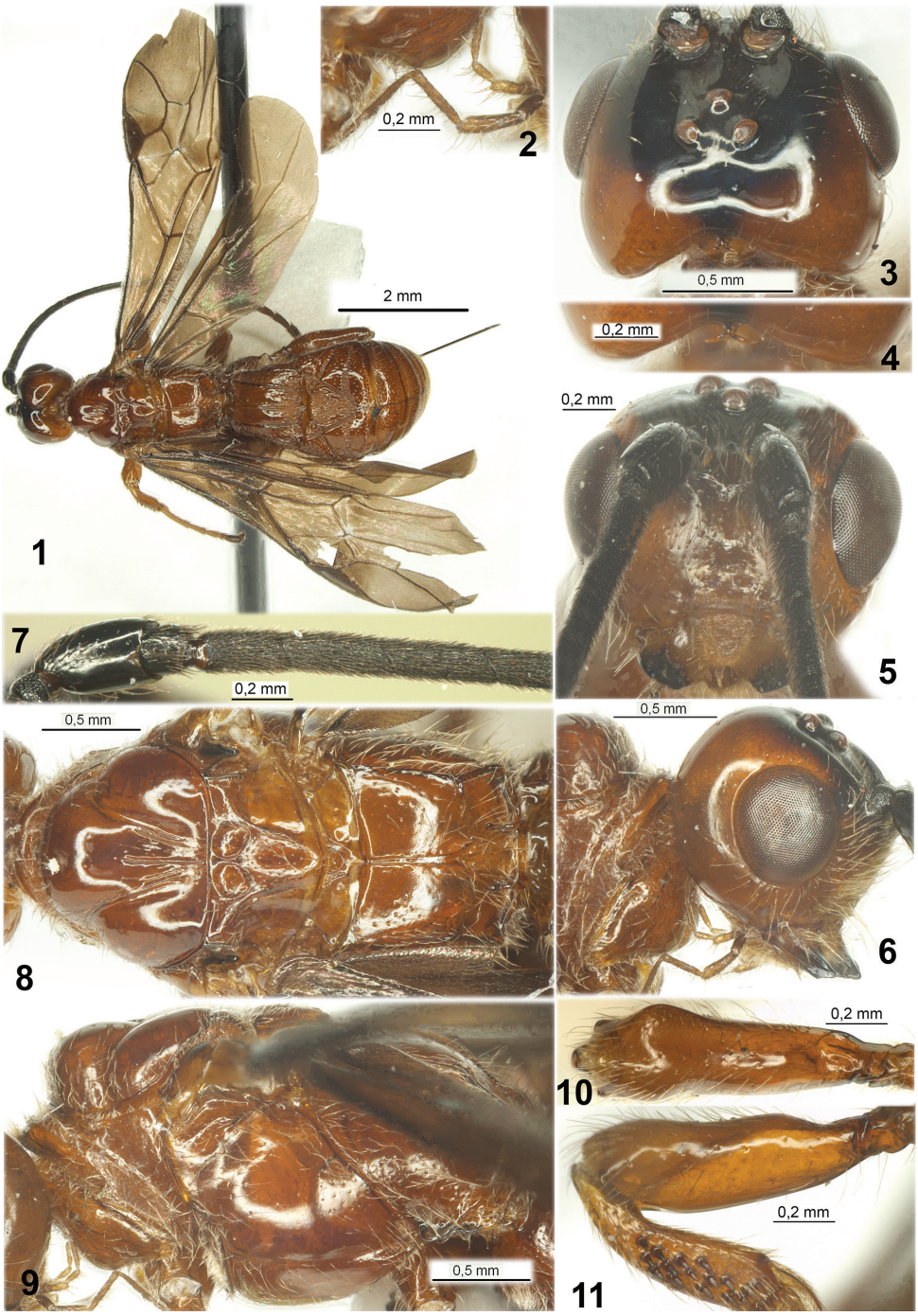
***Ivondrovia grangeri* sp. n.**
http://zoobank.org/11847BE7-9D54-4145-9242-14B868FCF6F6
Figs 1–20

Type material. Holotype: female, "Kenya: Nyanza Prov., Gembe Hills in dry gallery woodland *Olea europaea* ssp. *cuspidata* common, 1362 m, 0°29.36'S, 34°15.60'E, 22–29.i.2005, R. Copeland", "CNIN 3090" (ZISP). **Paratypes**. 1 female, with same first label, "CNIN 3326" (UNAM); 1 female, with same first label, but "8–15.i.2005", "CNIN 3609" (UNAM); 1 female, Kenya, "Nyanza Prov. Gembe Hills in dry gallery woodland *Olea europaea* ssp. *cuspidata* common, 1362 m, 0°29.36'S – 34°15.60'E, R. Copeland" (MNHN).

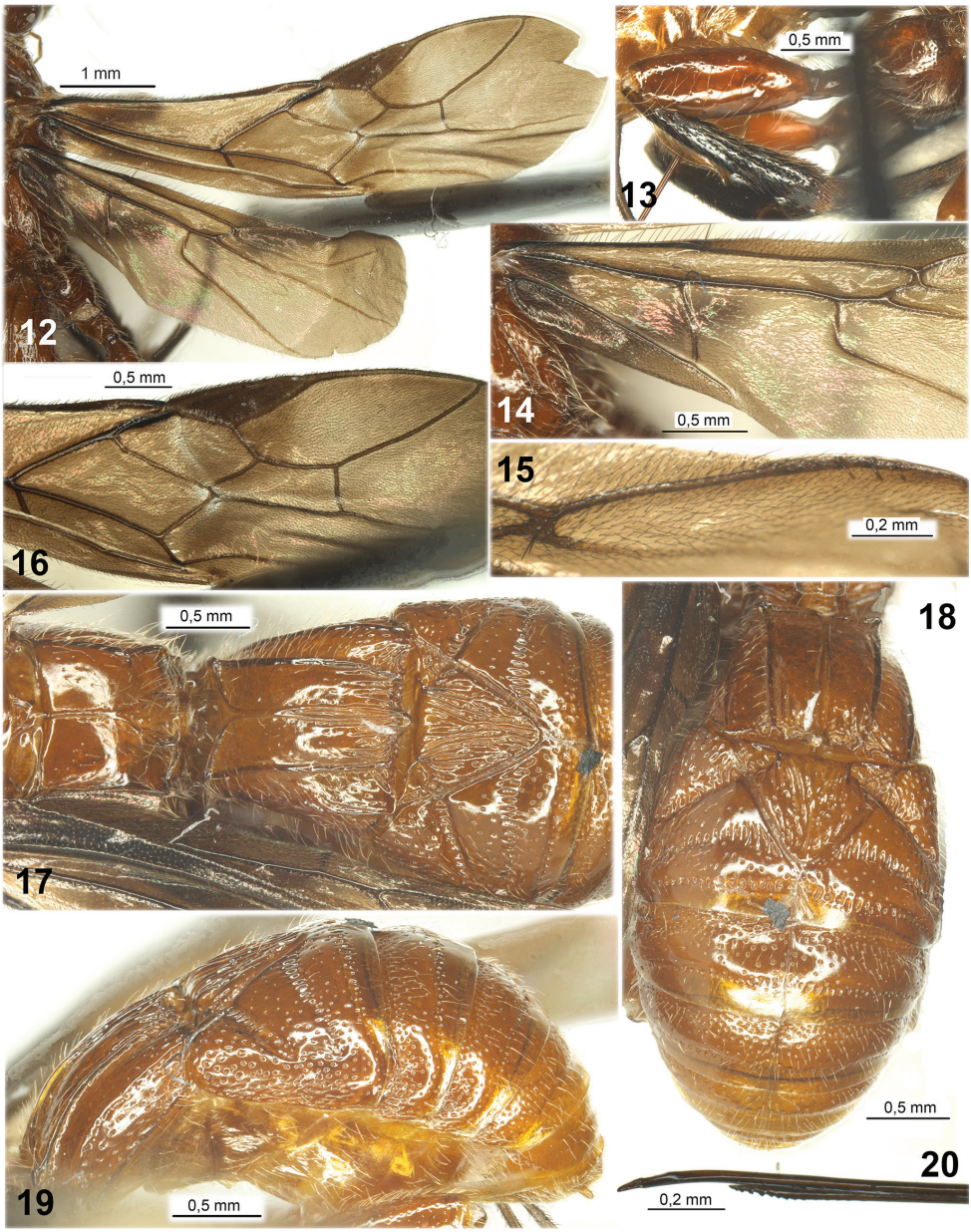
Comparative diagnosis. This new species is very similar to *I. seyrigi*; the differences between both species are indicated in the foregoing key.

Description. Female. Body length 7.3–7.9 mm; fore wing length 5.7–5.8 mm.

Head width 1.60–1.75 times its median length, 1.15–1.20 times width of mesoscutum. Occiput distinctly concave. Head behind eyes (dorsal view) slightly convex anteriorly and weakly roundly narrowed posteriorly. Transverse diameter of eye 1.2–1.3 times longer than temple. Ocelli enlarged, in triangle with base 1.1–1.2 times its sides, situated on median line of eyes. POL 1.10–1.25 times Od, 0.30–0.35 times OOL. Eye without emargination opposite antennal sockets, 1.1–1.2 times as high as broad. Malar space 0.4 times as high as eye, 0.75–0.80 times as high as basal width of mandible. Face width 1.3–1.4 times height of eye and 1.50–1.65 times height of face and clypeus combined. Clypeus almost flat (lateral view). Width of hypoclypeal depression 0.8–0.9 times distance from edge of depression to eye, 0.4–0.5 times width of face. Hypostomal flange narrow.



Figures 1–11. *Ivondrovia grangeri* sp. n., female, holotype. **1** habitus, dorsal view **2** palpi **3** head, dorsal view **4** upper median process of occiput **5** head, front view **6** head, lateral view **7** basal segments of antenna **8** mesosoma, dorsal view **9** mesosoma, lateral view **10** fore femur, dorsal view **11** fore femur and tibia, lateral view.



Figures 12–20. *Ivondrovia grangeri* sp. n., female, holotype. **12** fore and hind wings **13** hind leg **14** basal part of hind wing **15** upper apical part of hind wing **16** apical part of fore wing **17** propodeum and three basal tergites of metasoma, dorsal view **18** metasoma, dorsal view **19** metasoma, lateral view **20** apex of ovipositor, lateral view.

Antenna thickened, almost filiform, 51-segmented. Scape 1.5–1.7 times longer than its maximum width. First flagellar segment 2.4–2.6 times longer than its apical width, 0.90–0.95 times as long as second segment. Submedian segments 1.5 times longer than their widths.

Mesosoma. Length 1.7 times its height. Lateral side of pronotum without longitudinal carina, mainly smooth. Median lobe of mesoscutum distinctly convex, protruding forwards and weakly rounded anteriorly. Notauli entirely deep and distinct, rather wide, smooth. Prescutellar depression (scutellar sulcus) deep, long, only with strong median carina, smooth, 0.3–0.4 times as long as scutellum. Scutellum 1.15–1.20 times longer than its maximum width. Subalar depression shallow, entirely smooth. Precoxal sulcus (sternaulus) shallow, narrow, smooth, connected anteriorly with prepectal carina, running along all lower part of mesopleuron. Metapleural lobe without dense pubescence along posterior margin. Propodeum (lateral view) distinctly and evenly convex.

Wings. Fore wing 3.4–3.5 times longer than its maximum width. Pterostigma 3.5–4.2 times longer than width. Metacarpus (R1a) 1.1–1.2 times longer than pterostigma, 1.5–2.0 times longer than distance between apex of radial (marginal) cell and apex of wing. Radial vein (r) arising from basal 0.4 of pterostigma. Second radial abscissa (3RSa) 1.9–2.1 times longer than first abscissa (r), 0.4 times as long as the slightly, evenly curved third abscissa (3RSb), 1.3–1.5 times longer than the almost straight and oblique first radiomedial vein (2RS). Second radiomedial (submarginal) cell slightly widened towards apex, 2.6–2.9 times longer than its maximum width, 0.85 times as long as the rather wide brachial (first subdiscal) cell. Brachial (first subdiscal) cell slightly convex anteriorly. First medial abscissa ((RS+M)a) slightly sinuate. Recurrent vein (1m-cu) 1.1–1.2 times longer than first radiomedial vein (2RS), 0.6 times as long as basal vein (1M); recurrent (1m-cu) and basal (1M) veins subparallel. Discoidal (first discal) cell long, 2.5–2.6 times longer than its maximum width. Distance from nervulus (1cu-a) to basal vein (1M) 0.25–0.30 times nervulus (1cu-a) length. Hind wing 3.6 times longer than its maximum width. First abscissa of mediocubital vein (M+CU) 0.9–1.0 times as long as second abscissa (1M); basal part of second abscissa (1M) (before recurrent vein (m-cu)) 3.5 times longer than apical part of second abscissa (1M) (behind recurrent vein (m-cu)). Recurrent vein sclerotised, blackish.

Legs. Hind coxa 1.2–1.4 times longer than maximum width, 0.80–0.85 times as long as propodeum. Hind femur 2.4–2.6 times longer than width. Hind tarsus 0.9–1.0 times as long as hind tibia. Second segment of hind tarsus 0.5 times as long as basitarsus, 0.75–0.80 times as long as fifth segment (without pretarsus).

Metasoma 1.2 times longer than head and mesosoma combined. First tergite rather strongly and obliquely widened basally, then distinctly and weakly-roundly widened from almost base to subapex, slightly narrowed apically, without oblique apico-lateral furrows. Maximum width of first tergite 1.5–1.6 times its width at dorsope level, 2.1–2.3 times its minimum width; length 1.1 times its apical width. Median length of second tergite 0.5 times its basal width, 2.3–2.5 times length of third tergite. Ovipositor sheath almost equal to metasoma, 1.7 times longer than mesosoma, 0.7 times as long as fore wing.

Sculpture and pubescence. Head (including frons and clypeus) smooth. Mesosoma mainly smooth; mesoscutum in medioposterior third with longitudinally median carina and striation on rather wide area, metapleuron posteriorly punctate. Propodeum with medial length and subtriangular or suboval areola situated in posterior 0.4–0.5 of segment, with coarse long mediobasal carina in anterior half of segment, basolateral areas almost fused posteriorly with apico-lateral areas, mainly smooth. Hind coxa and femur entirely smooth. First tergite almost smooth widely in basal two-thirds and mostly laterally, distinctly striate in medio-apical third, with distinct longitudinal medial carina narrowly branched in apical half, lateral carinae slightly convergent. Second tergite medially strongly striate on large leaf-shaped median area, densely and distinctly punctate laterally; third tergite sparsely punctate and partly smooth, with crenulated and rather narrow transverse submedian furrow. Third and fourth tergites sub-posteriorly with transverse narrow punctate furrows. Remaining tergites distinctly sparsely punctate, smooth posteriorly. Vertex almost entirely glabrous, usually with not long and semi-erect setae laterally. Mesoscutum mainly glabrous, with rather dense, short and semi-erect pale setae laterally and in medioposterior third. Mesopleuron widely glabrous medially. Hind tibia dorsally with rather dense, short, and semi-erect golden setae, ventrally with dense or very dense, short and semi-erect golden setae and additionally with sparse, long and semi-erect setae; length of setae on dorsal margin of tibia 0.3–0.5 times maximum width of hind tibia.

Colour. Body almost entirely light reddish brown, head with large black spot on all or most part of frons and on median part of vertex. Antenna entirely black. Palpi reddish brown, darker basally. Legs light reddish brown or partly reddish brown, apical segments of fore and middle tarsi dark brown to black; hind tibia and tarsus entirely black, tarsus sometimes medially dark reddish brown. Ovipositor sheaths black. Fore and hind wings entirely distinctly infuscate, without yellowish tint. Pterostigma entirely black.

Male. Unknown.

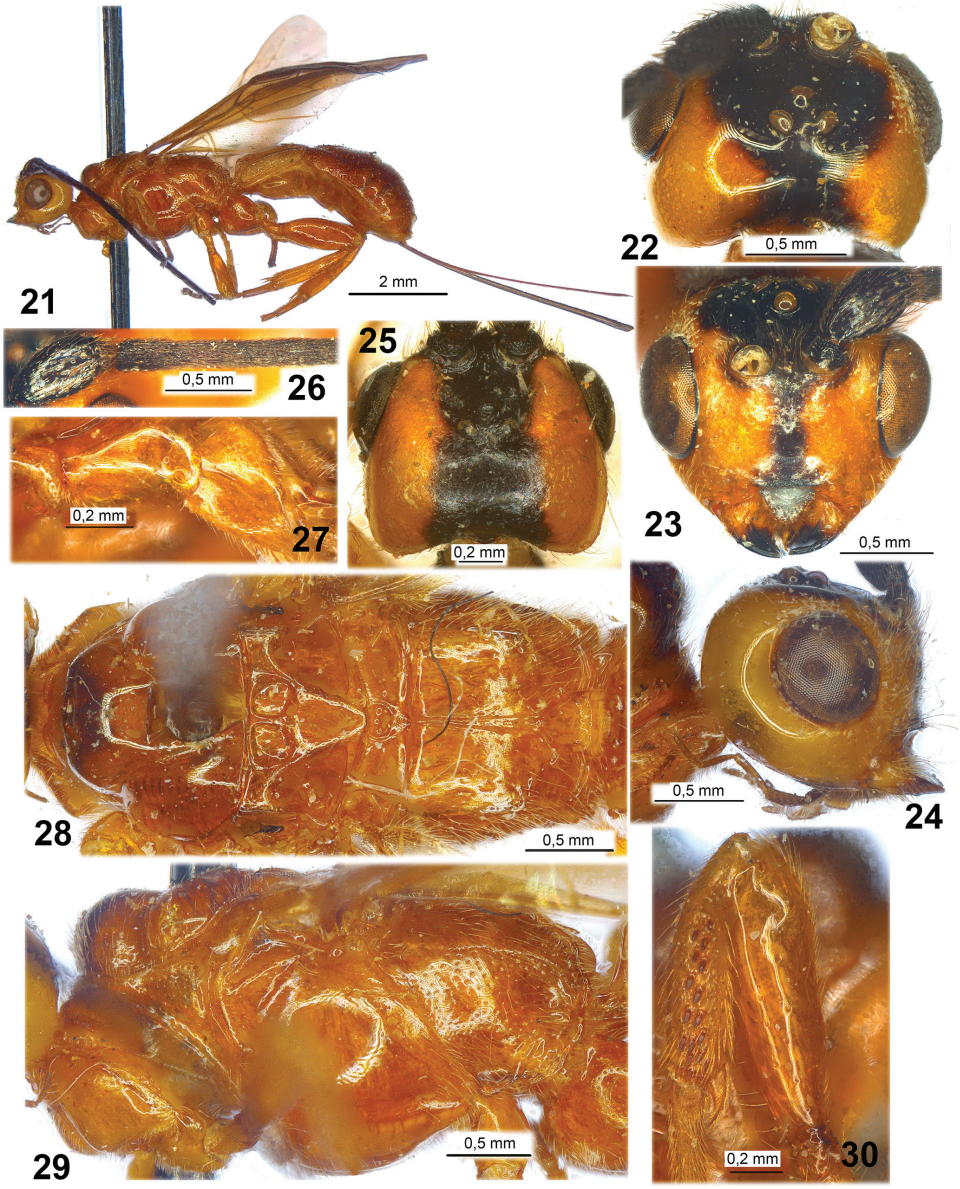
Ivondrovia seyrigi **(Granger, 1949)**

Figs 21–38

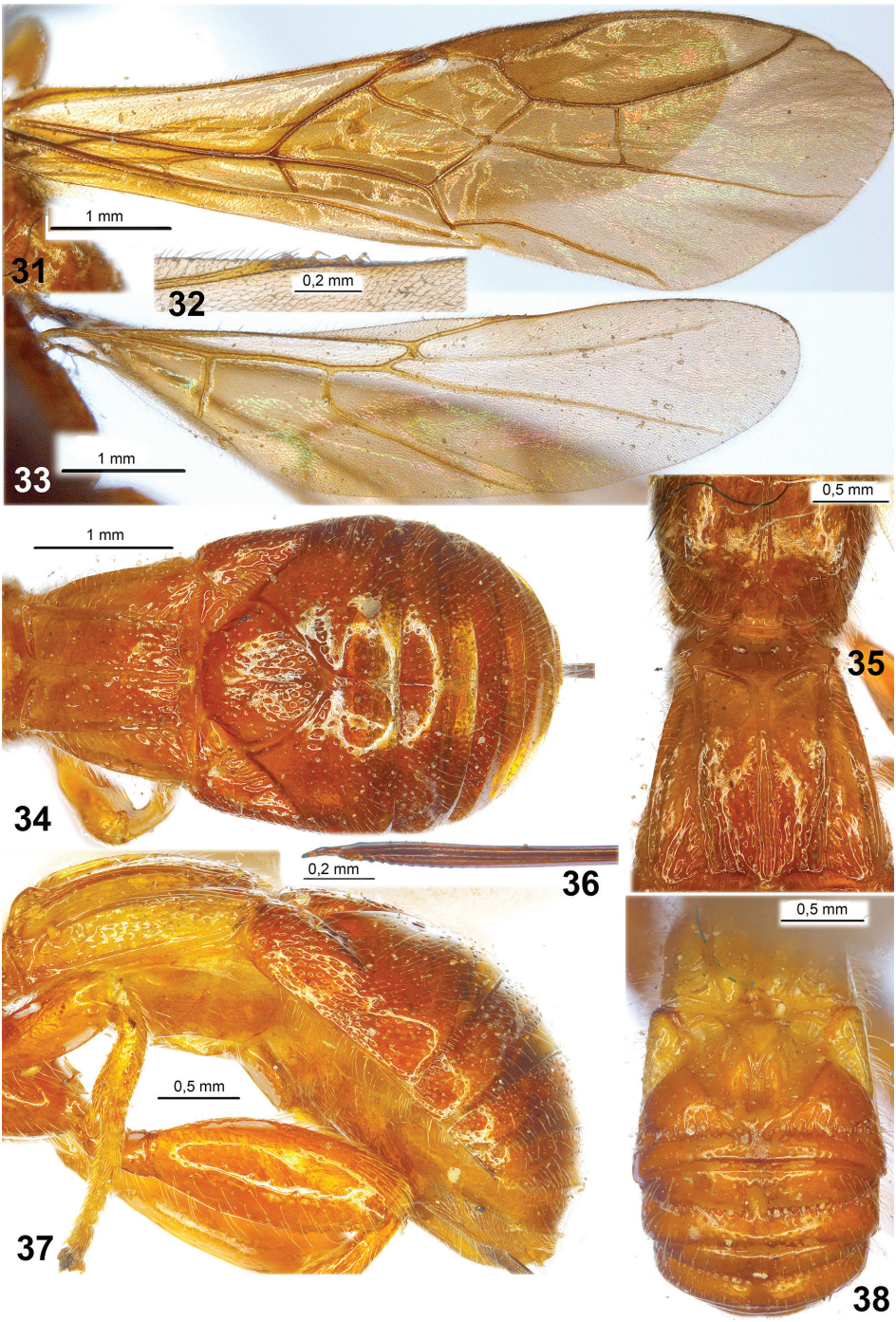
Lophogaster seyrigi Granger, 1949: 93.
Ivondrovia seyrigi (Granger, 1949): Shenefelt and Marsh 1976: 1364; Yu et al. 2005.

