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Aretopsis sandybrucei, a new deep-water shrimp (Malacostraca: Decapoda: Caridea: Alpheidae) from the Coral Sea

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Abstract. A new alpheid shrimp, *Aretopsis sandybrucei* sp. nov., is described on the basis of three specimens collected from three deep-water banks in the Chesterfield Plateau of the Coral Sea, between New Caledonia and Queensland, Australia, at a depth range of 280–550 m. The new species is the first known deep-water species of the genus *Aretopsis* De Man, 1910, with its two congeners, *A. amabilis* De Man, 1910 and *A. manazuruensis* Suzuki, 1971, being confined to the lower intertidal and shallow subtidal areas, to a maximum depth of 50 m. Based on morphological grounds, *A. sandybrucei* sp. nov. can be easily separated from *A. amabilis* and *A. manazuruensis* by the generally much stouter third to fifth pereiopods, with their dactyli each bearing a very small secondary unguis on the flexor margin, in comparison to a much stronger one in the other two species. *Aretopsis sandybrucei* sp. nov. also differs from *A. amabilis* and *A. manazuruensis* by the less contrasting colour pattern, including the more translucent, dull yellowish chelae and tail fan. An association of *A. sandybrucei* sp. nov. with a deep-water hermit crab appears to be highly likely due to the presence of several large hermit crabs (Paguridae) in at least one of the three dredge/bottom trawl hauls, which was also containing a paratype of the new species. The taxonomic status of *A. amabilis* and *A. manazuruensis* is discussed.

Keywords. Marine biodiversity, crustacean, West Pacific, Chesterfield Plateau, symbiosis.

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Introduction

Aretopsis De Man, 1910 is a small genus within the large family Alpheidae Rafinesque, 1815, currently with only two recognised species, *A. amabilis* De Man, 1910, the type species, and *A. manazuruensis* Suzuki, 1971 (Banner & Banner 1973; Chace 1988; De Grave & Fransen 2011). A third nominal species, *A. aegyptiaca* Ramadan, 1936, was placed in the synonymy of *A. amabilis* by Banner & Banner (1973, misspelled as *A. aegyptica*). Accepting this synonymy, *A. amabilis* results in a widespread and morphologically variable species, occurring from the Red Sea and Madagascar across the Indian Ocean to Vietnam, southern Japan, Marshall Islands and eastern Australia (Holthuis 1958; Banner & Banner 1968, 1973; Bruce 1969, 1984; Chace 1988; Marin 2010), whereas *A. manazuruensis* remains known only from the type locality in Sagami Bay, Honshu, Japan (but see below).

The genus *Aretopsis* can easily be distinguished from all other alpheid genera by the combination of the following characters: (1) the short, laterally compressed rostrum, distally rounded in lateral view; (2) the absence of supra-orbital and extra-corneal teeth; (3) the presence of small infra-corneal teeth; (4) the coxa of the third maxilliped with a dorsally projecting lateral plate; (5) the first pereiopods (= chelipeds) typically unequal in size and asymmetrical in shape, sometimes equal and symmetrical, carried extended forward, with both chelae laterally compressed and dactylus in ventral position; (6) the second pereiopod carpus composed of five units; (7) the third to fifth pereiopods with biunguiculate dactyli; and (8) the strap-like epipods present on the third maxilliped and first and second or (typically) first to third pereiopods (De Man 1910, 1911; Bruce 1969; Suzuki 1971; Banner & Banner 1973; Nomura 1986; Chace 1988). The rostro-orbital region, especially the very short, distally blunt rostrum, and the general shape of the chelipeds, are particularly diagnostic for the genus. In addition, *Aretopsis* is well defined ecologically, with both species typically encountered inside large gastropod shells occupied by hermit crabs, especially larger species of the genera *Dardanus* Paulson, 1875 and *Aniculus* Dana, 1852, in the lower intertidal and shallow subtidal areas (Bruce 1969; Suzuki 1971; Banner & Banner 1973; Nomura 1986; Marin 2010). However, *A. amabilis* was occasionally recorded from other shell-type microhabitats, for instance, an empty sea urchin test (Marin 2014) and a large clam, *Pterocera* sp. (Banner & Banner 1968). This species is presumed to be a protandric hermaphrodite, at least based on preliminary observations by Miyake & Miya (1967) and Banner & Banner (1968, 1973), as well as examination of the secondary sexual characters by Nomura (1986).

In 2017, three specimens clearly assignable to the genus *Aretopsis* were collected during the KANADEEP cruise targeting deep-water banks on the Chesterfield Plateau of the Coral Sea, between New Caledonia and Queensland, Australia (see Acknowledgements). One of them was photographed alive/freshly dead, shortly after the collection. After examination of the morphology of these specimens and colour photographs of one of them, it was concluded that they belong to an undescribed species of *Aretopsis*. In the present study, an opportunity is taken to describe this interesting deep-water shrimp species as new to science.