Material examined. Type specimens. Lectotype: female, "Madagascar, Ivondro", "Museum Paris, I. 39", "Type", "♀ *Lophogaster seyrigi* Granger, C. van Achterberg, 1980, Lectotype" (MNHN). Paralectotype: 1 male, "Madagascar, Bekily, reg. sud de l'ile", "Museum Paris, III.37, A. Seyrig", "♂ *Lophogaster seyrigi* Granger, C. van Achterberg, 1980, Paralectotype" (MNHN).

Non-type specimen: 1 male, "Madagascar, Bekily, reg. sud de l'ile", "Museum Paris, I.39, A. Seyrig" (MNHN).



Figures 21–30. *Ivondrovia seyrigi* (Granger, 1949) (**21–24, 26–30** female, holotype; **25**, male, specimen). **21** habitus, lateral view **22**, **25** head, dorsal view **23** head, front view **24** head, lateral view **26** basal segments of antenna **27** tegula **28** mesosoma, dorsal view **29** mesosoma, lateral view **30** fore femur and tibia, lateral view.



Figures 31–38. *Ivondrovia seyrigi* (Granger, 1949) (**31–37**, female, holotype; **38**, male, specimen). **31** fore wing **32** hamuli of hind wing **33** hind wing **34**, **38** metasoma, dorsal view **35** propodeum and first tergites of metasoma, dorsal view **36** apex of ovipositor, lateral view **37** metasoma, lateral view.

Comparative diagnosis. The differences between the type species and *I. grangeri* sp. n. are given in the above-mentioned key.

Description. Female. Body length 9.7 mm; fore wing length 8.0 mm.

Head width 1.5 times its median length, 1.1 times width of mesoscutum. Occiput strongly concave. Head behind eyes (dorsal view) slightly convex anteriorly and slightly roundly narrowed posteriorly. Transverse diameter of eye 1.45 times longer than temple. Ocelli enlarged, in triangle with base 1.1 times its sides, situated distinctly before median line of eyes. POL 0.8 times Od, 0.25 times OOL. Eye without emargination opposite antennal sockets, 1.15 times higher than broad. Malar space 0.45 times as high as eye, 0.8 times as high as basal width of mandible. Face width 1.4 times height of eye and 1.5 times height of face and clypeus combined. Clypeus almost flat (lateral view). Width of hypoclypeal depression equal to distance from edge of depression to eye, 0.4 times width of face. Hypostomal flange narrow.

Antenna thickened, weakly setiform, more than 35-segmented (apical segments missing). Scape 1.6 times longer than its maximum width. First flagellar segment slightly thickened, 2.0 times longer than its apical width, almost as long as second segment. Submedian segments 1.8 times longer than their width.

Mesosoma. Length 1.8 times its height. Lateral side of pronotum without longitudinal carina, mainly smooth. Median lobe of mesoscutum distinctly convex, protruding forwards and weakly rounded anteriorly. Notauli entirely deep, but slightly less deep posteriorly, narrow, almost smooth. Prescutellar depression (scutellar sulcus) deep, long, only with median carina, smooth, 0.3 times as long as scutellum. Scutellum 1.1 times longer than its maximum width. Subalar depression entirely smooth. Precoxal sulcus (sternaulus) very shallow, connected anteriorly with prepectal carina, running along all lower part of mesopleuron. Metapleural lobe without dense pubescence along posterior margin. Propodeum (lateral view) rather distinctly broken submedially.

Wings. Fore wing 3.2 times longer than its maximum width. Pterostigma 4.5 times longer than its width. Metacarpus (R1a) 0.9 times as long as pterostigma, 1.7 times longer than distance between apex of radial (marginal) cell and apex of wing. Radial vein (r) arising from basal 0.35 of pterostigma. Second radial abscissa (3RSa) 1.8 times longer than first abscissa (r), 0.4 times as long as the distinctly curved third abscissa (3RSb), 1.5 times longer than the almost straight and oblique first radiomedial vein (2RS). Second radiomedial (submarginal) cell slightly widened towards apex, 2.4 times longer than its maximum width, 0.75 times as long as the rather narrow brachial (second discal) cell. Brachial (second discal) cell slightly convex anteriorly. First medial abscissa ((RS+M)a) slightly sinuate. Recurrent vein (1m-cu) 1.25 times longer than first radiomedial vein (2RS), 0.65 times as long as basal vein (1M); recurrent (1m-cu) and basal (1M) veins subparallel. Discoidal (first discal) cell long, 2.7 times longer than its maximum width. Distance from nervulus (1cu-a) to basal vein (1M) 0.25 times nervulus (1cu-a) length. Hind wing 4.2 times longer than its maximum width. First abscissa of mediocubital vein (M+CU) 0.9 times as long as second abscissa (1M); basal part of second abscissa (1M) (before recurrent vein (m-cu)) approx. twice longer than

apical part of second abscissa (1M) (behind recurrent vein (m-cu)). Recurrent vein (m-cu) sclerotised, yellowish.

Legs. Middle tarsus 1.2 times longer than middle tibia. Hind coxa 1.2 times longer than maximum width, 0.85 times as long as propodeum. Hind femur 2.5 times longer than its width. Hind tarsus 0.9 times as long as hind tibia. Second segment of hind tarsus 0.5 times as long as basitarsus, 0.8 times as long as fifth segment (without pretarsus).

Metasoma almost as long as head and mesosoma combined. First tergite strongly and obliquely widened basally, then distinctly and weakly-roundly widened from subbase to subapex, slightly narrowed apically, without oblique furrows apico-laterally. Maximum width of first tergite 1.4 times its width at dorsope level, 1.9 times its minimum width; length almost equal to its apical width. Median length of second tergite 0.6 times its basal width, 2.3 times length of third tergite. Ovipositor sheath 1.15 times longer than metasoma, 1.5 times longer than mesosoma, 0.7 times as long as fore wing.

Sculpture and pubescence. Head (including frons and clypeus) smooth. Mesosoma mainly smooth (mesoscutum medioposteriorly broken by pin), metapleuron posteriorly punctate-striate. Propodeum with short and semi-round areola situated in posterior third of segment, with coarse long mediobasal carina in anterior two-thirds of segment, basolateral areas long, fused with apico-lateral areas, mainly smooth. Hind coxa and femur entirely smooth. First tergite weakly punctate-rugulose and slightly smooth in basal half and laterally, distinctly striate in medio-apical half. Second and third tergites rather distinctly and sparsely punctate, smooth posteriorly. Remaining tergites mainly smooth. Vertex with rather sparse, long and almost erect setae marginally, widely glabrous medially. Mesoscutum mainly glabrous, with rather sparse, short and semi-erect pale setae along notauli and laterally. Mesopleuron widely glabrous medially. Hind tibia dorsally with dense short and semi-erect yellow setae, ventrally with very dense, short, and semi-erect golden setae and additionally with sparse, long and semi-erect setae; length of setae on dorsal margin 0.3–0.4 times maximum width of hind tibia.

Colour. Head yellow, with black wide spot on most part of frons and on median part of vertex. Mesosoma brownish yellow, mesoscutum darker. Metasoma light reddish brown, first tergite yellow (basally) to brownish yellow or light reddish brown (apically). Antenna entirely black. Palpi reddish brown, darker basally. Legs brownish yellow to light reddish brown, apex of hind tibia, all hind tarsus and apical segments of fore and middle tarsi brown or reddish brown. Ovipositor sheaths dark brown to black. Fore wing entirely distinctly infuscate with yellowish tint (especially basally). Pterostigma entirely brown.

Male. Body length 7.2 mm; fore wing length 5.5 mm. Head width 1.25 times its median length. Temple long; transverse diameter of eye 1.1 times longer than temple. Malar space 0.3 times as high as eye, 0.5 times as high as basal width of mandible. Face medially weakly and densely granulate, dark brown to black. Antenna 57-segmented, 1.6 times longer than body. Penultimate segment 2.3 times longer than wide, 0.7 times as long as apical segment; apical segment distinctly pointed. Anterior part of mesosoma brown to dark brown. First metasomal tergite elongate, 1.4 times longer

than apical width; its sublateral carinae parallel. Second tergite with median triangular area distinctly separated by deep grooves, prolonged apically by distinct obtuse carina. Transverse groove on third tergite deep, wide and coarsely crenulated. Fourth to sixth tergites with deep, compete, crenulated and slightly curved transverse submedian furrow. Metasoma mainly smooth. Otherwise similar to female.

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Morphological and histological study of the forewing of *Orthezia urticae* (Linnaeus, 1758) (Hemiptera, Sternorrhyncha)

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Abstract

Wings of *Orthezia urticae* males were studied. Both ventral and dorsal surfaces of wings were examined under light and scanning electron microscopes. The structure regarded as vein cubitus anterior turned out to be a reinforcement element only. Two elements known as radius sector and media are almost transparent depressions in the wing membrane. Veins at the margin of the fold of the wing anal lobe were not confirmed. Studies indicated a row of sensilla cupola at the beginning of the subcostal ridge.

Cross sections of the wing membrane showed a two-layered membrane. The presence of two veins was confirmed in a common stem – subcostal and radius. The change of common stem shape was described. Neither tracheae nor nerves were observed. This is the second paper on cross-sections of wing within Sternorrhyncha.

Keywords

Coccoids, cross-section, forewing, morphology, ultrastructure, wing veins

Introduction

Infraorder Coccomorpha (Fallen 1814) comprises scale insects, also known as coccoids. They are sap-sucking hemipterans, divided into two main groups: more primitive archaeococcoids and "advanced" neococcoids (Gullan and Martin 2009). The genus *Orthezia* belongs to the first group (family Ortheziidae) and has the wings regarded as the most primitive within known scale insects because they retain all fundamental elements of venation (Shcherbakov 2007). However, on the basis of current studies of recent and fossil species, the family Ortheziidae does not seem to be as primitive as previously thought (Vea and Grimaldi 2012).

The analysis of the *O. urticae* forewing was made in detail by Koteja (1986) and partly by Shcherbakov (2007). The distinctive feature of coccoid females is the wing loss, which is complete and no organs replace them. It is most probably related to the parasitic life mode, i.e. life on host plant and feeding on it (Koteja 1985). In males, forewings are folded flat over the abdomen and overlap each other (Brodsky 1996), while hindwings are reduced to hamulohalteres (Koteja 1986). However, venation is strongly reduced in this insect group and the nomenclature of the veins is still highly questionable.

After Morrison (1925) and Schlee (1969), Koteja (1986) described wings in Ortheziidae as composed of five easily noticeable elements. These elements divide wing membrane into three fields (Koteja 1996) (1–3, Fig. 1A).

The first element, so-called Sc+R, is convex and composed of subcostal (Sc) and radial (R1) veins. Between the anterior wing edge and the subcostal ridge, there is a narrow field (1, Fig. 1A) called the costal field in most insects, and marginal thickening in coccoids. In the second field, the radial sector vein (Rs) (also known as the anterior diagonal vein) is visible as a long but weak patch. Below Rs, another vein is present – the medial sector vein (M) (= first diagonal clear line), which is also weak and long. These last two veins are placed in a triangular medial field (2, Fig. 1A). Another main vein on the wing membrane is a convex "basal diagonal vein" = cubital vein (Koteja 1986, Shcherbakov 2007 – Fig. 2A–B). Under this vein there is a transparent and concave part of the membrane (or shallow depression) called the anal fold contained within the third, posterior field of the wing (3, Fig. 1A).

To verify the above interpretations of the wing venation, we present the reconstruction of the course and the inner structure of wing veins in *Orthezia urticae* (Linnaeus, 1758). We also suggest changes in wing venation nomenclature (Fig. 2C; Table 1).

Recently, for the first time within Sternorrhyncha, cross-sections of wing were made for an aphid representative, *Aphis fabae* (Scopoli, 1763) (Franielczyk-Pietyra and Wegierek 2017). Thanks to that study it became possible to draw a broader comparison, which was an additional aim here.

Table 1. Wing vein nomenclature for *Orthezia urticae* (Linnaeus, 1758).

Author	Veins					
Koteja (1986)	scr	rs	ms	cu	–	–
Shcherbakov (2007)	Sc, R1	Rs	M	CuA	CuP	PCu+1A
Franielczyk-Pietyra et al. (2018)	Sc, R	"rs"	"m"	"cua"	–	–

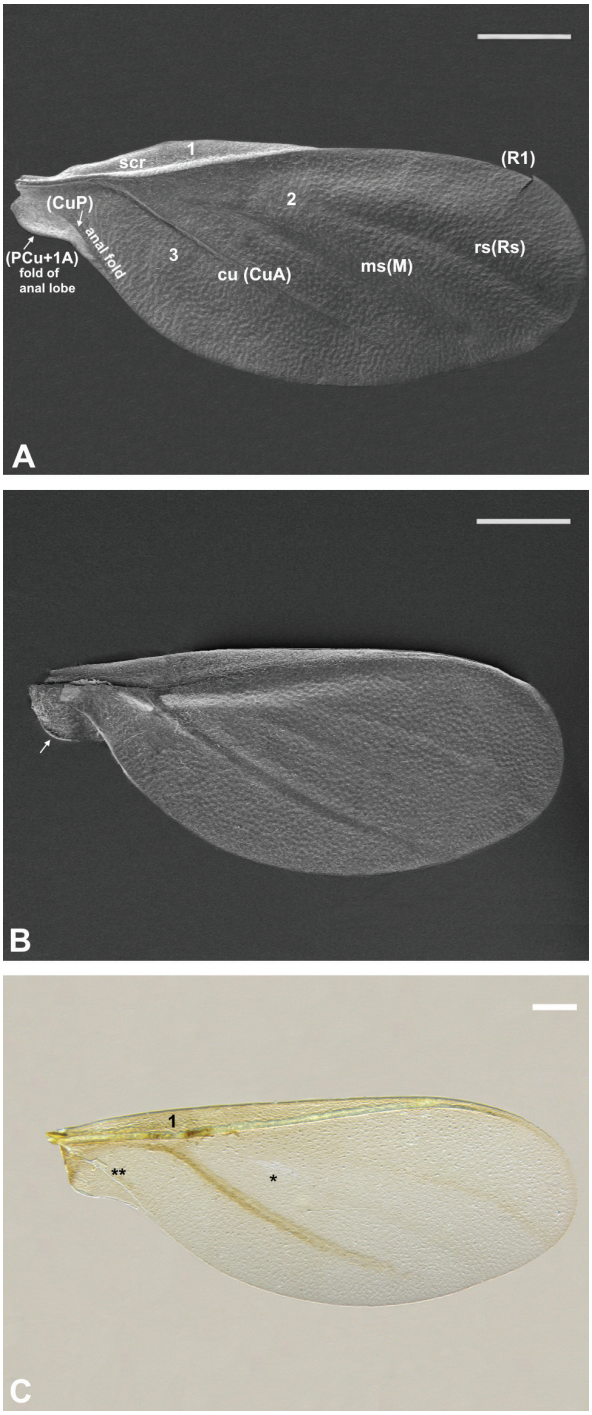

Figure 1. Forewing of *Orthezia urticae* (Linnaeus, 1758) **A** dorsal view under SEM **B** ventral view under SEM; Scale bar: 50 µm **C** dorsal view under LM; Scale bar: 250 µm; vein names without brackets after Koteja (1986), with brackets after Shcherbakov (2007); other symbols explained in the manuscript.

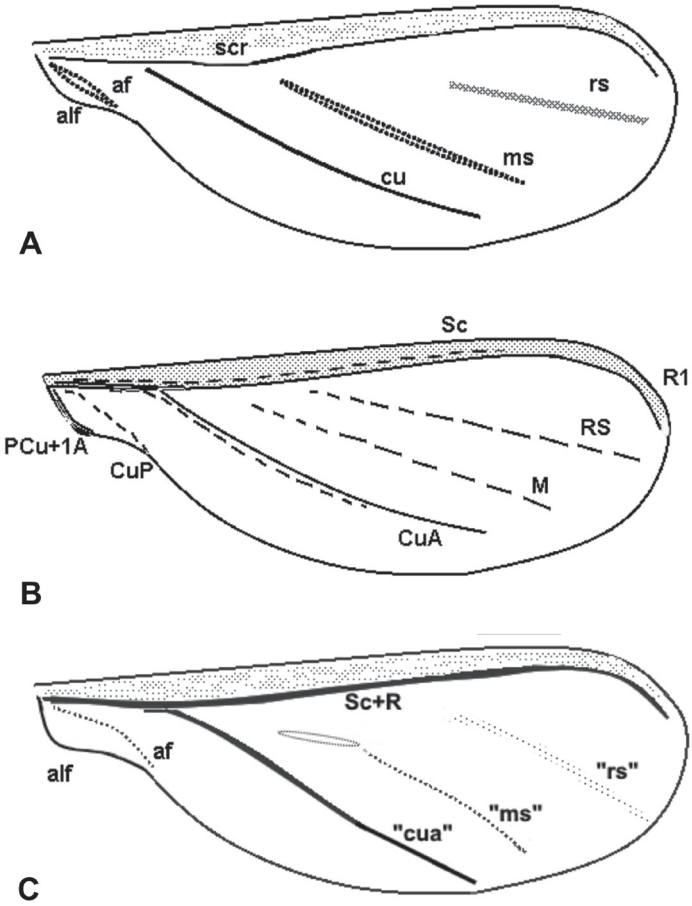

Figure 2. Schematic drawings of forewing of *Orthezia urticae* (Linnaeus, 1758) after **A** Koteja (1986) **B** Shcherbakov (2007) **C** present interpretation.

Materials and methods

Scanning electron microscopy (SEM) and histology

Methods were the same as in the previous article (Franielczyk-Pietyra and Wegierek 2017), both for SEM and histology. In the figures with cross-sections (Figs 3, 4) costal margin is at the top, anal margin at the bottom, upper surface to the right. Places of sectional cuts are presented in Fig. 5. Because of the delicacy of the wings, they were not cleaned and a large amount of wax is normal for this species.

Nomenclature of the veins is after Koteja (1986) and Shcherbakov (2007). The following abbreviations are used:

af	anal fold;
alf	fold of anal lobe;
als	alar setae;
cs	campaniform sensilla;
R	radius;
R1	first branch of radius (RA in the interpretation of Szwedo and Nel 2011);
"rs" (= Rs)	radius sector (RP in the interpretation of Szwedo and Nel 2011);
"ms" (= M)	media;
mt	marginal thickening;
"cua" (= CuA)	cubitus anterior;
CuP	cubitus posterior;
PCu+1A	fused postcubitus and first anal vein;
Sc	subcostal;
scr	subcostal ridge.

Results

Scanning electron microscopy

The dorsal surface shows a tuberculate sculpture formed by polygonal cells of cuticle. There are no microtrichia (Fig. 1A).

Subcostal ridge and cubital veins are convex, whereas medial and radial sectors look like small depressions. From the wing base to the place where CuA appears, the subcostal ridge is strongly convex and vertical, then the ridge turns closer to the cubital vein. It is still convex but not as much as at the beginning. Scr almost reaches the apex of the wing in that manner (Fig. 1A).

There are a few small alar setae (als) at the beginning of subcostal ridge (Fig. 6A) and a row of about 30 campaniform sensilla (cs) (Fig. 6B).

Between the wing base and the concave anal fold there is a small anal lobe (Fig. 1A).

The ventral surface also shows a tuberculate sculpture (Fig.1B). The whole course of scr and CuA veins is concave. Veins M and Rs look like a weak slightly convex patch. The proximal edge of anal lobe has a narrow fold to hold hamuli of the second pair of wings (white arrow, Fig. 1B).

Light microscopy

Forewings are semitransparent and are elongate-oval in shape (Fig. 1C).

The subcostal ridge almost reaches the apex but turns towards the edge of the wing, so there is no pterostigma. No other vein reaches the wing apex. The costal field of the wing (1, Fig. 1C) is much more pigmented than other parts of the wing.

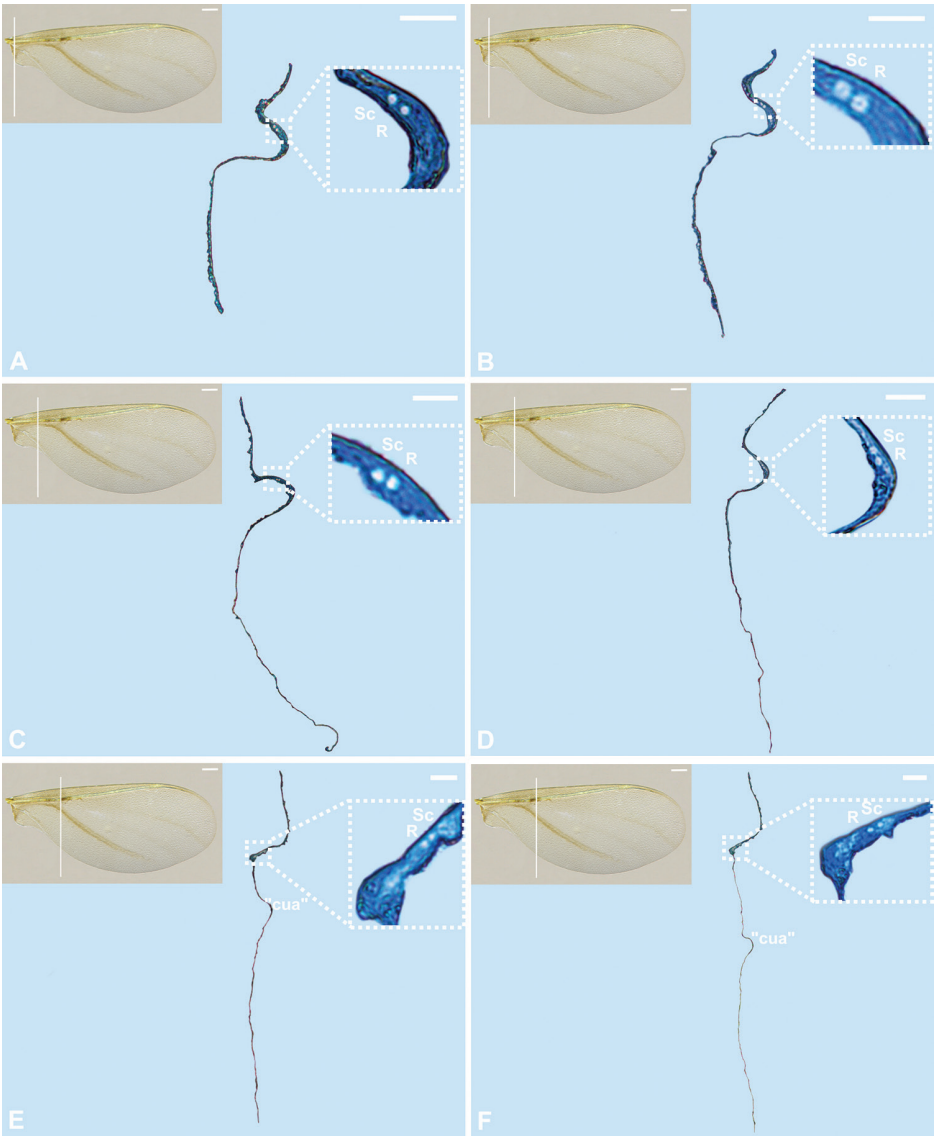

Figure 3. Cross-sections of the forewing of *Orthezia urticae* (Linnaeus, 1758); Scale bar: 50 µm. Scale bar of the forewing under light microscope 250 µm.

The cubital vein, which is strongly pigmented, does not seem to be directly connected with the subcostal ridge - it can be seen underneath as a separate element. The radial sector vein is less pigmented, and the medial vein is hardly visible. At the beginning of the latter, a small, narrow transparent patch is present (marked * in Fig. 1C).

The anal fold is a transparent element of the membrane (marked ** in Fig. 1C), visible as a thin line extending from the base of wing to the posterior margin of anal lobe.

The pterostigma is absent.

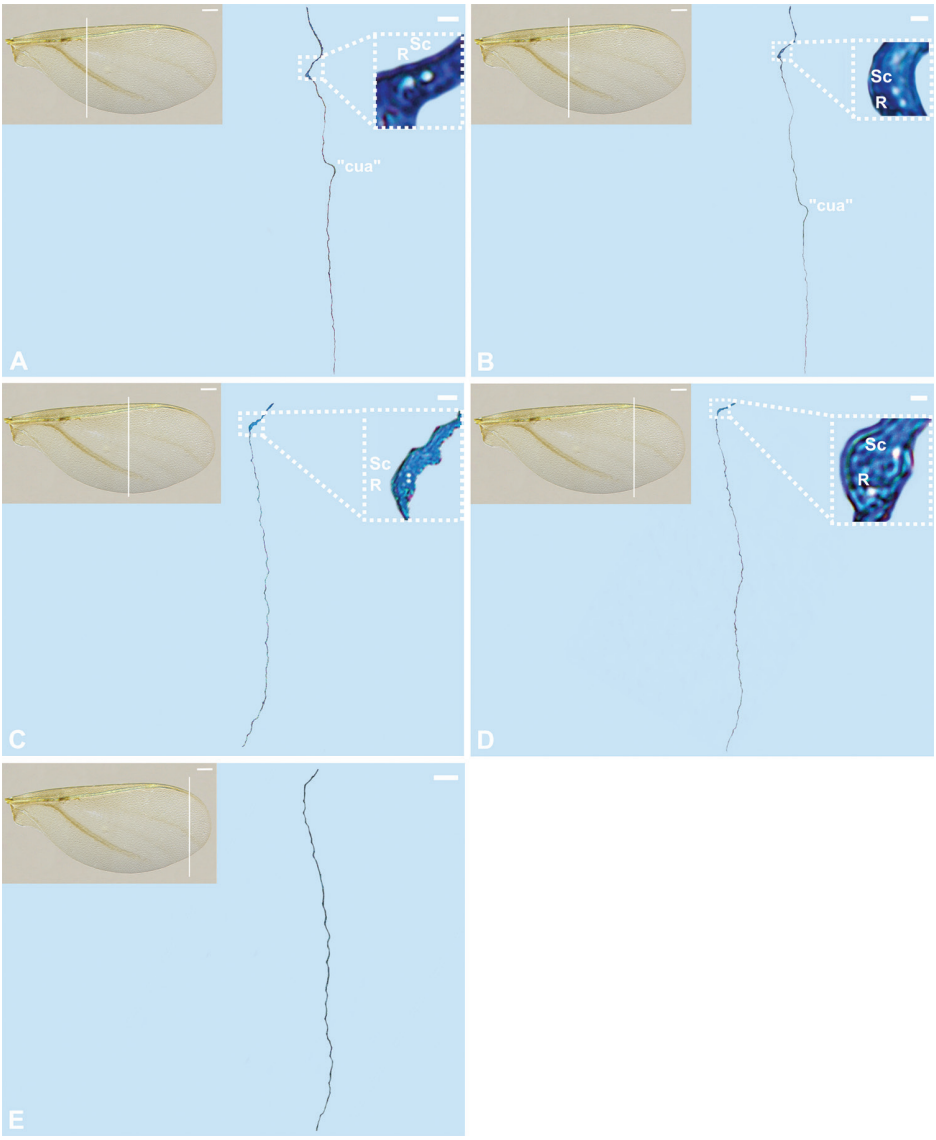

Figure 4. Cross-sections of the forewing of *Orthezia urticae* (Linnaeus, 1758); Scale bar: 50 µm. Scale bar of the forewing under light microscope 250 µm.

Histology cross-sections

The wing membrane, at the beginning of sections, is thicker at the proximal part (Fig. 3A–E), then becomes thinner (Figs 3F, 4A–E). The subcostal ridge, inverted U-shaped on sections, comprises two veins inside (Sc and R). These are firstly placed at the base of scr (Fig. 3A–D). When the cubital vein appears, as mentioned earlier, scr turns closer to it.

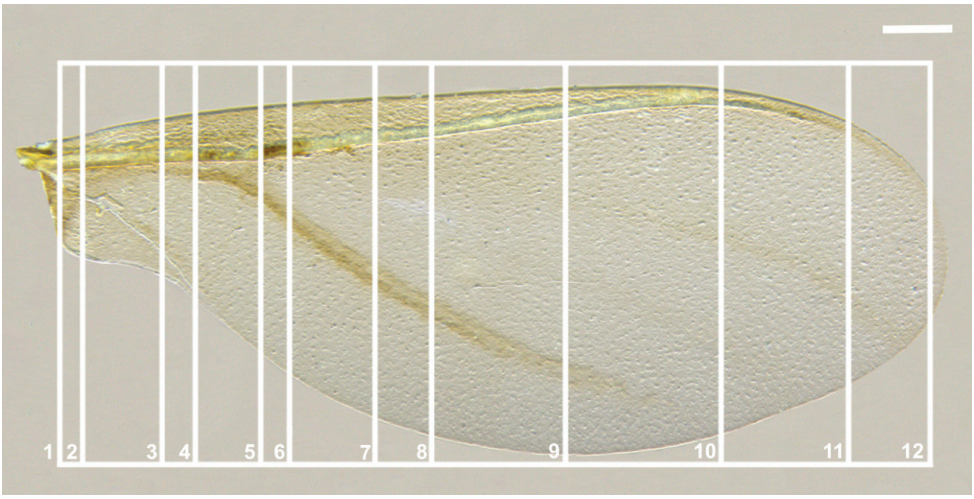

Figure 5. Light microscopy showing the forewing of *Orthezia urticae* (Linnaeus 1758), places of sectional cuts; Scale bar: 250 μm.

From this point the subcostal and radial veins run in scr closer to the triangular medial field (Fig. 3E). Both veins are present till the end of scr on cross-sections (Fig. 3A–4D). No nerves or tracheae are observed inside them. The cubital vein is present as a convex reinforcement of the wing membrane without any lumen inside (Figs 3E–F, 4A–B). The medial and radial sector veins are not visible on sections (Fig. 4C, D).

Discussion

There is certainly no costal vein on cross-sections (which is equivalent to the lack of trachea). It is in contrast to aphid forewings, where a costal vein is present but there are no tracheae (Franielczyk-Pietyra and Wegierek 2017). This vein functions mainly as a reinforcement of the wing. In coccoids it was replaced by the subcostal ridge. The lack of costal trachea was regarded as a synapomorphy of Aphidomorpha and Coccomorpha by Shcherbakov (2007). According to the above results, this statement can be confirmed: neither costal vein nor costal trachea was observed.

The subcostal ridge, also known as the subcostal complex, comprises two veins – the subcostal and the radial ones, which run together from the wing base to the apex, where they turn towards the wing margin and disappear. Cross-sections confirm the theory of Koteja (1986) and confirm that these veins can be considered to have lumens which create tunnels for haemolymph. The subcostal complex can be regarded as a common stem for these two veins, which is similar to the situation in *Aphis fabae* (Franielczyk-Pietyra and Wegierek 2017). However, in aphids the common stem is composed of radius, media and cubital anterior veins as well as their tracheae. Besides the content of the common part, the difference is reflected in the fact that in coccoids both veins run together to the wing apex, while in aphids R, M and Cu veins spread apart.

The presence of the subcostal vein is note-worthy because it is reported for the first time in a representative of the Sternorrhyncha. Neither aphids (Franielczyk-Pietyra and Wegierek 2017) nor psyllids (Franielczyk-Pietyra and Wegierek unpubl. data) have this vein. This brings coccoids closer to the Naibiidae family, which is considered as ancestral to true scale insects (Shcherbakov 2007).

Darker parts of the membrane, regarded as medial and radial sector veins, are only more pigmented (sclerotized) parts of the wing. Probably they are remnants of veins, as evidenced by Koteja (1986). The tracheal system which he drew is more complex than the system of veins (Fig. 7). So far it has been believed, that Patch (1909) in her work showed tracheal and vein systems for all coccoids. However, two coccoid species studied by her, *Planococcus citri* (Risso 1813) (= *Pseudococcus citri*) (Pseudococcidae) (Fig. 8) and an unidentified species of *Dactylopius* Costa, 1829 (Dactylopiidae), belong to the group of neococcoids. Also, the only visible veins on those wings are called Sc, Rs and M by Patch. Judging by the course of the tracheae in the presented neococcoid wing, the medial vein should probably be considered as the cubital anterior, and the radial sector as the radial vein (because of no further branching). As there is no trace of other veins, the reduction of venation proves to have taken place in more advanced species. It is the reason why Rs and M should not be called veins but only slight depressions or transparent patches and marked as "rs" and "m".

In aphids, radial sector and medial veins are very clearly outlined and in *A. fabae* the latter is divided into three branches: M_1, M_2 and M_{3+4} (Franielczyk-Pietyra and Wegierek 2017); it additionally stiffens the wing, but these veins are not equally well developed in all aphids. Some have media with two branches or unbranched.

Additionally, Shcherbakov (2007) described Rs and M as concave veins in coccoids, which cannot be confirmed, as it is only pigmentation. Also, he claimed that veins Sc+R and CuA are twofold; both contain convex and concave parts. This idea may have been drawn from the shadow formed in SEM under a strongly convex subcostal ridge and the element called the cubital vein. Histological methods did not confirm this. Moreover, two cubitus anterior veins (CuA_1, CuA_2) are distinctive of aphids. Atrophy of this veins in the coccoids forewing is probably associated with the existence of the anal lobe and with hindwing diminution (Shcherbakov 2007).

The same author indicated the presence of PCu+1A vein on the edge of the anal lobe, as a synapomorphy for both aphids and coccoids. Likewise, Koteja (1986) described the presence of the anal vein as a common feature for the Ortheziidae and most archaeococcoids (absent in neococcoids). Both authors were probably referring to the same vein, PCu+1A. However, its presence cannot be confirmed, due to the fact that neither aphids (Franielczyk-Pietyra and Wegierek 2017), nor scale insects (coccoids) show such an element in cross-sections. Probably this vein is moved to the anal wing margin. In coccoids the wing anal lobe is always present in species with halteres (Giliomee 1967). In such species the edge of the anal lobe has a narrow fold on the ventral surface, the place where hamuli are attached (two hooked setae from halteres) (Koteja 1986). The wing anal lobe has not been described in aphids; they have two similar pairs of wings linked together by a wing-coupling apparatus (Franielczyk-Pietyra and We-

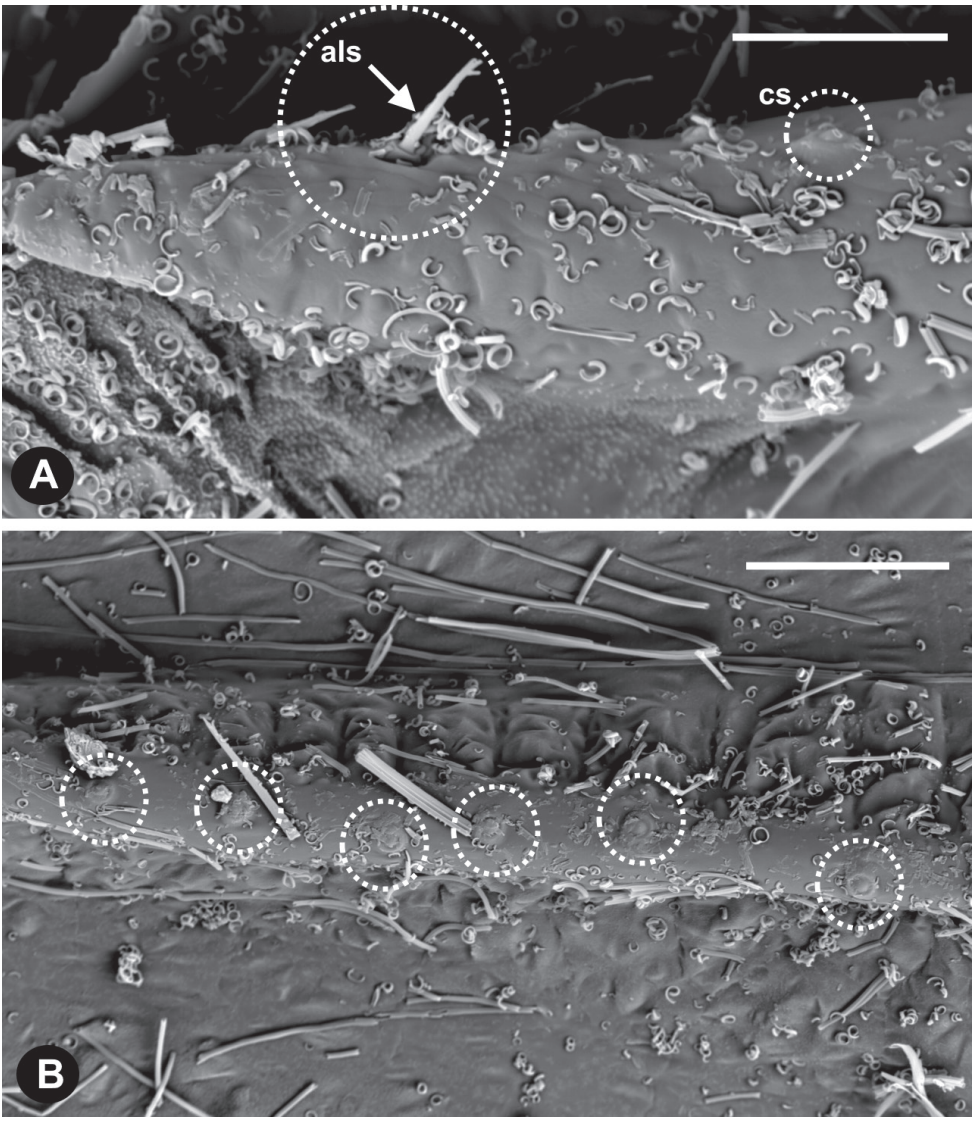

Figure 6. A Alar setae (als) and campaniform sensilla (cs) on the wing base of *Orthezia urticae* forewing; scale bar 20 μm **B** campaniform sensilla at the subcostal ridge. Scale bar: 25 μm.

gierek 2017). As suggested by Koteja (1996), the occurrence of a connection between both wings could be regarded as synapomorphy of aphids and coccoids.

No archaeococcoids have developed microtrichia, which are characteristic of the wing surface of neococcoids (Koteja 1996). It explains the absence of these structures on the wings examined.

Alar setae and campaniform sensilla observed at the subcostal ridge (Fig. 6) confirm data presented by Koteja (1986), and the number is congruent with his opinion. According to this author, 3–8 alar setae are located on the subcostal ridge near the wing

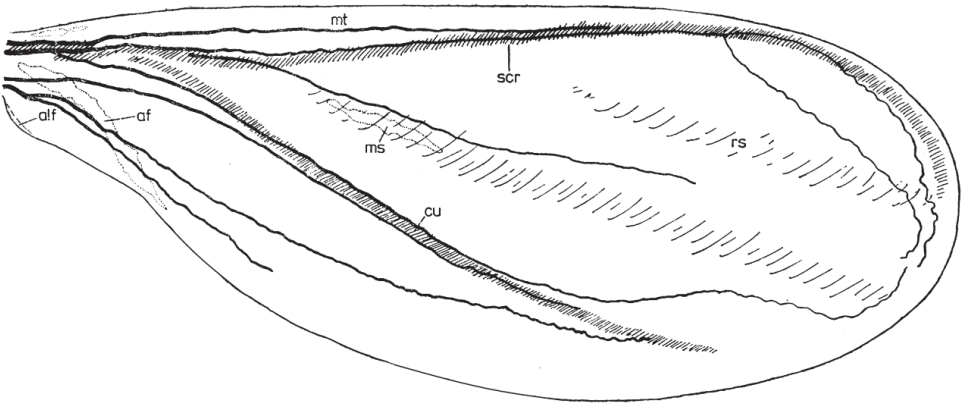

Figure 7. Tracheal system of forewing of *Orthezia urticae* (Linnaeus 1758) after Koteja (1986).