Material and methods

Type material of the new species is deposited in the collections of the Muséum national d'Histoire naturelle, Paris, France (MNHN). Comparative material of *A. amabilis* is deposited in the Museum of Tropical Queensland, Townsville, Queensland, Australia (MTQ) and National Museum of Natural History, Smithsonian Institution, Washington DC, USA (USNM). Carapace length (cl) was measured from the tip of the rostrum to the mid-posterior end of the carapace.

Total genomic DNA was isolated from the tissues of the fourth and/or fifth pleopods using the DNeasy Blood & Tissue Isolation Kit (QIAGEN) according to the manufacturer's protocol. To amplify a partial fragment of the CO1 gene, the primers JgLCO1490 and JgHCO2198 (Geller et *al.* 2013) were used for PCR. The thermocycler conditions were set as follows: 5 min at 94°C, followed by 40 cycles of 30 s at 90°C, 1 min 30 s at 48°C, and 1 min at 72°C, and a final extension step at 72°C for 10 min. The final products were purified by the GenElute PCR Clean-up kit (Sigma-Aldrich), and sent to Macrogen, Amsterdam, for sequencing.

Results

Subphylum Crustacea Brünnich, 1772
Class Malacostraca Latreille, 1802
Order Decapoda Latreille, 1802
Infraorder Caridea Dana, 1852
Family Alpheidae Rafinesque, 1815
Genus *Aretopsis* De Man, 1910

Aretopsis sandybrucei sp. nov.
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Figs 1–4

Etymology

The new species is named after Dr. Alexander J. Bruce, or Sandy Bruce for his friends and colleagues, for his tremendous contribution to the taxonomy of caridean shrimps, including an important article on the genus *Aretopsis* (Bruce 1969).

Material examined

Holotype

NEW CALEDONIA • ♂ (cl 5.31 mm); Coral Sea; Chesterfield Plateau between New Caledonia and Queensland; 25°29′ S, 159°49′ E; depth 360–400 m; 4 Sep. 2017; MNHN exped.; KANADEEP 1 sta. DW4941; Capel Bank; MNHN-IU-2017-2924.

Paratypes

NEW CALEDONIA • 1 ovigerous ♀ (cl 4.95 mm); same locality for holotype; 27°07′ S, 159°19′ E; depth 340–550 m; 19 Sep. 2017; MNHN exped.; KANADEEP 1 sta. DW5011; Nova Bank; GenBank COI gene: MZ389775; MNHN-IU-2017-3144 • 1 ovigerous ♀ (cl 6.58 mm); same locality as holotype; 23°08′ S, 159°31′ E; depth: 280 m; 6 Sep. 2017; MNHN exped.; KANADEEP 1 stn. CP4958; Argo Bank; MNHN-IU-2017-2770.

Comparative material

Aretopsis amabilis De Man, 1910

AUSTRALIA • 1 ♂ (cl 6.7 mm), 1 ♀ (cl 6.8 mm); Queensland; Great Barrier Reef; Lizard Island; Coconut Beach; 14.6842° S, 145.4700° E; depth 1 m; 25 Aug. 2010; I. Marin leg.; MTQ-W33075.

PHILIPPINES • 1 ♂ (cl 5.2 mm); Negros Island; Bonbonon Point; 9.0625 N, 123.1260 E; depth: 0–3m; 12 May 1978; Smithsonian exped.; stn. SP-5-2A, R/V Sting Ray V; USNM 213482 [examined by Anker (2001)].

Description

Carapace (Fig. 1A, C). Carapace glabrous, slightly swollen (more in females), poorly covering eyes dorsally and laterally, with deep cardiac notch. Rostrum (Fig. 1A–B) very short, triangular in dorsal view, slightly wider than long, compressed laterally, with short dorsal carina and feebly marked lateral lamella; tip rounded, distinctly overreaching distal half of first article of antennular peduncle, falling slightly short of its distal margin. Orbital teeth present in form of small, triangular, subacute infra-corneal teeth (Fig. 1A), reaching to about one third of eye length in lateral view; extra-corneal and supra-corneal teeth absent. Anterolateral margin of carapace (Fig. 1A) between infra-corneal tooth and pterygostomial angle somewhat sinuous; pterygostomial angle broadly rounded.

PLEON (Fig. 1C). Pleura of first to fifth pleonites rounded antero- and postero-ventrally; second pleuron greatly expanded in females; sixth pleonite with distinct, fairly large articulated plate.