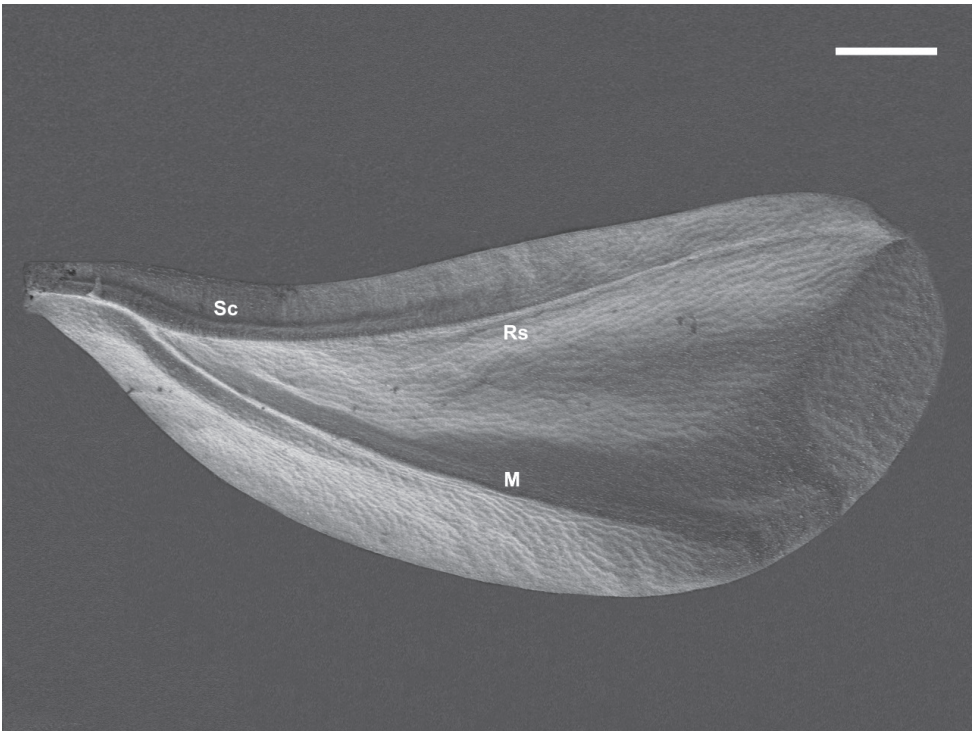

Figure 8. Forewing of *Planococcus citri* (Risso 1813) under SEM. Scale bar: 100 μm.

base, whereas campaniform sensilla create a row of 25–43 setae along the subcostal ridge. Our observations make it possible to state that alar setae do occur, but their number is hard to estimate because of their fragility. Due to the fact that there is a very dense wax covering, some sensilla may not be clearly visible, so it is not easy to count them correctly. We counted about 30 of them. As campaniform sensilla are the only example

of mechanoreceptors known to be involved in flight stabilization (Chapman 2013), their number and placement is understandable. These sensilla are distributed along the subcostal ridge to take on the role of non-existing veins. A recent study of campaniform sensilla in the aphid genus *Mindarus* (Montagano & Favret, 2016) revealed fewer elements on the forewing. It is probably associated with frequent wing flexing and different distribution of sensilla on aphid forewings in comparison with scale insects.

The hypodermal club-shaped thickening (structure similar to pterostigma in other insects) without any veins around (Koteja 1996; Koteja and Azar 2008), is known only in some coccoids within the Margarodidae family *sensu lato*. Therefore, the lack of this structure in our results is not surprising.

Comparing forewings in aphids and coccoids, we can conclude that the elements distinctive of coccoids include only two veins, subcostal and radial ones in the common stem and the presence of the wing anal lobe (Table 2). It seems that this very delicate structure in coccoid representatives is related to the short life span of scale insect males (Koteja 1985).

Based on morphological (Hennig 1981; Carver, Gross, Woodward 1991) and molecular studies (von Dohlen and Moran 1995; Xie et al. 2008), aphids and coccoids are considered as sister groups. The results summarized in Table 2 do not show many affinities between the forewings in these groups. This only indicates that wing venation may not be a good character for the analysis of similarities or phylogeny.

Due to the fact that histological methods revealed only two veins, the subcostal and the radial ones in the subcostal ridge, it seems necessary to change the nomenclature of wing veins for *Orthezia urticae* Linnaeus 1758. The element known as cubitus anterior vein should be regarded as a convex sclerotized part used only to strengthen the wing and should be marked as "cua". Two other elements, known as radial sector and medial sector veins, should be marked as "rs" and "m", but not considered any longer as veins.

Table 2. Comparison of the forewing structures between a representative of aphids and of coccoids.

Structure	*Aphis fabae*	*Orthezia urticae*
C	+	–
Sc	–	+
R	+	+
R_1	+	–
Rs	+	„rs"
M	+	„m"
M_1	+	–
M_2	+	–
M_{3+4}	+	–
CuA	+	„cua"
CuA_1	+	–
CuA_2	+	–
pterostigma	+	–
common stem	R+M+CuA	Sc+R
anal lobe	–	+

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RESEARCH ARTICLE

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First record of *Ianiropsis* cf. *serricaudis* in Maryland Coastal Bays, USA (Crustacea, Peracarida, Janiridae)

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Abstract

During monthly sampling of benthic invertebrates at 13 stations in the Maryland Coastal Bays (MCBs) from March to December 2012, a total of 29 individuals of *Ianiropsis* cf. *serricaudis* were collected. This species is being reported for the first time in MCBs. A detailed illustration and description of an adult male of *I.* cf. *serricaudis* from MCBs is presented. An illustrated key of males of *Ianiropsis* species belonging to the palpalis-group is also presented. The size of the largest male was 3.0 mm and that of the largest female was 2.5 mm. It is possible that *I.* cf. *serricaudis* was present in the MCBs, but overlooked during previous surveys of marine benthic invertebrates in the area because of its small body size and lack of taxonomic expertise.

Keywords

Ianiropsis cf. *serricaudis*, Isopoda, Maryland Coastal Bays (MCBs), mid-Atlantic Region

Introduction

Ianiropsis serricaudis Gurjanova, 1936 is a janirid isopod that was described from the Russian coast of the Sea of Japan (Fig. 1). Unfortunately, the original description is poor and the illustrations are incomplete (Gurjanova 1936). Specimens of *I. serricaudis*

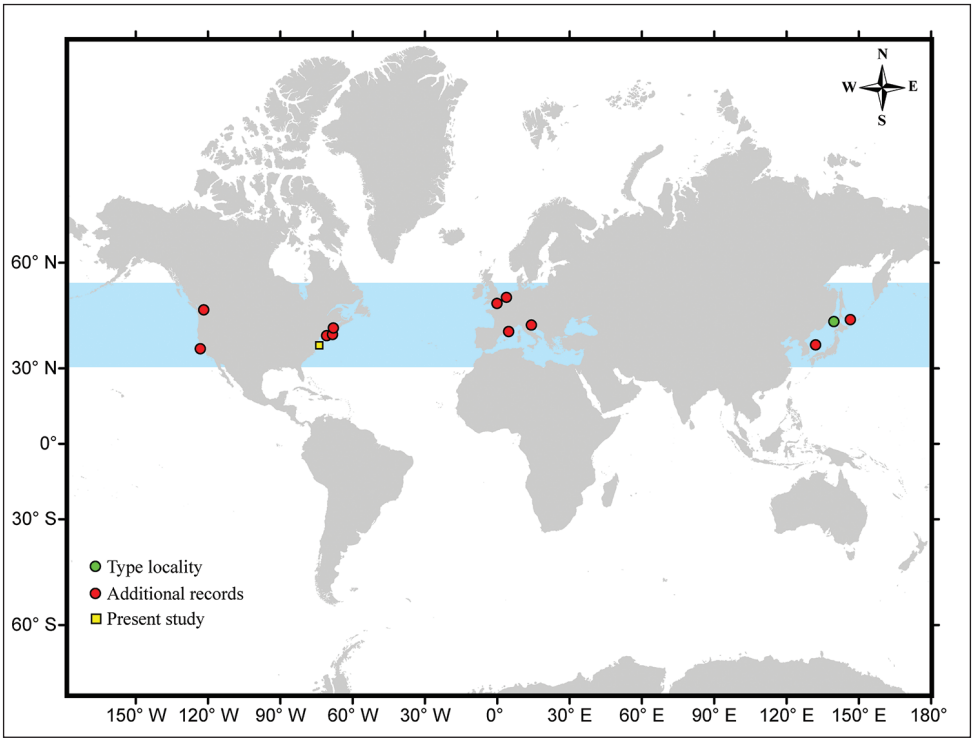

Figure 1. Map showing the worldwide distribution of *Ianiropsis serricaudis* and *I.* cf. *serricaudis*. *Ianiropsis serricaudis* – type material (green circle), *I. serricaudis* – additional records (red circle), *I.* cf. *serricaudis* (yellow square). Data from: Gurjanova (1936); Kussakin (1962, 1988); Jang and Kwon (1990); Hobbs et al. (2015); Marchini et al. (2016); Ulman et al. (2017); Morales-Núñez and Chigbu (this study).

have also previously been reported in the Sea of Okhotsk, on the Coast of Iturup Island (one of the Kuril Islands) from Russia (Kussakin 1962, 1988), Korea (Jang and Kwon 1990), and recently as a successful invasive species of both coasts of the United States and Europe (Hobbs et al. 2015; Marchini et al. 2016; Ulman et al. 2017) (Fig. 1). In the coastal waters of the northeastern United States, it has only been reported from Gulf of Maine to Barnegat Bay, NJ whereas in Europe it is known only from England, Netherlands, Italy, and France (Hobbs et al. 2015; Marchini et al. 2016; Ulman et al. 2017) (Fig. 1). These authors presented additional descriptions of the body and/or appendages of specimens of the species and showed morphological differences among specimens from various geographic locations (see Kussakin 1962, 1988; Jang and Kwon 1990; Hobbs et al. 2015). Additionally, Saito et al. (2000) considered *I. notoensis* as a junior synonym of *I. serricaudis* despite exhibiting multiple differences with Gurjanova's original description. Despite these differences, no one has revised the original description of the type material of *I. serricaudis*, or at least specimens from the precise type locality (topotypes). Without such a revision, and more detailed morphological and molecular analyses of these populations, the records attributed to this species remain uncertain.

We have tried to find the type material of *I. serricaudis*, but the exact location (i.e., museum collection) where it was placed was not indicated in the original description; it is unknown whether or not it has been lost. For this reason, Dr. Viktor Petryashov (Zoological Institute, Russian Academy of Sciences, Saint Petersburg, Russia) was contacted and asked if the type material might be located at this institute, but, regrettably, the only material available is a female collected in 1948 (V. Petryashov pers. comm. 2017).

During examination of monthly samples of benthos collected in 2012 from the Maryland Coastal Bays (MCBs), a number of specimens attributable to *Ianiropsis* cf. *serricaudis* were observed (Figs 1–2). This study aims to report, for the first time, the presence of *I.* cf. *serricaudis* in the MCBs. Additionally, a detailed supplementary illustration and description of an adult male of *I.* cf. *serricaudis* from MCBs is presented herein.

Materials and methods

Study area

The Maryland Coastal Bays is a barrier-island system located on the eastern part of the Delmarva Peninsula in the United States of America (USA). The system consists of five principal lagoons distributed in two areas; Assawoman and Isle of Wight Bays located in the northern area of MCBs, and Sinepuxent, Newport, and Chincoteague Bays located in the southern area of MCBs (Fig. 3). These five bays differ with regard to depth, flushing rate, surface area, and anthropogenic activity. In general, the MCBs are shallow with an average depth of 1.2 m, predominantly polyhaline with salinity greater than 25, and surface area that ranges from 15.9 km^2 in Newport Bay to 189 km^2 in Chincoteague Bay (Chaillou et al. 1996; Wazniak et al. 2004).

Sample collection and processing

Samples were taken at 13 sites (eight sites in the southern area and five in the northern area) (Fig. 3). Sampling was conducted monthly for nine months from March to December 2012, although due to inclement weather conditions, samples were not collected in September. Samples were collected using an epibenthic sled (area = 0.39 m^2), with a 1.0 mm mesh size net. A flow meter Model 2030R (General Oceanics) was attached to the net frame in order to determine the volume of water that passed through the net during each sampling event. Field sampling was completed in two days each month. At each site, two horizontal tows were conducted at an average speed of 2 knots for 5 min. In the field, the net was rinsed and all macroinvertebrates were passed through a 0.5 mm sieve. Additionally, epifauna were separated from macroalgae by shaking each macroalgal fragment in a bucket filled with seawater. The macroinvertebrates retained were passed through a 0.5 mm sieve and all the invertebrates were fixed in 5% neutral buffered formalin. All macroalgae collected with the sled were stored in plastic bags with seawater in a cooler. The macroalgae were washed over a sieve with a 0.3 mm mesh size. Each macroalgal fragment was then visually examined further

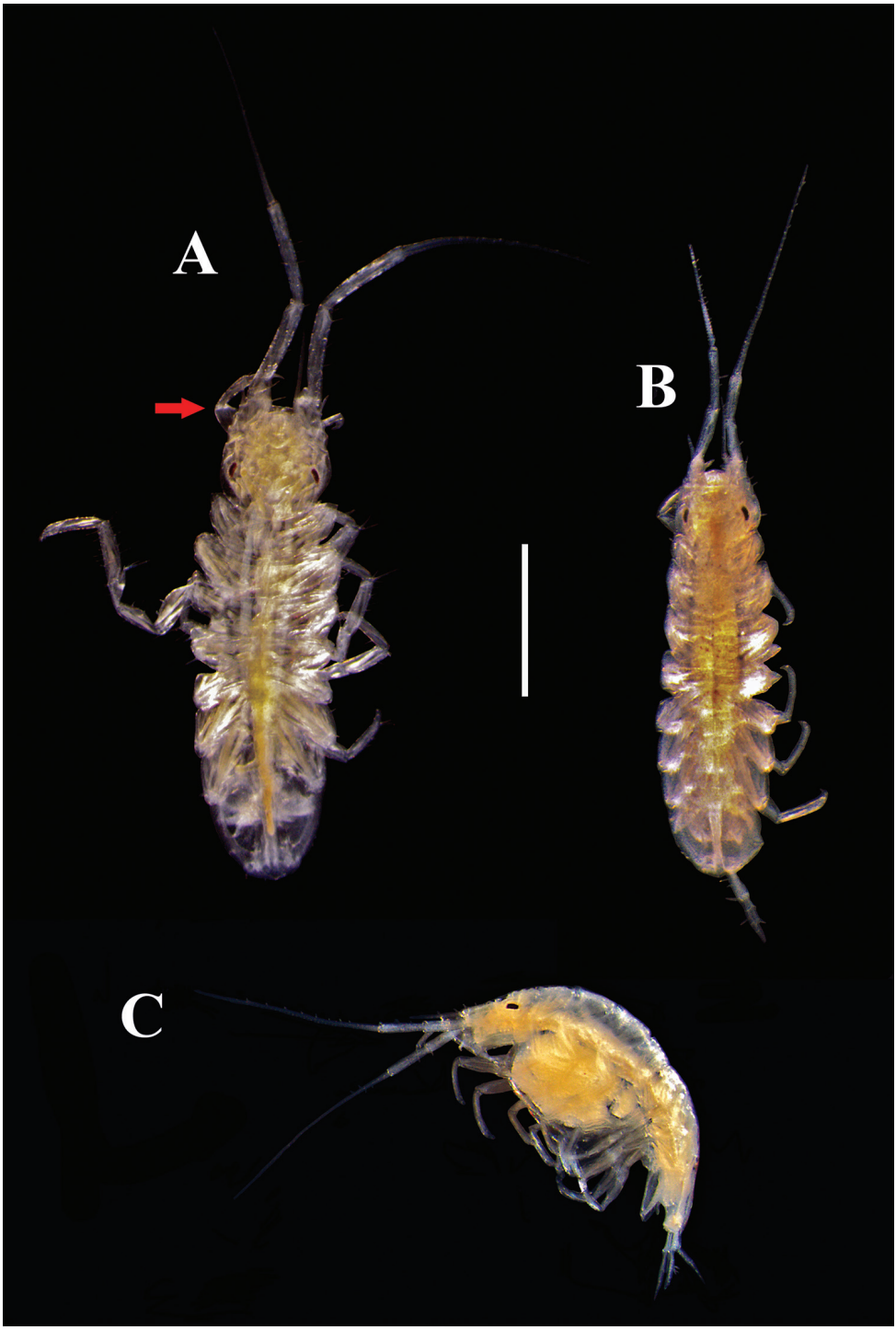

Figure 2. Pictures of habitus of *Ianiropsis* cf. *serricaudis* from Maryland Coastal Bays. **A** adult ♂, dorsal view, 3.0 mm TL **B** ♀ with oostegites, dorsal view, 2.7 mm TL **C** ovigerous ♀, lateral view, 2.26 mm TL. Arrow indicate the long maxillipedal palp from dorsal view on ♂. Scale bar: 1.0 mm.

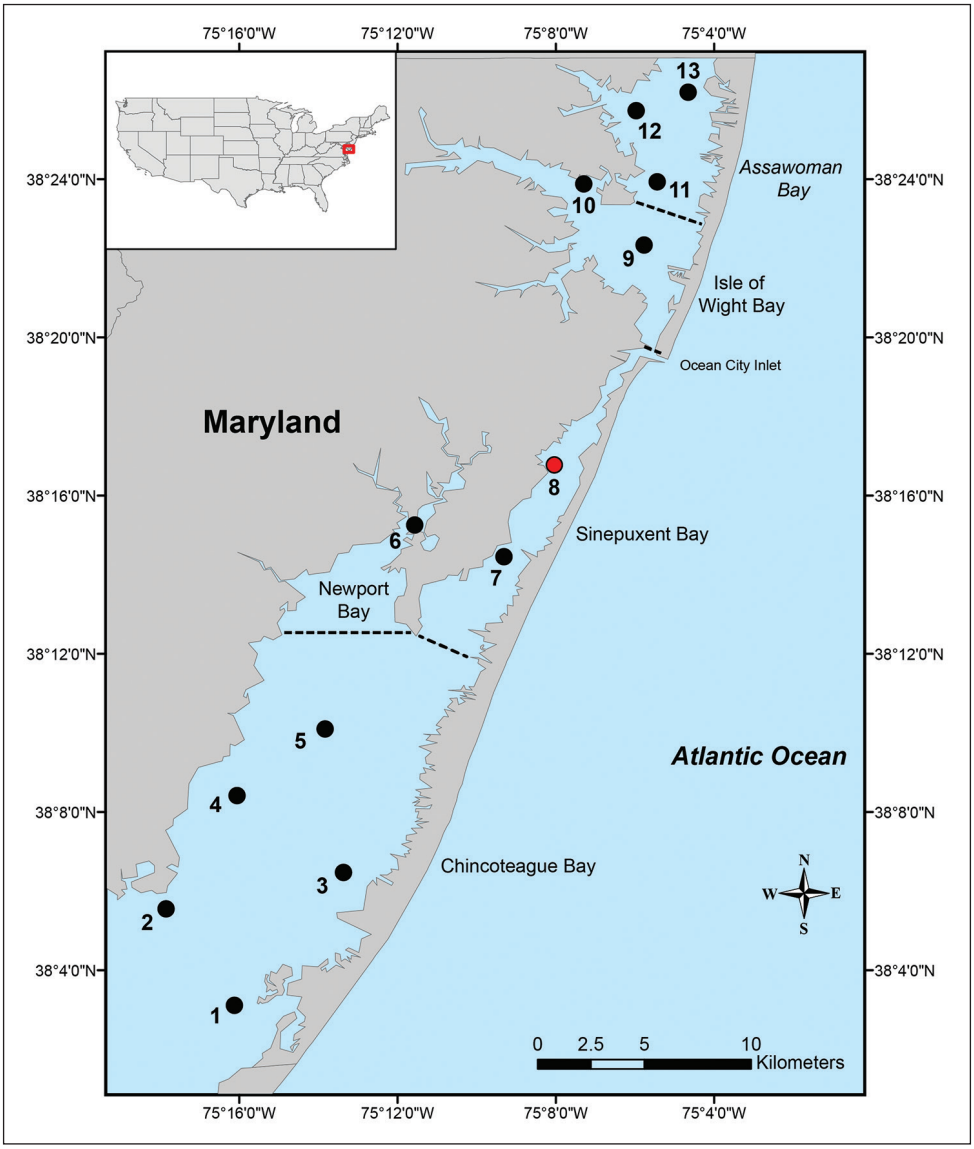

Figure 3. Map of Maryland Coastal Bays indicating the 13 stations sampled. Red circle (station 8) indicates the only station where *Ianiropsis* cf. *serricaudis* was collected; dotted lines separate bays.

to confirm that all epifaunal invertebrates had been removed. All invertebrates collected were counted, identified to the lowest practical taxonomic level, and preserved in ethanol (70 %).

Water quality data were collected *in situ* using a YSI 6600 Multi-Parameter Water Quality Sonde and included water temperature, salinity, dissolved oxygen, and pH, which were all recorded at 0.3 m from the bottom (Table 1). Additionally, water depth and clarity (i.e. Secchi disc transparency) were recorded at each site.

Specimens of *I.* cf. *serricaudis* were dissected under an Olympus SXZ16 stereomicroscope. Appendages were mounted on glass slides in glycerin and observed with an

Table 1. Mean ± SE monthly values of abiotic variables from March to December 2012 in MCBs. * No data were collected.

Months	Temperature (°C)	Salinity (PSU)	Dissolved Oxygen (mg L^{-1})	pH	Depth (m)	Secchi Depth (m)
March	11.8 ± 0.60	32.2 ± 1.20	9.1 ± 0.19	8.0 ± 0.05	*	*
April	14.7 ± 0.77	34.6 ± 0.76	7.9 ± 0.10	8.0 ± 0.02	1.9 ± 0.13	*
May	17.2 ± 0.49	34.1 ± 0.53	7.6 ± 0.19	8.0 ± 0.02	1.6 ± 0.26	0.7 ± 0.10
June	21.7 ± 0.34	32.5 ± 0.46	6.9 ± 0.13	7.8 ± 0.40	1.9 ± 0.14	0.7 ± 0.06
July	26.4 ± 0.23	32.9 ± 0.45	6.0 ± 0.16	7.8 ± 0.03	2.0 ± 0.13	0.6 ± 0.04
August	24.5 ± 0.11	34.4 ± 0.51	5.7 ± 0.24	7.7 ± 0.04	1.7 ± 0.21	*
October	17.6 ± 0.1	27.6 ± 0.6	8.1 ± 0.1	8.0 ± 0.0	2.1 ± 0.16	1.2 ± 0.06
November	9.6 ± 0.2	26.4 ± 0.8	10.4 ± 0.3	8.0 ± 0.0	2.2 ± 0.26	1.0 ± 0.10
December	8.0 ± 0.1	28.2 ± 0.6	10.3 ± 0.1	8.0 ± 0.0	2.1 ± 0.24	1.0 ± 0.20

Olympus BX41 compound microscope, and drawings were made with a *camera lucida*. Illustrations were prepared with Adobe Illustrator CS6 Extended. Photographs were taken using an Olympus DP73 digital camera mounted on a stereomicroscope Olympus SXZ16 and all specimens were measured with CellSens dimensions 1.11 software (Olympus). Specimens have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). All measurements are in millimeters (mm). Total body length (TL) was measured from the frontal margin of the head to the tip of the pleotelson.

All specimens of *Ianiropsis* cf. *serricaudis* were sexed and classified into three categories:

(1) males (Fig. 2a) with maxillipedal palp visible on dorsal view, nonetheless, when the maxillipedal palp could not be observed in dorsal view, the triangular shape at the apex of the pleopod-1 was used, (2) females with oostegites (Fig. 2b), and (3) ovigerous females (Fig. 2c) with embryos in the marsupium (Fig. 2c).

We were not able to re-examine the type material or topotypes of *Ianiropsis serricaudis* in order to clarify uncertainties about the morphology of this species. For this reason, identification of the specimens from this study is based on the morphological characters from previous descriptions (Gurjanova 1936; Kussakin 1962, 1988; Jang and Kwon 1990; Hobbs et al. 2015).

Nevertheless, specimens of *Ianiropsis* sp. from Florida and off Virginia coast logged at the USNM were examined to determine whether they are conspecific with *I. serricaudis*.

Abbreviations

MCBs Maryland Coastal Bays
PSU Practical Salinity Unit
USNM National Museum of Natural History, Smithsonian Institution, Washington DC
TL Total body length

Results

Abiotic variables

The mean (±SE) values of environmental parameters measured in the MCBs during this study period are summarized in Table 1. Mean temperature (°C) ranged from 8.0 ± 0.1 to 26.4 ± 0.23, salinity (PSU) from 26.4 ± 0.8 to 34.6 ± 0.76, and dissolved oxygen (mg l^{-1}) from 6.0 ± 0.16 to 10.4 ± 0.3. Furthermore, pH ranged from 7.7 ± 0.04 to 8.0 ± 0.05, depth (m) from 1.7 ± 0.21 to 2.2 ± 0.26, and Secchi depth (m) transparency from 0.6 ± 0.04 to 1.2 ± 0.06.

Composition of population

A total of 29 individuals of *Ianiropsis* cf. *serricaudis* was counted and sexed. Among them, 13 were females with oostegites, three were ovigerous females, and 13 were males (Table 2). Specimens of *I.* cf. *serricaudis* were only found in one of thirteen stations along the bays (Fig. 2); all of them were found in October (2012) (Fig. 4).

Size-distribution of population

The body sizes of individual *Ianiropsis* cf. *serricaudis* measured in the MCBs during this study are presented in Table 2. Females with oostegites varied from 0.95 to 2.52 mm; mean TL was 1.98 ± 0.15 (n = 12). The smallest observed ovigerous female was 1.91 mm, while the largest was 2.34 mm, mean TL was 2.17 ± 0.13 (n = 3). Males ranged from 1.38 mm to 3.0 mm; mean TL was 2.21 ± 0.13 (n = 13).

Systematics

Order Isopoda Latreille, 1817
Suborder Asellota Latreille, 1802
Superfamily Janiroidea Sars, 1897
Family Janiridae Sars, 1897
Genus *Ianiropsis* Sars, 1897

***Ianiropsis* cf. *serricaudis* Gurjanova, 1936**
Figures 2, 5–12, 13D

Material examined. 13 ♂♂ (three USMN: 1480972, 1480973, and 1480974), one ovigerous ♀, two ♀♀ carrying juveniles (one USNM 1480975), and 13 ♀♀ with oostegites (two USNM: 1480976 and 1480977), station-8 (38°16.825'N – 75°08.032'W), Sinepuxent Bay, USA, depth 3.1 m, October 25-2012, collected by A.G. Morales-Núñez.

Table 2. TL and comparison of morphological features of stages of *Ianiropsis* cf. *serricaudis* from Maryland Coastal Bays.

Stages	TL (mm)	No. of antennular articles (Left–Right)	Length–Antenna (mm)	Length antennal articles 5–6 (Left–Right)	No. of lateral spines of pleotelson (Left–Right)	Maxilliped–dorsal view
Females with oostegites						
1	0.99	7–7	1.0	0.23–0.22	3–3	
2	0.95	7–7	1.0	0.21–0.23	3–3	
3	1.98	10–10	Missing	Missing	4–4	Not visible
4	2.26	11–11	1.68	0.60–missing	2–2	Not visible
5	1.95	10–10	1.86	0.48–0.45	4–4	Not visible
6	2.52	9–10	2.22	0.73–0.57	4–3	Not visible
7	2.44	12–12	2.09 (broken)	0.77–missing	4–2?	Not visible
8	2.36	11–11	2.28	0.67–0.71	4–4	Not visible
9	2.33	11–11	2.28	0.57–0.61	3–4	Not visible
10	2.21	10–11	Missing	Missing	4–2?	Not visible
11	1.89	Missing	Missing	Missing	3–3	Not visible
12	1.86	10–10	2.23	Missing–0.47	3–4	Not visible
13	Broken	12–12	Missing	Missing	Missing	Not visible
Mean ± SE	1.98 ± 0.15					
Ovigerous females						
1	1.91	10–10	Missing	Missing	3–4	Not visible
2	2.26	10–10	2.22	0.57–0.56	3–3	Not visible
3	2.34	11–11	2.39	Missing–0.60	2–2	Not visible
Mean ± SE	2.17 ± 0.13					
Males						
1	2.14	Damaged	2.45	0.76–0.78	4–3	Not visible
2	2.2	11–12	2.39	0.64–0.65	3–3	Not visible
3	3.0	13–14	3.02	1.21–1.17	4–4	Visible
4	1.76	10–10	Missing	Missing	3–3	Not visible
5	1.53	Missing–10	1.12	0.31–missing	4–4	Not visible
6	1.38	9–9	1.4	0.34–0.37	3–3	Not visible
7	2.43	13–13	3.0	1.02–0.76	3–3	Visible
8	2.7	14–13	1.20 (broken)	0.36–missing	3–4	Visible
9	2.93	12–13	3.1	1.29–1.24	4–4	Visible
10	2.22	12–12	Missing	Missing	3–3	Visible
11	2.19	12–12	1.59 (broken)	0.63–0.49	4–4	Not visible
12	2.17	12–12	1.49 (broken)	Missing–0.76	4–4	Visible
13	2.09	11–11	2.28	0.61–0.58	4–2	Not visible
Mean ± SE	2.21 ± 0.13					

Description. Based on adult terminal ♂ of *Ianiropsis* cf. *serricaudis* from Maryland Coastal Bays. *Body* (Fig. 5A). TL 3.0 mm, about 3.1 times as long as wide, pigmentation in preservative scattered brown pigment.

Head (Fig. 5A). ~0.15 TL, 1.7 width, anterior margin with a light median convexity, posterior margin linear, each lateral margin with small simple setae of various

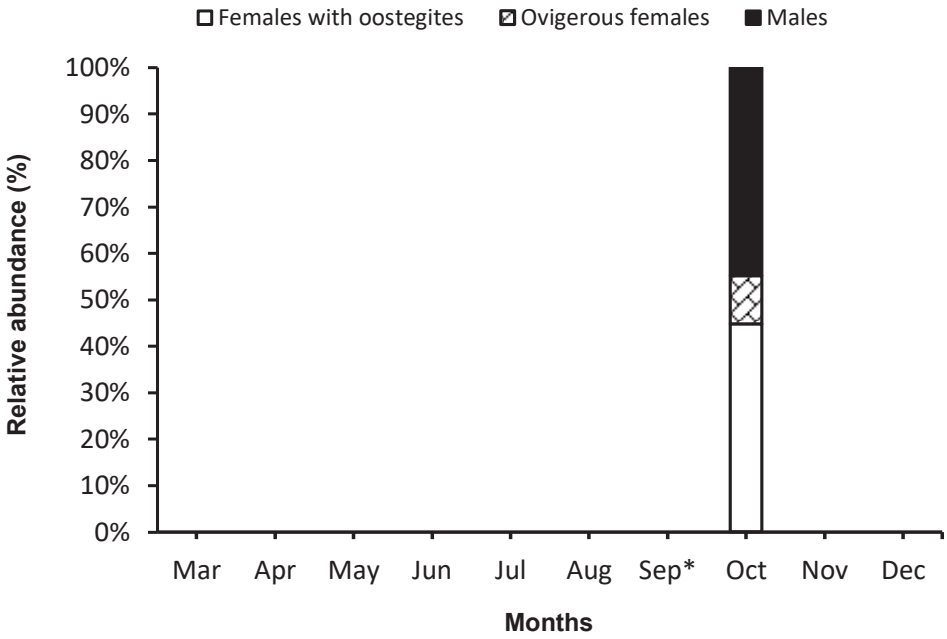

Figure 4. Relative abundance of developmental stages of *I.* cf. *serricaudis* in 2012. *Samples were not taken in September.

lengths, longer than pereonite 1. Eyes dorsal, set back from lateral margin, pigmented with more than 15 well-developed ommatidia.

Pereon (Fig. 5A). ~0.6 TL, all pereonites wider than long, pereonites 1–3 sub-equal in length, pereonites 4 and 5 shorter than pereonites 1–3 and 5–6, both lateral margins of each pereonite with small simple setae of various lengths.

Pleotelson (Fig. 5A–B). ~0.25 TL, ovate, with three to four denticles on each lateral margin (Fig. 5A–B).

Antennule (Figs 5A, 6A). ~0.25 TL, tip reaching 0.73 of length of antennal article 5, with 13–14 articles. Article 1 widest, 1.1 times as long as wide, inner margin with a sub-proximal small simple seta and two (one simple and one sensory) distal setae; outer margin with three (two short) distal setae. Article 2, 1.3 times as long as wide, distal margin with row of seven simple setae of unequal lengths; outer mid-margin with sensory seta. Article 3, 1.2 times as long as wide, asetose. Flagellum with ten articles; articles 8, 10 and 13 with one aesthetasc. Article 13 minute, with three distal simple setae of various lengths.

Antenna (Figs 5A, 6B). As long as body, articles 1–6 about ½ of TL. Articles 1 and 2, wider than long, with simple seta on distal outer margin. Article 3 sub-quadrate, with small seta near to the insertion of the antennal scale. Article 4, wider than long, with two simple setae on inner distal margin. Article 5, twice as long as combined

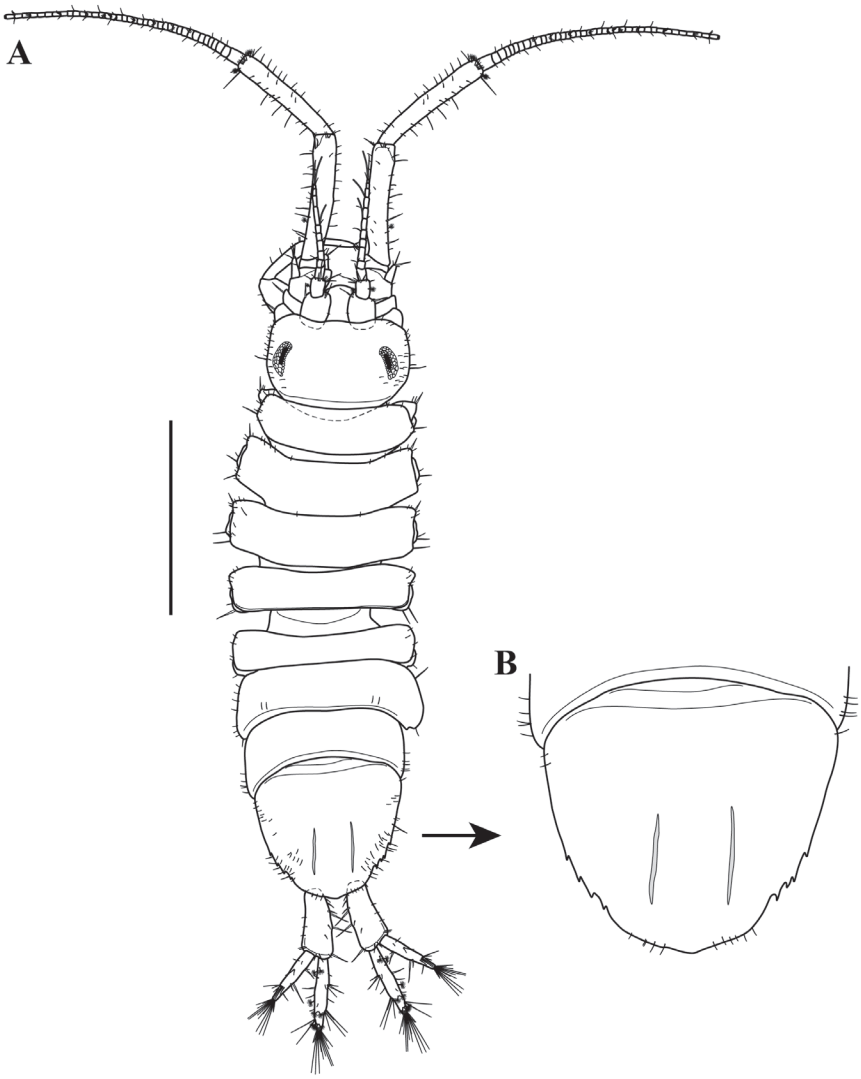

Figure 5. *Ianiropsis* cf. *serricaudis* from MCBs, Adult ♂. **A** dorsal view **B** enlargement of pleotelson. Scale bar: 1.0 mm (**A**).

lengths of articles 1–4. Article 6, slightly shorter than article-5. Flagellum with 39–45 sub-equal articles. Antennal scale longer than article 4, with five simple setae on distal margin of varying lengths.

Mouthparts. *Upper lip* (Fig. 7A) broad, with fine apical setae.

Mandibles (Fig. 7B–E). Molar process well developed with two denticulate setae (Fig. 7B and 7E, respectively); left mandible with strong incisor bearing five teeth (Fig. 7C), *lacinia mobilis* with five teeth and two rows of simple setae in the middle area (Fig. 7B, D); setal row with five denticulate setae (Fig. 7B); right mandible with incisor bearing five teeth, setal row with eight denticulate setae and two bifid setae (Fig. 7E).

Palp article 1, 3.5 times as long as wide, with small simple seta on mid-margin and two (one longer and one small) simple setae on distal margin; article 2 longest, 2.9 times as long as wide, with three (two long and one short) denticulate setae on sub-distal lateral margin, with small simple seta on distal margin; article 3, 3.9 times as long as wide, with row of ± 25 denticulate setae along the lateral margin (Fig. 7E).

Lower lip (Fig. 7F). Two pairs of lobes with inner margins setulate.

Maxillule (Fig. 7G–I). Inner lobe with four setulate distal setae, outer and distal margin with simple setae. Outer lobe with 12–13 robust denticulate distal setae (Fig. 7H–I), with one simple seta on mid sub-distal margin, both margins finely setose (Fig. 7G).

Maxilla (Fig. 7J–M). Inner lobe with seven denticulate setae (Fig. 7K), both margins finely setose. Outer and middle lobes having one "comb-like" seta (Fig. 7L) and three finely setulate setae (Fig. 7M), both margins finely setose.

Maxilliped (Fig. 8A–G). Basis, 1.2 times wider than long. Endite, 2.0 times as long as wide, outer margin with 11–12 simple setae (Fig. 8B); inner proximal margin with two coupling hooks (Fig. 8B, F–G), sub-distal inner margin with one setulate seta and ~seven simple setae, sub-distal margin with seven (six on dorsal view (Fig. 8B) and one on ventral view (Fig. 8G), respectively) fan setae (Fig. 8C), distal margin with 12 (seven (Fig. 8B) and five (Fig. 8G), respectively) setulate setae (Fig. 8D), inner distal margin with three simple setae (Fig. 8E). Palp 7.4 times longer than basis (Fig. 8A): article 1, wider than long; article 2, wider than long, 3.4 times as long as article-1, inner distal margin with two clusters of simple setae of varying lengths; article 3, longer than wide, 1.7 times as long as wide, slightly longer than twice of article 2; mid-proximal inner margin greatest wide, with a row of simple setae of varying lengths; article 4 longest, 5.6 times as long as wide, with row of 12–13 simple setae on inner distal margin; article 5 sub-equal length of that of article 3, 9.5 times as long as wide, with a row of 10–11 simple setae on inner margin.

Pereopod I (Fig. 9A–B). Extremely longer, 1.2 times longer than TL, basis to propodus longer than other six pereopods. Basis elongate, 8.3 times as long as wide; with eight small simple setae along dorsal margin; with one simple seta and 13 robust setae along ventral margin. Ischium elongate, 5.6 times as long as wide; with 11 simple setae along dorsal margin; with one simple seta on disto-medial margin; with six simple small setae along ventral margin. Merus elongate, 2.7 times as long as wide, widest distally; with five simple setae including two small setae along dorsal margin, disto-dorsal lobe with three distal setae; with simple seta on disto-lateral margin; with six simple setae of varying lengths on ventral margin. Carpus elongate, 4.6 times as long as wide; with eight (one small) simple setae along dorsal margin and three small disto-dorsal simple setae; with 18 simple setae and three robust setae along ventral margin. Propodus elongate, 8.0 times as long as wide; with 11 (two small) simple setae along dorsal margin and cluster of four simple setae on sub-distal dorsal margin; with four simple setae on lateral margin; with 12 simple setae along ventral margin, with five simple setae of varying lengths and one robust seta on disto-ventral margin (Fig. 9B); articular plate absent. Dactylus with two distal claws, with three simple setae on disto-medial margin between the claws, with four simple setae on disto-dorsal margin (Fig. 9B).

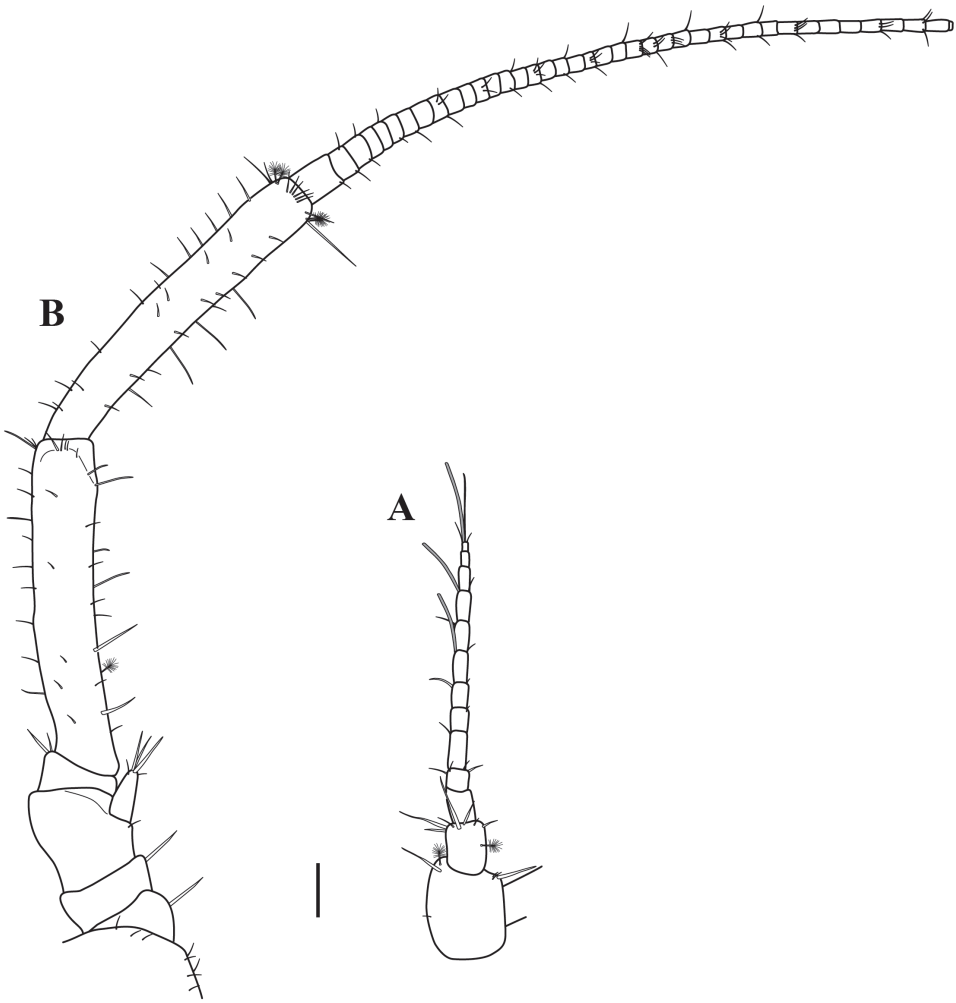

Figure 6. *Ianiropsis* cf. *serricaudis* from MCBs, Adult ♂. **A** antennule **B** antenna. Scale bar: 0.1 mm.

Pereopod II (Fig. 9C–H). Basis, 2.4 times as long as wide; with six simple setae of varying lengths (Fig. 9D), and one sensory seta (Fig. 9E); with three small simple setae along ventral margin. Ischium, 2.6 times as long as wide; with eight simple setae along dorsal margin; with one small simple seta on distal lateral margin; with five simple setae along ventral margin. Merus, 2.0 times as long as wide, widest distally; with two simple setae along dorsal margin, disto-dorsal lobe with three robust setae (Fig. 9F); with simple setae on disto-lateral margin; with five (three distally) simple setae on ventral margin. Carpus, 3.2 times as long as wide; with seven simple setae along dorsal margin and a cluster of one sensory and six simple setae on disto-dorsal margin; with two robust setae (Fig. 9G) and ten simple setae of varying lengths along ventral margin. Propodus, 5.3 times as long as wide, with six simple setae of varying lengths

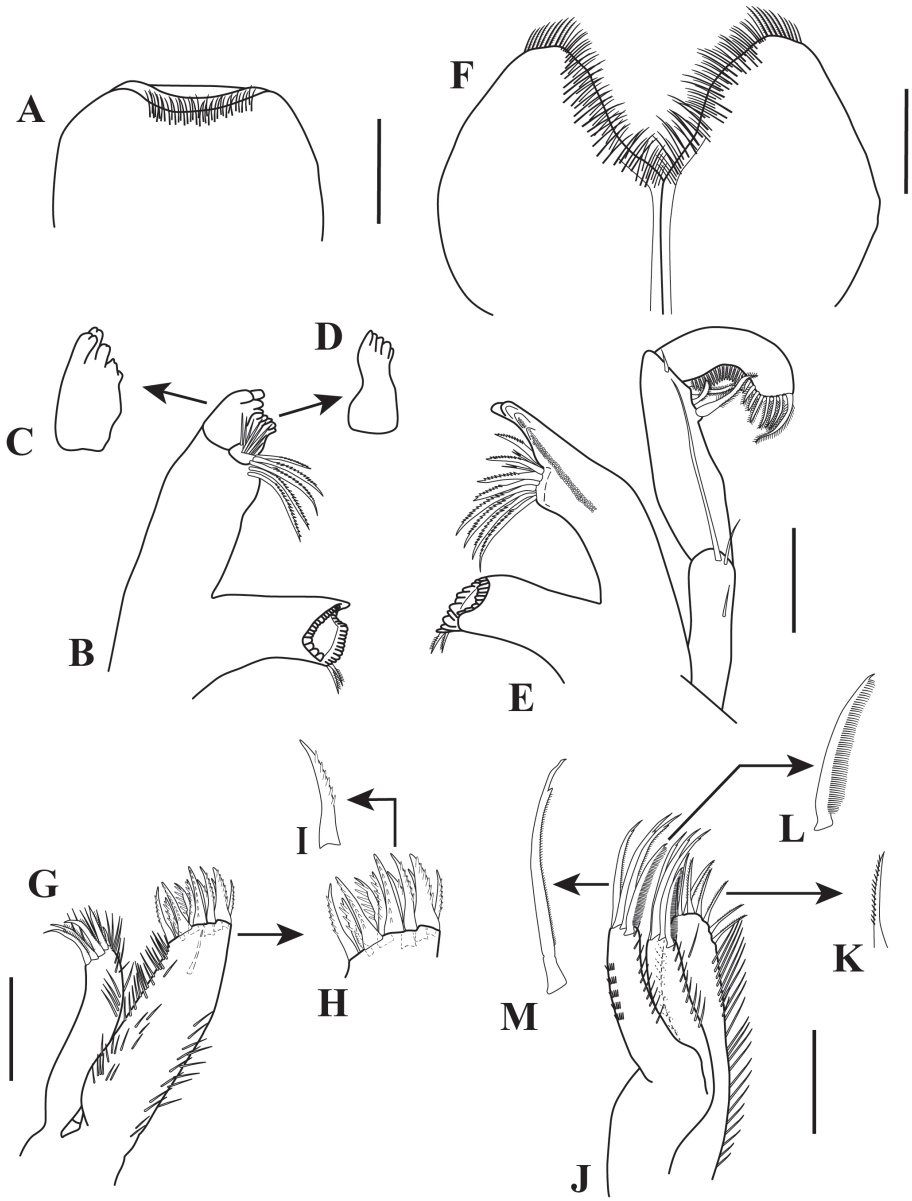

Figure 7. *Ianiropsis* cf. *serricaudis* from MCBs, Adult ♂. **A** labrum **B** left mandible **C** enlargement of incisor process **D** enlargement of *lacinia mobilis* **E** right mandible **F** lower lip **G** maxillule **H** enlargement of tip of outer lobe **I** denticulate seta **J** maxilla **K** denticulate setae **L** enlargement of "comb-like" setae **M** enlargement of finely setulate seta. Scale bars: 0.1 mm (**A–B, E, F, G, J**).

and one robust seta along dorsal margin and one sensory seta and eight simple setae of varying lengths on disto-dorsal margin (Fig. 9C); with six robust setae and five simple setae along ventral margin; articular plate present on disto-lateral margin. Dactylus

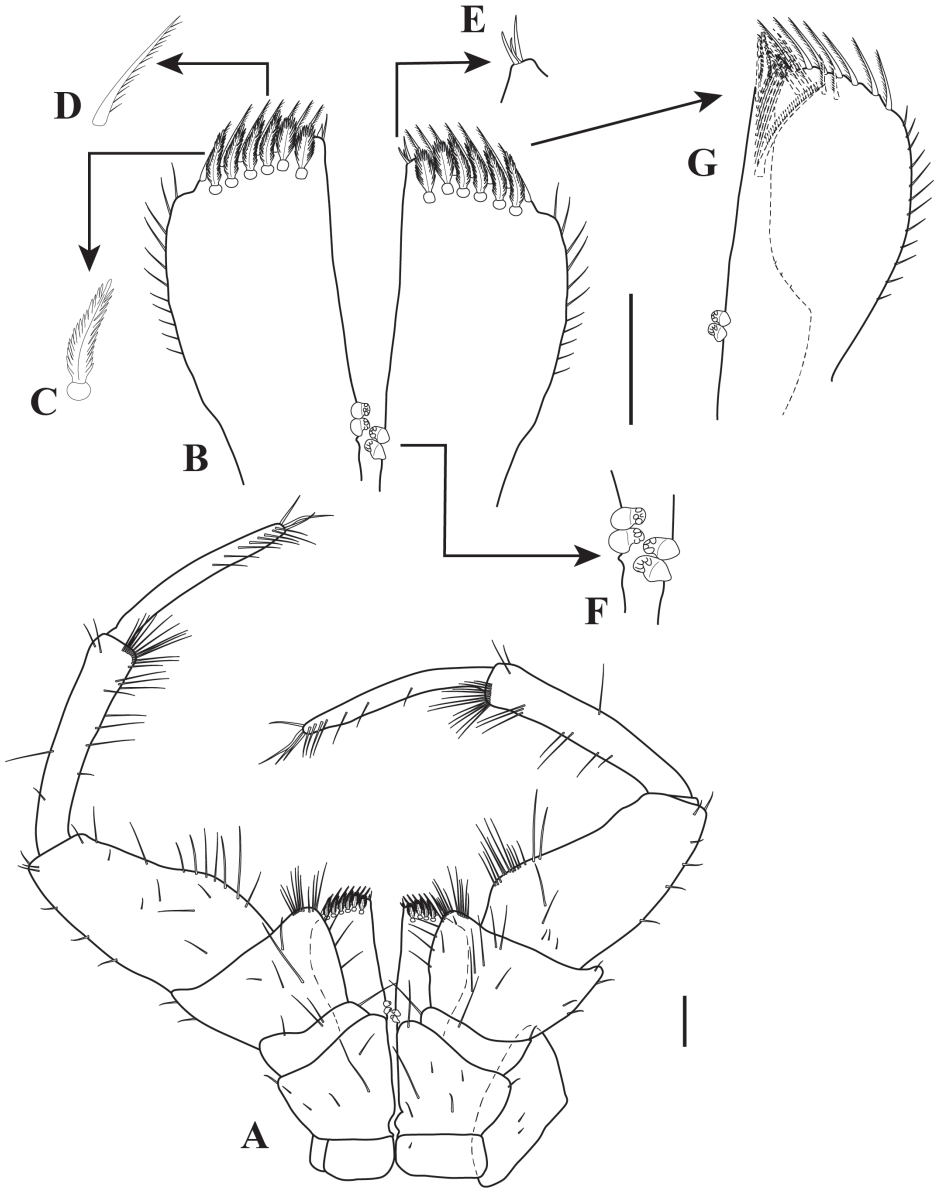

Figure 8. *Ianiropsis* cf. *serricaudis* from MCBs, Adult ♂. **A** maxilliped **B** endite **C** enlargement of fan setae **D** enlargement of setulate setae **E** enlargement of the distal inner margin of endite **G** detail of endite sub-distal end **F** enlargement of coupling hooks. Scale bars: 0.1 mm (**A–B, G**).

with three (one mid-lateral and two distal) claws, with two simple setae on distal lateral margin between the claws, with four simple setae on disto-dorsal margin (Fig. 9H).

Pereopods III–VII (Figs. 9I–J; 10A–H, respectively). *Pereopod III* (Fig. 9I–J): 0.54 times as long as pereopod I. *Pereopod IV* (Fig. 10A–B): 0.46 times as long as pereopod I. *Pereopod V* (Fig. 10C–D): Shortest, 0.39 times as long as pereopod I. *Pereopod VI*

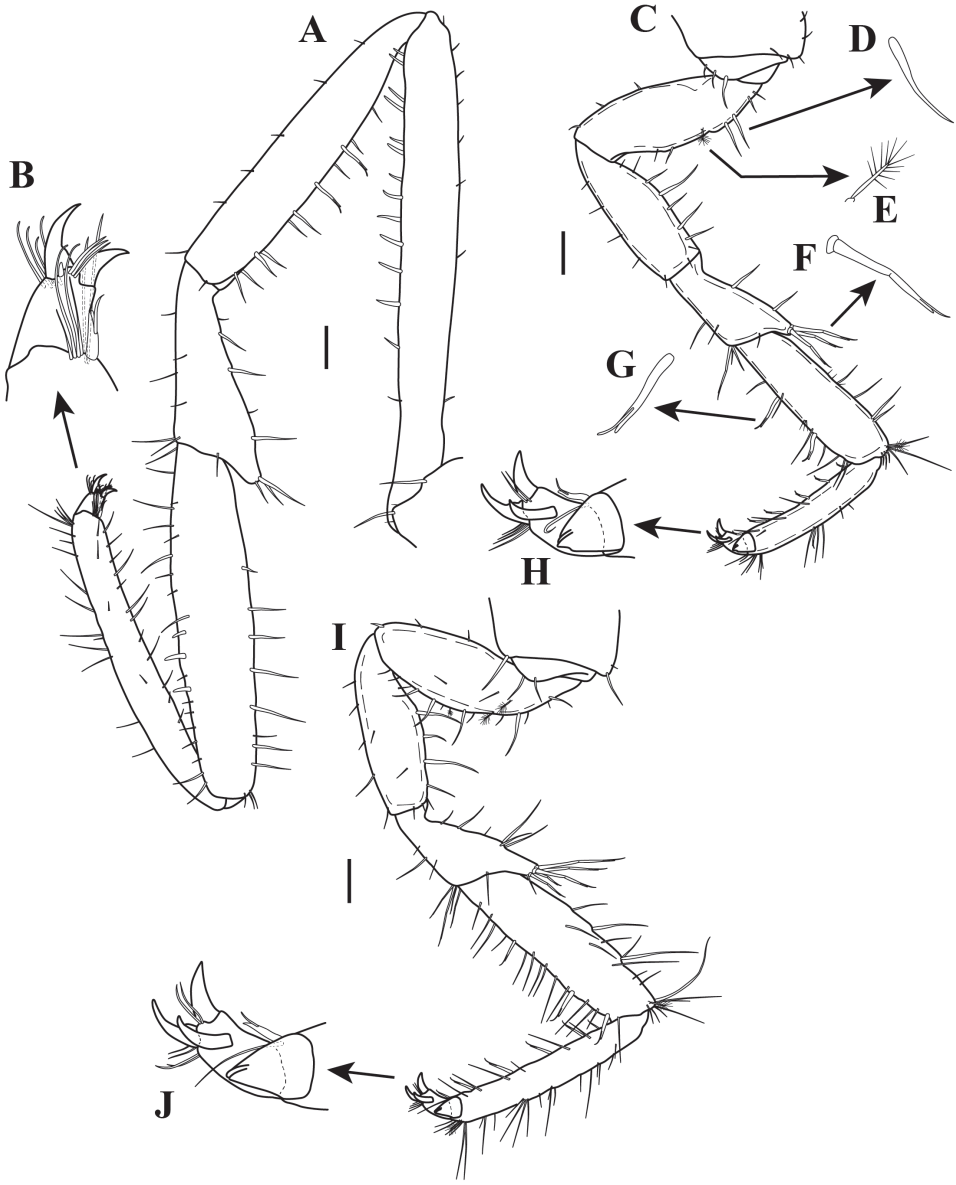

Figure 9. *Ianiropsis* cf. *serricaudis* from MCBs, Adult ♂. **A–B** pereopod I **C–H** pereopod II **I–J** pereopod III. Scale bars: 0.1 mm (**A, C, I**).

(Fig. 10E–F): 0.45 times as long as pereopod I. *Pereopod VII* (Fig. 10G–H): 0.49 times as long as pereopod I.

Pleopod I (Fig. 11A). 8.3 times as long as wide, lateral apex pointed and directed obliquely backward, distal margin with 13–15 simple setae of unequal lengths, subdistal outer margin with 6–7 simple setae.

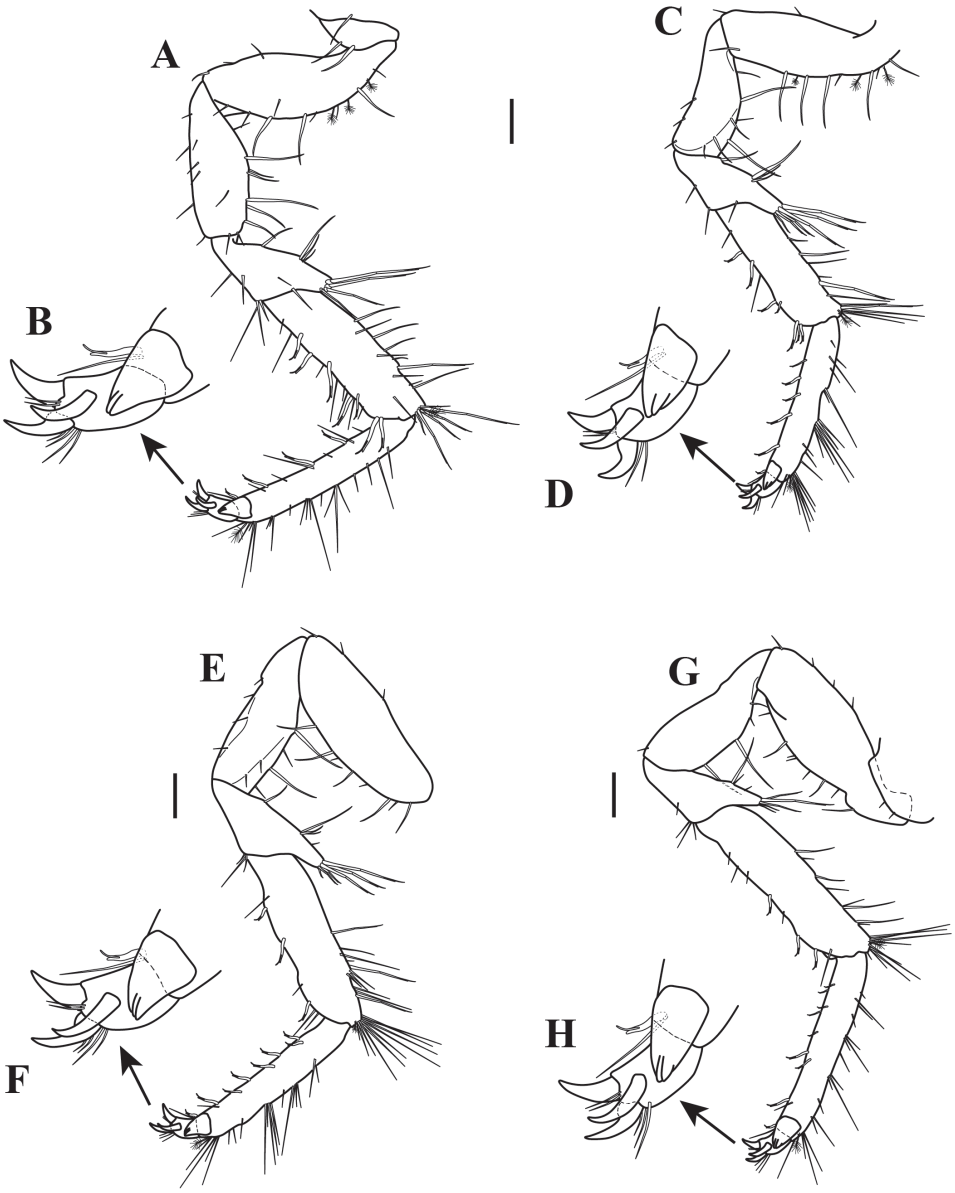

Figure 10. *Ianiropsis* cf. *serricaudis* from MCBs, Adult ♂. **A–B** pereopod IV **C–D** pereopod V **E–F** pereopod VI **G–H** pereopod VII. Scale bars: 0.1 mm (**A, C, E, G**).

Pleopod II (Fig. 11B). Protopod, 1.8 times as long as wide, robust, long-oval asetose, distal margin setae absent. Endopod, stylet bi-articulated, distal tip narrow, curved inwards; exopod distal margin convex, asetose.

Pleopod III (Fig. 11C). Endopod, 2.0 times as long as wide, distal margin rounded, inner margin setulate with plumose seta distally, outer distal margin with two plumose

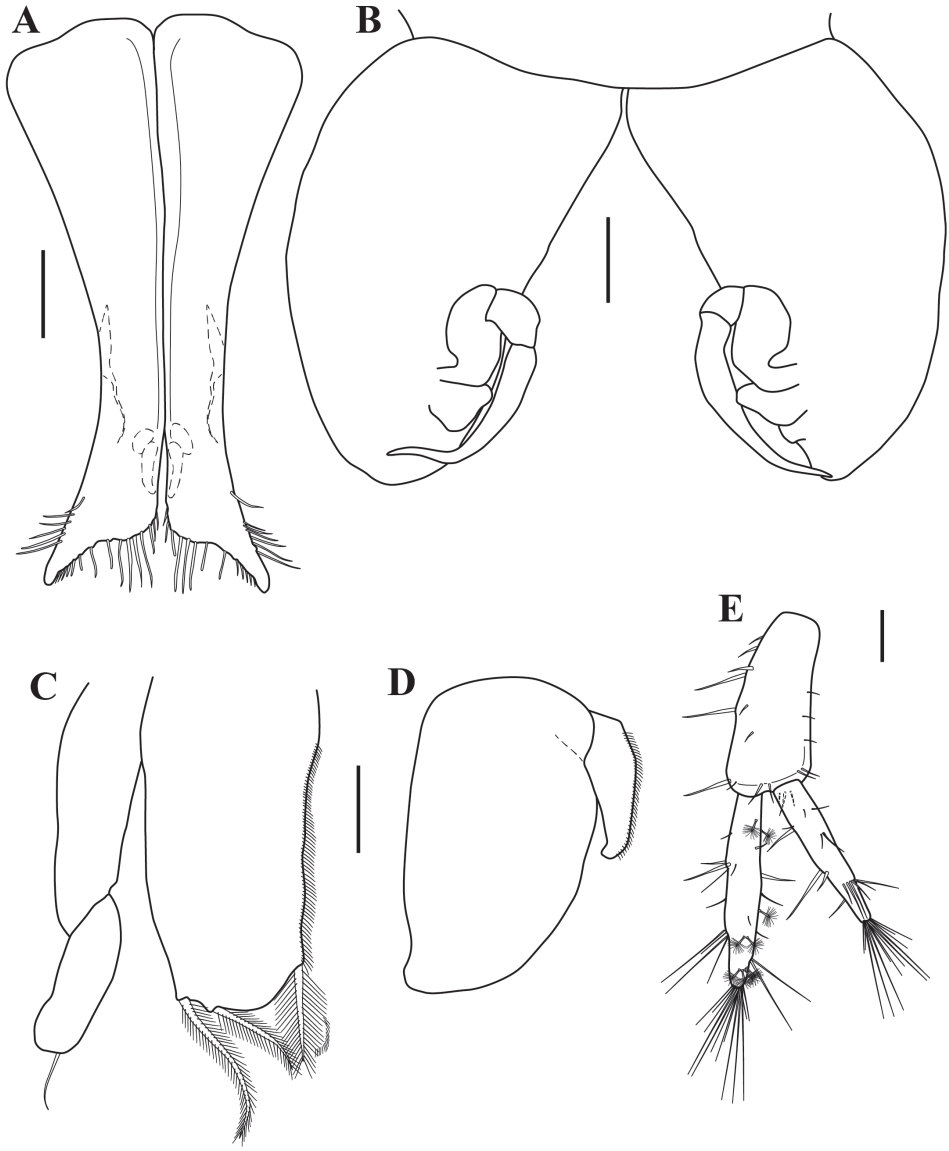

Figure 11. *Ianiropsis* cf. *serricaudis* from MCBs, Adult ♂. **A** pleopod I **B** pleopod II **C** pleopod III **D** pleopod IV. Scale bars: 0.1 mm.

setae; exopod 1.2 times as long as endopod, bi-articulated, articulation between two articles oblique, article 2 distal margin broadly rounded, with simple seta.

Pleopod IV (Fig. 11D). Endopod, 1.7 times as long as wide, asetose; exopod 2.4 times as long as wide, reduced, 0.27 times as long as endopod, half as long as endopod, with outer margin setulate.

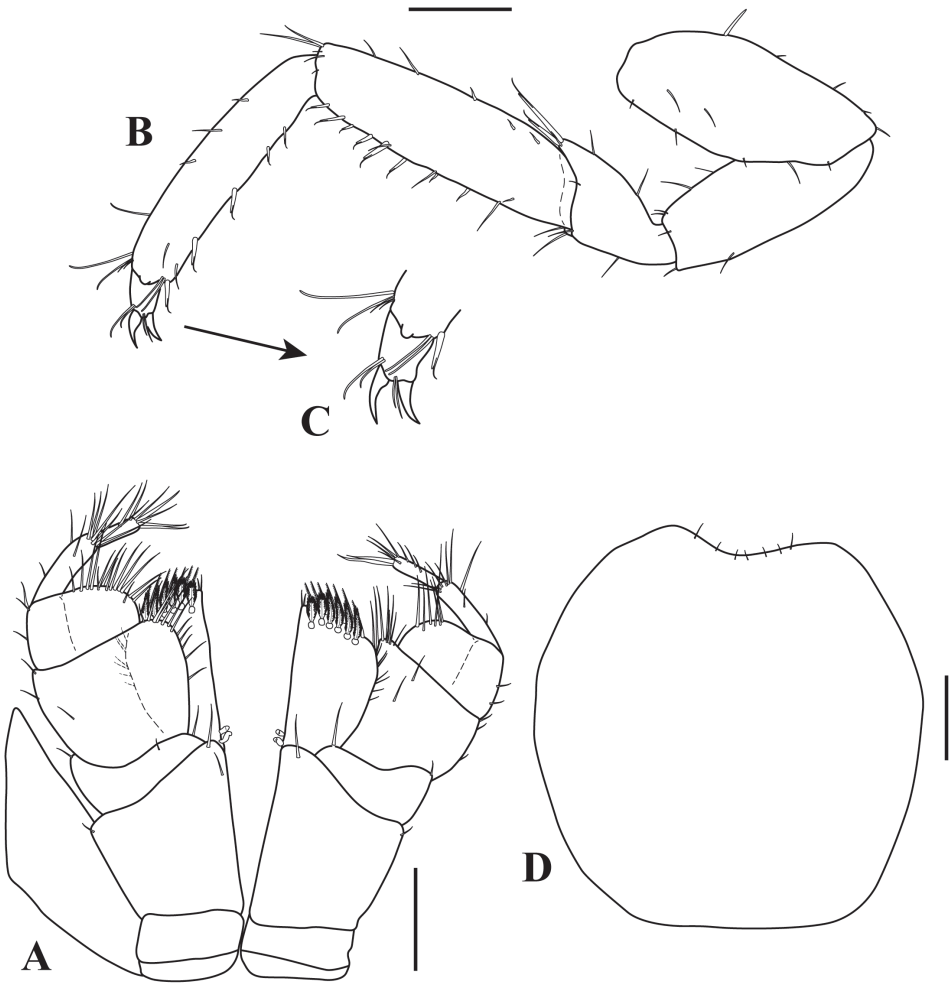

Figure 12. *Ianiropsis* cf. *serricaudis* from MCBs, ♀ with oostegites. **A** maxilliped **B** pereopod I **D** operculum. Scale bar: 0.1 mm.

Uropod (Figs 5A, 11E). 1.1 times as long as pleotelson, slightly longer than pleotelson. Protopod 1.8 times as long as wide, 1.2 times as long as exopod and slightly shorter than endopod, with six spiniform and three simple setae along the inner margin, with two simple setae on distal margin, with five simple setae along outer margin. Endopod, 5.7 times as long as wide, longer than exopod, with several plumose, spiniform and simple setae along both margins, distal margin with 13 simple setae of varying lengths. Exopod, 5.5 times as long as wide, with spiniform and simple setae along both margins, distal margin with 13 simple setae of varying lengths.

Females with oostegites. Smaller than males, mean TL 1.98 mm; TL ranges from 0.95 to 2.52 mm (Table 2). Antennule with 7–12 articles (Table 2). Antenna generally

shorter than TL (Table 2); lengths of antennal articles 5–6 combined, shorter than half TL (Table 2).

Maxilliped (Fig. 12A). Maxillipedal palps cannot be observed on dorsal view, not passing well beyond the basal articles of the antenna. Basis, as long as wide. Endite, 2.0 times as long as wide, outer margin with 7–8 simple setae; inner proximal margin with two coupling hooks, sub-distal margin with seven (six on dorsal view and one on ventral view (not shown), respectively) fan setae (Fig. 8C), distal margin with 12 (seven and five (not shown), respectively) setulate setae (Fig. 8D), inner distal margin with two simple setae. Palp 2,4 times longer than basis: article 1, wider than long; article 2, wider than long, 1.3 times as long as article 1, inner distal margin with 7–8 simple setae of varying lengths; article 3, wider than long, 1.8 times as wide as long, slightly shorter than twice of article 2; inner distal margin with a row of 14–15 simple setae of varying lengths, outer margin with three (one on middle and two on distal) simple setae; article 4, 3.3 times as long as wide, with row of 6–7 simple setae on inner distal margin; article 5, slightly shorter than twice of article 4, 2.3 times as long as wide, with a row of 7–8 simple setae on inner margin.

Pereopod I (Fig. 12B–C). Shorter than male pereopod I, 0.48 times shorter than TL, Basis 2.0 times as long as wide; with six small simple setae along dorsal margin; with two simple seta on proximal-medial margin, and one robust and five simple setae along ventral margin. Ischium, 1.8 times as long as wide; with four simple setae along dorsal margin; with one simple seta on disto-medial margin; with two simple small setae along ventral margin. Merus, 1.5 times as long as wide, widest distally; disto-dorsal lobe with one simple and three robust distal setae, with two small setae along dorsal margin; with simple seta on disto-lateral margin; with four simple setae of varying lengths on ventral margin. Carpus, 3.4 times as long as wide; with five (three small) simple setae along dorsal margin and four disto-dorsal simple setae of unequal lengths; with simple seta on disto-lateral margin, with six simple setae and six robust setae along ventral margin. Propodus, 4.9 times as long as wide; with four simple setae along dorsal margin and cluster of four simple setae of varying lengths on distal dorsal margin (Fig. 12B–C); with simple seta on sub-distal lateral margin, with three (one sub-distal and two distal) simple setae and five robust setae along ventral margin, articular plate absent. Dactylus with two distal claws, with two simple setae on disto-medial margin between the claws, with two simple setae on disto-dorsal margin (Fig. 12B–C).

Operculum (Fig. 12C). As long as wide distal margin concave with small simple distal setae.

Ovigerous females. Slightly smaller than males; mean TL 2.17 mm, ranges from 1.91 to 2.34 mm (Table 2). Antennule with 10–11 articles (Table 2). Antenna usually shorter than TL (Table 2); lengths of antennal articles 5–6 combined, shorter than half TL (Table 2). Maxillipedal palps cannot be observed on dorsal view, not passing well beyond the basal articles of the antenna.

Variations. *Ianiropsis* cf. *serricaudis* from MCBs shows some degree of variations among the individuals as: 1) overall, the number of antennular articles varied between females and males; females have less articles than males (7–12 *versus* 9–14, respectively)

(Table 2); 2) the total lengths of the antennal articles 5–6 combined is shorter than half TL of females and males (Table 2); 3) long maxillipedal palps can be easily observed in dorsal view on largest adult males (2.43–3.0 mm) (Table 2), but elongated maxillipedal palps can be observed also in males of less size (e.g. 2.17–2.22 mm); and 4) the number of denticles on the lateral margins of the pleotelson, ranged from 2 to 4; the three most common denticles combinations were 3–3 (32%), 4–4 (29%), and 3–4 (14%) (Table 2); sometimes the denticles are much less conspicuous.

Other material examined. *Ianiropsis* sp. (USNM 99317): four ovigerous ♀♀, two ♂♂, station II-19 (29.6533 N, -80.38 W), off the coast of Florida, USA, depth 42 m, April-26-1953, identified by Bowman, Thomas E., Smithsonian Institution, National Museum of Natural History. *Ianiropsis* sp. (USNM 190327): one specimen (damaged, apparently ♀), (37.1017N – -74.5533 W), off the coast of Virginia, USA, depth 180 to 200 m, Sep-01-1976, identified by Virginia Institute of Marine Sciences.

Discussion

The original description of *Ianiropsis serricaudis* given by Gurjanova (1936) was based on an apparently adult male with body length of about 3.0 mm that was not fully developed (e.g., pereopod I not elongate; p. 251, fig. 1). Conversely, *I.* cf. *serricaudis* male from MCBs with body length comparable to that of the original description shows a well-developed pereopod I, and males not fully developed (< 2.2 mm) from MCBs have a pereopod I that is not elongate. We corroborated that long maxillipedal palps can be easily observed in dorsal view on the largest adult males (G.D.F. Wilson, pers. comm.). Although, maxillipedal palps with the last three articles elongated are present in males less than 2.2 mm in body length, they are not complete or fully elongated as in adult males to be easily observed in dorsal view (Gurjanova 1936, Kussakin 1988, and this study, Table 2).

Recent studies, Hobbs et al. (2015), Marchini et al. (2016), and Ulman et al. (2017), suggest that *I. serricaudis* is well established along both coasts of the United States and the North-eastern Atlantic. The *I.* cf. *serricaudis* material collected and examined from MCBs is morphologically similar to the materials collected, reported, and illustrated (some characters) of *I. serricaudis* in USA (Hobbs et al. 2015) by having males with: (1) a pleotelson with three to four denticles on lateral margin, (2) adult males with elongated maxillipedal palp which can be seen on dorsal view, (3) dactylus of pereopod I with two claws, and (4) dactylus of pereopods II to VII with three claws. Nevertheless, there are subtle but significant differences between these materials such as: (1) lengths of the antennal articles 5–6 combined, shorter than half TL of males from MCBs *versus* longer than half TL of males from upper areas of North-east coast of USA; and (2) the lowest number of denticles on the lateral margins of the pleotelson registered on MCBs populations was two *versus* three from upper areas of North-east coast of USA. Clearly, there is a need to conduct a detailed revision of the original type material or specimens of *I. serricaudis* from the precise type locality (topotypes),

and more detailed morphological and molecular analysis of the genus to determine the degree of similarity among the populations. To aid in identification of the species especially in the area, we have included a complementary detailed description of an adult male of *I.* cf. *serricaudis* from MCBs.

This is the first time that individuals attributable to *I.* cf. *serricaudis* have been reported from MCBs. This is also the first detailed illustration and description of an adult male of *I.* cf. *serricaudis* from MCBs in the western Atlantic. It is possible, however, that this new finding or possible new record is the result of a more intensive screening effort and careful examination of coastal marine invertebrates in MCBs. The small size of individuals belonging to the species and lack of taxonomic expertise might have led to them being overlooked or misidentified in samples collected previously from the bays by other investigators (Llansó et al. 2002, 2003, 2004, 2005, 2006; Llansó and Dew 2010; Llansó 2015). Furthermore, until a molecular study similar to the work on the isopod, *Asellus* (Verovnik et al. 2009) is conducted to determine if *I. serricaudis* populations from both coasts of the United States and worldwide are conspecifics, the possibility of the existence of undescribed species cannot be rule out.

Unfortunately, all the specimens from Florida examined in this study were in such a bad condition that it was difficult to conduct a detailed taxonomic identification. All of them had a pleotelson without denticles on lateral margin, implying that the specimens are not conspecific with *I. serricaudis*. The only specimen from off Virginia coast that was also examined in this study was equally in bad condition; nonetheless, it has a pleotelson with three denticles on lateral margin. Since this character has been reported in other species within the genus *Ianiropsis* and without the presence of an adult male, we cannot definitely state that the specimen belongs to *I. serricaudis*. In fact, the presence of this *Ianiropsis* specimen collected in 1976 indicates that this genus has been present on the East coast of the United States much earlier than the most recent records of this genus from Maine to New Jersey (Hobbs et al. 2015), and MCBs (this study). Besides, it is interesting that this specimen was collected within a depth range of 190 to 200 m. All members of *Ianiropsis* that have been reported around USA were collected in shallow waters (<10 m).

An illustrated key of males of *Ianiropsis* species belonging to the palpalis-group (Wilson and Wägele 1994) is presented. Wilson and Wägele (1994) established the term "palpalis-group" to include within the genus *Ianiropsis* all the males that have long maxillipedal palps, which can be observed on dorsal view, passing well beyond the basal articles of the antenna (Wilson and Wägele 1994; Doti and Wilson 2010).

Key to species of *Ianiropsis* "*palpalis*-group"

1 Pleotelson without denticles on each lateral margin (Fig. 13A) ....***Ianiropsis palpalis*** **Barnard, 1914** [South Africa]

– Pleotelson with two to four denticles on each lateral margin (Fig. 13B–D) **2**

2 Pleotelson with two denticles on each lateral margin (Fig. 13B)..... ..... ***Ianiropsis epilittoralis*** **Menzies, 1952** [North East Pacific: California]

– Pleotelson with three to four denticles on each lateral margin (Fig. 13C–D)..... ***Ianiropsis serricaudis*** **Gurjanova, 1936** ***sensu*** **Hobbs et al. 2015** [North West Atlantic: Maine to New Jersey]; and ***Ianiropsis*** **cf.** ***serricaudis*** **Gurjanova, 1936** ***sensu*** **Morales-Núñez and Chigbu, this study** [North West Atlantic: Maryland)

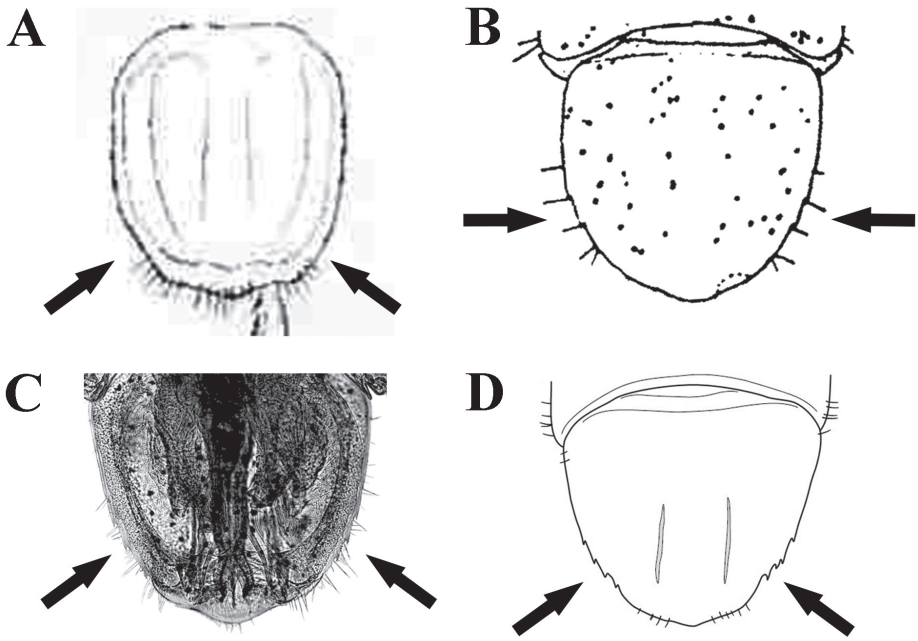

Figure 13. Denticles on lateral margin of pleotelson: **A** *Ianiropsis palpalis* **B** *I. epilittoralis* **C** *I. serricaudis sensu* (Hobbs et al. 2015) – Gulf of Maine to Barnegat Bay **D** *I.* cf. *serricaudis* this study – Maryland Coastal Bays. [Figures modified from (Barnard 1914; Menzies 1952; Hobbs et al. 2015), and this study]; not to scale.

Habitat

Marine epibenthic, in coastal shallow waters (≤ 3.1 m); *Ianiropsis* cf. *serricaudis* was collected with a small mixture of macroalgae (e.g., *Gracilaria* sp. and *Ulva lactuca*). Physicochemical parameters of the surrounding waters were: temperature, 17.94 °C; salinity, 31.63 PSU; dissolved oxygen (mg l^{-1}), 8.35; pH, 7.97, and Secchi depth transparency, 1.7 (m).

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DATA PAPER

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Antarctic and Sub-Antarctic Asteroidea database

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Abstract

The present dataset is a compilation of georeferenced occurrences of asteroids (Echinodermata: Asteroidea) in the Southern Ocean. Occurrence data south of 45°S latitude were mined from various sources together with information regarding the taxonomy, the sampling source and sampling sites when available. Records from 1872 to 2016 were thoroughly checked to ensure the quality of a dataset that reaches a total of 13,840 occurrences from 4,580 unique sampling events. Information regarding the reproductive strategy (brooders vs. broadcasters) of 63 species is also made available. This dataset represents the most exhaustive occurrence database on Antarctic and Sub-Antarctic asteroids.

Keywords

Antarctic, Asteroidea, presence-only data, Southern Ocean, Sub-Antarctic

Introduction

Mapping and understanding life diversity are major issues for the community of biologists and ecologists who focus on the Southern Ocean (SO). For several years, many initiatives such as the International Polar Year, the Census of Antarctic Marine Life (CAML 2005–2010), the Scientific Committee on Antarctic Research: Marine Biodiversity Information Network (SCAR MarBIN, www.biodiversity.aq) or the Biogeographic Atlas of the Southern Ocean (De Broyer et al. 2014) have also gathered information from distinct and transversal scientific domains to provide new multidisciplinary insights in the study of the SO marine ecosystems, linking biogeographic, phylogeographic, physiological, oceanographic, and biogeochemistry data. Such programs have established the most exhaustive and accurate inventories of scientific data ever, since the first historical researches of James Cook in 1772–1775 in the region, and have provided open source information systems (e.g., Register of Antarctic Marine Species, De Broyer and Danis 2010; Global Biodiversity Information Facility, http://www.gbif.org; Ocean Biogeographic Information System http://www.iobis.org/; Van de Putte et al. 2015, http://www.biodiversity.aq).

This extensive assessment was pursued by major improvements in methodologies and data analyses. Improvement of dataset completeness and resolution facilitates modelling approaches (Gutt et al. 2012) that provide interesting tools to better understand distribution patterns in this poorly documented part of the world.

Among benthic taxonomic groups, Asteroidea (Echinodermata) are well represented in the SO with 12% of the global species richness present in the region (Mah and Blake 2012). Around 300 species (Moreau et al. 2015) were reported at all depths including some potential keystone species in benthic communities (McClintock et al. 1988, 2008). As for many taxonomic groups, adaptations of invertebrates to the polar conditions of the SO environments have been widely reported (Peck 2002, 2016) and have led to unique biological traits and life-strategies as well as high levels of endemism in the region (Chown et al. 2015). In particular, reproductive strategies are diversified in the SO with a distinction between brooding and broadcasting species (Poulin et al. 2002; Pearse et al. 2009). In asteroids, the two distinct reproductive strategies strongly

drive species distribution patterns and the biogeography of the class in the SO (Moreau et al. 2017).

The present dataset is a compilation of georeferenced occurrences, at species level, for the whole class Asteroidea in the SO. Records from 1872 to 2016 have been gathered from various open source databases. Data collected during recent and unpublished campaigns were also added including records from literature, reaching a total of 13,840 occurrences from 4,580 unique sampling events. This dataset represents the most exhaustive database on Antarctic and Sub-Antarctic asteroids.

Project description

Project title: Antarctic and Sub-Antarctic Asteroidea database

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Study area descriptions / descriptor: This study focuses on the Antarctic and Sub-Antarctic regions located at latitudes south of 45°S. The Southern Ocean is a vast region characterised by the paucity of its scientific data (Griffiths 2010; Griffiths et al. 2011) and available collections are the compilation of several historical campaigns. The objective of this work is to integrate the most complete database of species occurrences for the class Asteroidea in the described geographic extent.

Design description: The compilation of occurrence data of asteroid species over the extent of the SO was realised by gathering data available from various biodiversity information systems (OBIS, GBIF, biodiversity.aq, PANGAEA https://www.pangaea.de/) as well as published literature, including original manuscripts (e.g., Gutt et al. 2014; Moles et al. 2015), data papers and cruise reports. Compiled occurrences were complemented with data from personal communications of unpublished works and museums registered collections. This extensive dataset was developed to describe distribution patterns in the SO as well as faunal affinities among 25 Antarctic and Sub-Antarctic bioregions (see Moreau et al. 2017). Several analytical methods such as Bootstrap Spanning Network, non-metrical multidimensional scaling (nMDS) and clustering contributed to highlight the importance of the reproductive strategy on the contemporary observed distribution patterns. The importance of environmental parameters such as influence of Antarctic Circumpolar Current (ACC), the influence of the Polar Front (PF), the pres-

ence of gyres or the geographic distance among locations has also been emphasised. This dataset helped to better describe the different biogeographic patterns within asteroids, which are overall congruent with other taxa and differs according to species reproductive strategy. This suggests a differential influence of dispersal capabilities on species distribution patterns. Analyses at genus levels also revealed the underlying legacy of past oceanographic and geodynamic processes in present-day patterns such as the existence of a trans-Antarctic pathway that split the Antarctic continent into two entities in the past. The detailed results are available from Moreau et al. (2017).

Data description: Asteroids are common invertebrates of Antarctic benthic communities considering the relative high species richness of the group in the region with regards to the world total diversity (Danis et al. 2014). They play a significant ecological role in Antarctic ecosystems, including in trophic networks (most species being predators) (Dayton 1972; Lawrence 2013). The present dataset, that focuses on regions located at latitudes higher than 45°S, compiles 28 families out of the 39 known worldwide (Mah 2017) with 13,840 occurrences gathered from various sources. The time coverage of the collection starts in 1872 with the HMS Challenger expedition and ends in 2016 with sampled collected during the *RRS James Clark Ross* JR15005 SO-AntEco cruise.

Associated to occurrence data, depth, relative position to the PF, taxonomic information and bioregion were implemented when available. Depth data were extracted from www.gebco.net. Information regarding the reproductive strategy (brooding or broadcasting) of 63 species out of the 299 described was included in the database. Corresponding bioregions of the observed occurrences were specified following Moreau et al. 2017. A significant part of the specimens is deposited in various institutions: e.g., National Museum of Natural History (NMNH), Museum national d'Histoire naturelle (MNHN), Museo Nazionale dell'Antartide (MNA), Université Libre de Bruxelles (ULB), Museo Argentino de Ciencias Naturales (MACN), National Institute of Water and Atmospheric Research (NIWA).

Quality control description: Data are available at species level. Nomenclature was thoroughly checked using the Taxon Match Tool implemented in the World Register of Marine Species (WoRMS Editorial Board 2016), to delete all potential discrepancies and update the taxonomy determination. All replicates originating from overlapping origins as well as errors regarding the georeferencing, species synonymy, or misspelling were removed. Most of the occurrences additions originating from recent campaigns were identified by Christopher Mah and Camille Moreau.

Taxonomic coverage

General taxonomic coverage description

The present dataset is the most exhaustive and up-to-date list of available occurrences for the class Asteroidea (Echinodermata), in the entire Southern Ocean. This collection

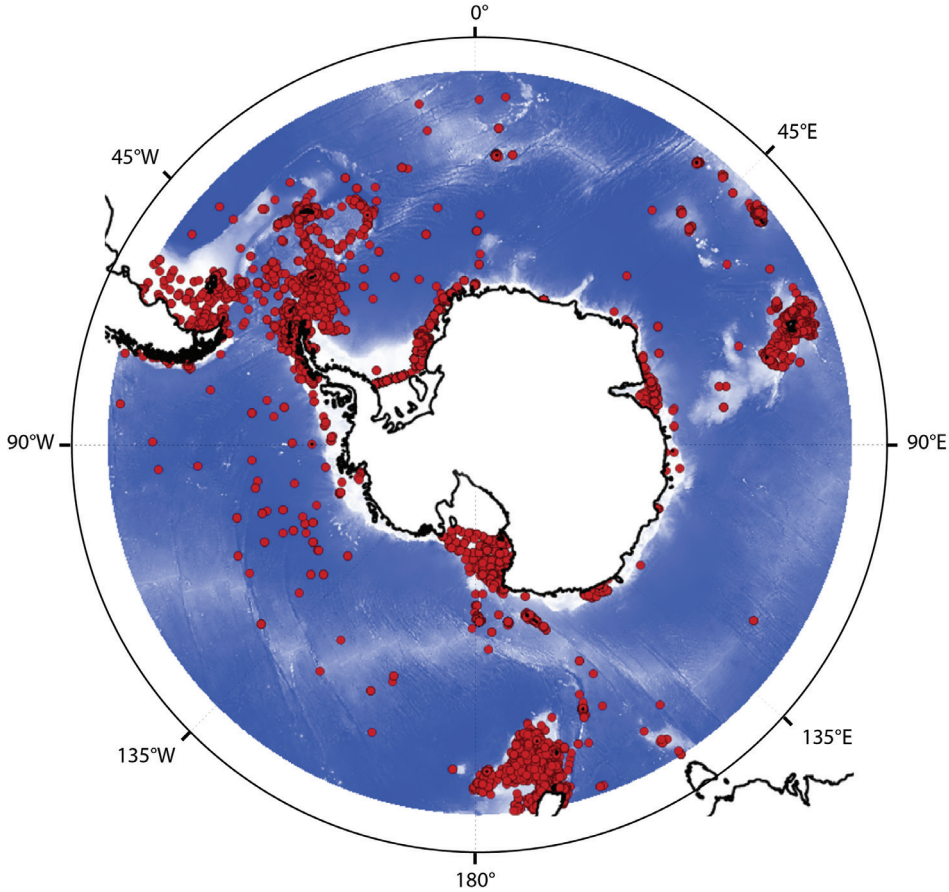

Figure 1. Map of the 13,840 asteroid species occurrences available in the present database, within the boundaries of the Southern Ocean (45°S). Projection: South Pole Stereographic.

provides information about the occurrence of 28 asteroid families, 118 genera, and 299 species. Occurrence distribution is illustrated on Figure 1.

Species richness in the different regions of the SO was estimated based on 1° × 1° grid cell resolution (Figure 2A). Maximum richness (55 species per cell) was found along the Western Antarctic Peninsula. High richness values were also reported in the Weddell Sea as well as in Sub-Antarctic Islands (Kerguelen, Crozet, Marion, and South Georgia Islands). Richness distribution needs to be interpreted carefully considering the patchy and uneven sampling effort of past oceanographic cruises carried out in the SO (Figure 2B). Indeed, considerable parts of the SO present a crucial lack of sampling. In the context of this study, richness values and sampling effort present a significant positive correlation in space (Pearson $r = 0.52$, $p < 0.001$) indicating the need to extend the development of this unique synthesis work and to strengthen the effort for other taxonomic groups.

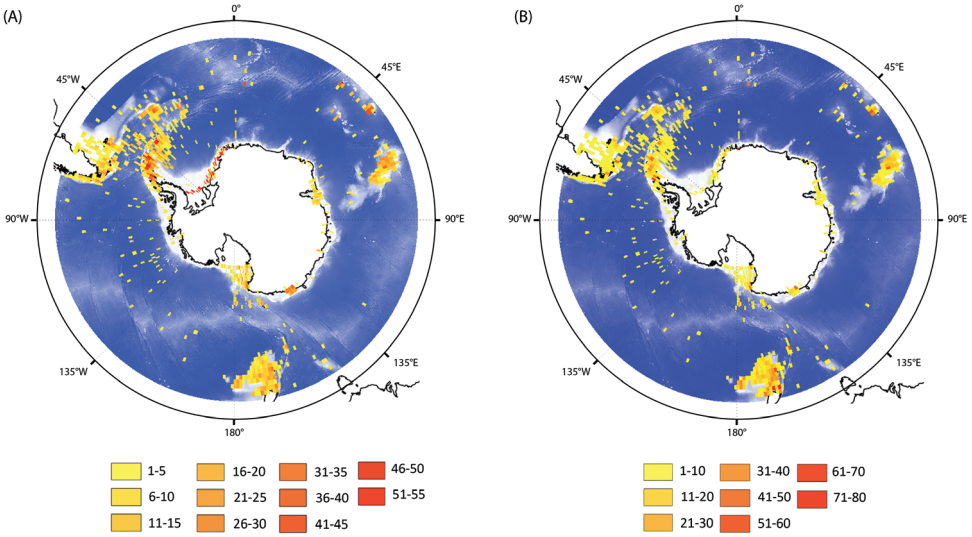

Figure 2. A Species richness in the Southern Ocean. The number of asteroid species present in 1° × 1° grid cells are reported using yellow-red colour chart **B** Sampling effort in the Southern Ocean for the class Asteroidea. The number of sampling station per 1° × 1° grid cell is reported using yellow-red colour chart. Projection: South Pole Stereographic.

Phylum: Echinodermata

Class: Asteroidea

Order: Brisingida, Forcipulatida, Notomyotida, Paxillosida, Spinulosida, Valvatida, Velatida

Family: Acanthasteridae, Asteriidae, Asterinidae, Astropectinidae, Benthopectinidae, Brisingidae, Ctenodiscidae, Echinasteridae, Freyellidae, Ganeriidae, Goniasteridae, Heliasteridae, Korethrasteridae, Leilasteridae, Luidiidae, Myxasteridae, Odontasteridae, Ophidiasteridae, Paulasteriidae, Pedicellasteridae, Poraniidae, Porcellanasteridae, Pseudarchasteridae, Pterasteridae, Radiasteridae, Solasteridae, Stichasteridae, Zoroasteridae.

Genus: *Abyssaster*, *Acanthaster*, *Acodontaster*, *Adelasterias*, *Allostichaster*, *Anasterias*, *Anseropoda*, *Anteliaster*, *Anthenoides*, *Asterina*, *Asthenactis*, *Astromesites*, *Astropecten*, *Astrostole*, *Bathybiaster*, *Belgicella*, *Benthopecten*, *Brisinga*, *Brisingenes*, *Caimanaster*, *Calyptraster*, *Ceramaster*, *Cheiraster*, *Chitonaster*, *Chondraster*, *Cladaster*, *Clavaporania*, *Coscinasterias*, *Cosmasterias*, *Crossaster*, *Cryptasterias*, *Ctenodiscus*, *Cuenotaster*, *Cycethra*, *Diplasterias*, *Diplodontias*, *Diplopteraster*, *Dipsacaster*, *Dytaster*, *Echinaster*, *Eratosaster*, *Eremicaster*, *Freyastera*, *Freyella*, *Freyellaster*, *Fromia*, *Ganeria*, *Gaussaster*, *Gilbertaster*, *Glabraster*, *Granaster*, *Henricia*, *Hippasteria*, *Hymenaster*, *Hymenodiscus*, *Hyphalaster*, *Kampylaster*, *Kenrickaster*, *Labidiaster*, *Leptychaster*, *Lethasterias*, *Lithosoma*, *Lonchotaster*, *Lophaster*, *Luidia*, *Lysasterias*, *Macroptychaster*, *Mediaster*, *Meridiastra*, *Mimastrella*, *Mirastrella*, *Myxoderma*, *Neosmilaster*, *Notasterias*, *Notioceramus*, *Novodinia*, *Odinella*, *Odontaster*, *Odontohenricia*, *Ophidias-*

ter, *Paralophaster*, *Paranepanthia*, *Patiriella*, *Paulasterias*, *Pectinaster*, *Pedicellaster*, *Pentagonaster*, *Pergamaster*, *Peribolaster*, *Perissasterias*, *Perknaster*, *Persephonaster*, *Pillsburiaster*, *Plutonaster*, *Poraniopsis*, *Porcellanaster*, *Proserpinaster*, *Psalidaster*, *Pseudarchaster*, *Pseudechinaster*, *Psilaster*, *Pteraster*, *Radiaster*, *Remaster*, *Rhopiella*, *Saliasterias*, *Sclerasterias*, *Scotiaster*, *Smilasterias*, *Solaster*, *Sphaeriodiscus*, *Stichaster*, *Styracaster*, *Taranuiaster*, *Tarsaster*, *Tremaster*, *Vemaster*, *Zoroaster*.

Species: *Abyssaster diadematus*, *Abyssaster planus*, *Acanthaster planci*, *Acodontaster capitatus*, *Acodontaster conspicuus*, *Acodontaster elongatus*, *Acodontaster hodgsoni*, *Acodontaster marginatus*, *Adelasterias papillosa*, *Allostichaster capensis*, *Allostichaster farquhari*, *Allostichaster insignis*, *Allostichaster polyplax*, *Anasterias antarctica*, *Anasterias asterinoides*, *Anasterias directa*, *Anasterias laevigata*, *Anasterias mawsoni*, *Anasterias pedicellaris*, *Anasterias perrieri*, *Anasterias rupicola*, *Anasterias sphoerulata*, *Anasterias spirabilis*, *Anasterias studeri*, *Anasterias suteri*, *Anseropoda antarctica*, *Anteliaster australis*, *Anteliaster scaber*, *Anthenoides cristatus*, *Asterina fimbriata*, *Asthenactis australis*, *Astromesites primigenius*, *Astropecten brasiliensis*, *Astrostole scabra*, *Bathybiaster loripes*, *Belgicella racowitzana*, *Benthopecten munidae*, *Benthopecten pedicifer*, *Benthopecten pikei*, *Brisinga chathamica*, *Brisingenes multicostata*, *Caimanaster acutus*, *Calyptraster tenuissimus*, *Calyptraster vitreus*, *Ceramaster australis*, *Ceramaster grenadensis*, *Ceramaster patagonicus*, *Cheiraster (Cheiraster) otagoensis*, *Cheiraster (Luidiaster) antarcticus*, *Cheiraster (Luidiaster) gerlachei*, *Cheiraster (Luidiaster) hirsutus*, *Cheiraster (Luidiaster) planeta*, *Chitonaster cataphractus*, *Chitonaster felli*, *Chitonaster johannae*, *Chitonaster trangae*, *Chondraster elattosis*, *Cladaster analogus*, *Clavaporania fitchorum*, *Coscinasterias calamaria*, *Coscinasterias muricata*, *Cosmasterias dyscrita*, *Cosmasterias lurida*, *Crossaster campbellicus*, *Crossaster multispinus*, *Crossaster penicillatus*, *Cryptasterias brachiata*, *Cryptasterias turqueti*, *Ctenodiscus australis*, *Ctenodiscus procurator*, *Cuenotaster involutus*, *Cycethra frigida*, *Cycethra macquariensis*, *Cycethra verrucosa*, *Diplasterias brandti*, *Diplasterias brucei*, *Diplasterias kerguelenensis*, *Diplasterias meridionalis*, *Diplasterias octoradiata*, *Diplasterias radiata*, *Diplodontias dilatatus*, *Diplodontias robustus*, *Diplodontias singularis*, *Diplopteraster clarki*, *Diplopteraster hurleyi*, *Diplopteraster otagoensis*, *Diplopteraster peregrinator*, *Diplopteraster semireticulatus*, *Diplopteraster verrucosus*, *Dipsacaster magnificus*, *Dytaster felix*, *Echinaster farquhari*, *Echinaster smithi*, *Eratosaster jenae*, *Eremicaster crassus*, *Eremicaster pacificus*, *Eremicaster vicinus*, *Freyastera benthophila*, *Freyastera tuberculata*, *Freyella attenuata*, *Freyella drygalskii*, *Freyella echinata*, *Freyella formosa*, *Freyella fragilissima*, *Freyella giardi*, *Freyella heroina*, *Freyella mutabilia*, *Freyellaster polycnema*, *Fromia monilis*, *Ganeria attenuata*, *Ganeria falklandica*, *Ganeria hahni*, *Gaussaster antarcticus*, *Gilbertaster anacanthus*, *Glabraster antarctica*, *Granaster nutrix*, *Henricia aucklandiae*, *Henricia compacta*, *Henricia diffidens*, *Henricia fisheri*, *Henricia lukinsii*, *Henricia obesa*, *Henricia ornata*, *Henricia pagenstecheri*, *Henricia parva*, *Henricia praestans*, *Henricia ralphae*, *Henricia simplex*, *Henricia smilax*, *Henricia spinulfera*, *Henricia studeri*, *Hippasteria falklandica*, *Hippasteria phrygiana*, *Hymenaster caelatus*, *Hymenaster campanulatus*, *Hymenaster carnosus*, *Hymenaster coccinatus*, *Hymenaster crucifer*, *Hymenaster densus*, *Hymenaster edax*, *Hymenaster*

estcourti, *Hymenaster formosus*, *Hymenaster fucatus*, *Hymenaster graniferus*, *Hymenaster latebrosus*, *Hymenaster nobilis*, *Hymenaster pellucidus*, *Hymenaster perspicuus*, *Hymenaster praecoquis*, *Hymenaster pullatus*, *Hymenaster sacculatus*, *Hymenodiscus aotearoa*, *Hymenodiscus distincta*, *Hymenodiscus submembranacea*, *Hyphalaster giganteus*, *Hyphalaster inermis*, *Hyphalaster scotiae*, *Kampylaster incurvatus*, *Kenrickaster pedicellaris*, *Labidiaster annulatus*, *Labidiaster radiosus*, *Leptychaster flexuosus*, *Leptychaster kerguelenensis*, *Leptychaster magnificus*, *Leptychaster melchiorensis*, *Lethasterias australis*, *Lithosoma novaezelandiae*, *Lonchotaster tartareus*, *Lophaster densus*, *Lophaster gaini*, *Lophaster stellans*, *Lophaster tenuis*, *Luidia clathrata*, *Luidia porteri*, *Lysasterias adeliae*, *Lysasterias belgicae*, *Lysasterias chirophora*, *Lysasterias digitata*, *Lysasterias hemiora*, *Lysasterias heteractis*, *Lysasterias joffrei*, *Lysasterias lactea*, *Lysasterias perrieri*, *Macroptychaster accrescens*, *Mediaster arcuatus*, *Mediaster dawsoni*, *Mediaster pedicellaris*, *Mediaster sladeni*, *Meridiastra medius*, *Meridiastra oriens*, *Mimastrella cognata*, *Mirastrella biradialis*, *Myxoderma qawashqari*, *Neosmilaster georgianus*, *Neosmilaster steineni*, *Notasterias armata*, *Notasterias bongraini*, *Notasterias candicans*, *Notasterias haswelli*, *Notasterias pedicellaris*, *Notasterias stolophora*, *Notioceramus anomalus*, *Novodinia novaezelandiae*, *Odinella nutrix*, *Odontaster aucklandensis*, *Odontaster benhami*, *Odontaster meridionalis*, *Odontaster pearsei*, *Odontaster penicillatus*, *Odontaster pusillus*, *Odontaster roseus*, *Odontaster validus*, *Odontohenricia anarea*, *Odontohenricia endeavouri*, *Ophidiaster confertus*, *Paralophaster antarcticus*, *Paralophaster godfroyi*, *Paralophaster hyalinus*, *Paralophaster lorioli*, *Paranepanthia aucklandensis*, *Patiriella regularis*, *Paulasterias tyleri*, *Pectinaster filholi*, *Pectinaster mimicus*, *Pedicellaster hypernotius*, *Pentagonaster pulchellus*, *Pergamaster incertus*, *Pergamaster triseriatus*, *Peribolaster folliculatus*, *Peribolaster lictor*, *Peribolaster macleani*, *Perissasterias monacantha*, *Perknaster antarcticus*, *Perknaster aurantiacus*, *Perknaster aurorae*, *Perknaster charcoti*, *Perknaster densus*, *Perknaster fuscus*, *Perknaster sladeni*, *Persephonaster facetus*, *Pillsburiaster aoteanus*, *Pillsburiaster indutilis*, *Plutonaster complexus*, *Plutonaster fragilis*, *Plutonaster hikurangi*, *Plutonaster jonathani*, *Plutonaster knoxi*, *Plutonaster sirius*, *Poraniopsis echinaster*, *Porcellanaster ceruleus*, *Proserpinaster neozelanicus*, *Psalidaster fisheri*, *Psalidaster mordax*, *Pseudarchaster discus*, *Pseudarchaster garricki*, *Pseudechinaster rubens*, *Psilaster acuminatus*, *Psilaster charcoti*, *Pteraster affinis*, *Pteraster bathami*, *Pteraster florifer*, *Pteraster gibber*, *Pteraster hirsutus*, *Pteraster koehleri*, *Pteraster robertsoni*, *Pteraster rugatus*, *Pteraster spinosissimus*, *Pteraster stellifer*, *Radiaster gracilis*, *Remaster gourdoni*, *Rhopiella hirsuta*, *Saliasterias brachiata*, *Sclerasterias eustyla*, *Sclerasterias mollis*, *Scotiaster inornatus*, *Smilasterias clarkailsa*, *Smilasterias irregularis*, *Smilasterias scalprifera*, *Smilasterias triremis*, *Solaster longoi*, *Solaster notophrynus*, *Solaster regularis*, *Solaster torulatus*, *Sphaeriodiscus mirabilis*, *Stichaster australis*, *Styracaster armatus*, *Styracaster chuni*, *Styracaster horridus*, *Styracaster robustus*, *Taranuiaster novaezealandiae*, *Tarsaster stoichodes*, *Tremaster mirabilis*, *Vemaster sudatlanticus*, *Zoroaster actinocles*, *Zoroaster alternicanthus*, *Zoroaster fulgens*, *Zoroaster macracantha*, *Zoroaster spinulosus*, *Zoroaster tenuis*.

Spatial coverage: Southern Ocean: from 45°S to higher latitudes
Temporal coverage: 1872: HMS Challenger to 2016: JR15005.
Dataset: Asteroid occurrences available in the Southern Ocean from 1872 to 2016, collected during different campaigns and gathered from different deposit resources.
Object name: Antarctic and Sub-Antarctic Asteroidea Database
Character encoding: UTF/8
Format name: Darwin Core Archive Format
Format version: 1.4
Distribution: http://ipt.biodiversity.aq/resource?r=asteroidea_southern_ocean
Publication date of data:
Language: English
Metadata language: English
Date of metadata creation:
Hierarchy level: Dataset

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