TELSON (Fig. 1D–E). Telson relatively broad, subrectangular in shape, gradually tapering distally; dorsal surface with anterior and posterior pairs of spiniform setae situated at about 0.5 and 0.7 of telson length, respectively; distolateral angle feebly projecting, with two pairs of spiniform setae, lateral about half as long as mesial; posterior margin between mesial pair of spiniform setae broadly convex.

ANTENNULE (Fig. 1A–B). Antennular peduncle short, stout; dorsally visible portion of first article wider than long; stylocerite well developed, distally blunt, reaching beyond half-length of second article to almost reaching its distal margin; second article very short, wider than long in dorsal view; third article slightly longer than second; lateral flagellum biramous, with fused portion consisting of six or seven units and short accessory ramus consisting of three feebly distinct units; groups of aesthetascs extending from third unit of fused portion to end of accessory ramus.

ANTENNA (Fig. 1A–B). All antennal articles robust; basicerite moderately developed, with subacute distoventral tooth; scaphocerite broad, ovate, with strong distolateral tooth reaching far beyond distally rounded blade, not or only slightly overreaching antennular peduncle, lateral margin straight; carpocerite relatively stout, reaching slightly beyond distolateral tooth of scaphocerite and to end of third article of antennular peduncle; flagellum moderately stout.

MOUTHPARTS. Mandible with well-developed palp. Third maxilliped (Fig. 2A), with coxa stout, bearing strap-like epipod, lateral plate produced anteriorly with tip pointing slightly laterally; antepenultimate article robust, about four times as long as wide, with blunt distodorsal margin; penultimate article short, noticeably more slender than antepenultimate article, about 2.3 times as long as wide and 0.3 times as long as antepenultimate article; ultimate article slender, tapering distally, about 2.5 times as long as penultimate article, with rows of numerous serrulate setae ventromesially and some long setae at tip, latter without spiniform setae; exopod well developed, reaching to middle of penultimate article.

FIRST PEREIOPODS (= CHELIPEDS) (Fig. 2B–G). Chelipeds unequal in size, subsymmetrical in shape, carried extended with dactylus in ventral to ventrolateral position. Male major cheliped (Fig. 2B–D) (on the right side in the holotype) larger and more voluminous than minor cheliped by about 20% in male. Coxa with strap-like epipod and set of setobranchs. Basis short, stout, with small exopod-like lobe. Ischium slightly longer than basis, widening distally, somewhat cup-shaped, armed with one spiniform seta on distodorsal margin. Merus robust, swollen, somewhat vase-shaped, about 1.5 times as long as maximal width, distoventral margin with subrectangular projection. Carpus robust, about 0.7 times as long as merus and complex in lateral view, with broad prominence, ventral surface smaller, much wider than long. Palm compressed laterally, ovate in general shape, about 1.7 times as long as high, with two small tubercles on dorsomesial surface, near base of pollex; blunt ridge extending along dorsolateral margin of palm onto pollex. Fingers subequal in length, about 0.8 times as long as palm, crossing distally when closed with strongly curved fingertips; pollex with row of low irregular teeth along entire cutting edge; dactylus with small irregular teeth on proximal two thirds, distal third unarmed. Male minor cheliped (Fig. 2E–G) (on the left side in the holotype) generally similar to major cheliped, except for some proportions. Coxa and basis as in major cheliped, smaller in size. Ischium more slender, about three times as long as wide. Merus less robust and less swollen compared to that of major cheliped, vase-shaped, about twice as long as maximally wide. Carpus about cup-shaped, with small bump on lateral surface. Chela generally similar to that of major cheliped. Palm 1.5 times as long as high, bearing three small tubercles on dorsomesial surface, near base of pollex. Fingers about 0.7 times as long as palm; both pollex and dactylus armed with small teeth along their entire cutting edges. Female major cheliped overall similar to that of male (see Fig. 4); female minor cheliped unknown (missing in both paratypes).

Second to fifth pereiopods. Second pereiopod (Fig. 3A) relatively short; coxa with strap-like epipod and single setobranch; basis short, with small exopod-like lobe; ischium and merus subequal in length, latter about 4.5 times as long as maximally wide, ventral margin slightly convex; carpus about 1.2 times as long as merus, with five subdivisions, proximal longest, slightly shorter than length sum of remaining four, palm slightly longer than fingers. All walking legs (third to fifth pereiopods) very stout. Third pereiopod (Fig. 3B) with coxa bearing strap-like epipod and single setobranch; basis distally with one minute spiniform seta on ventrolateral surface; ischium stout, distally widening, with two small spiniform setae on ventrolateral surface; merus robust, about 2.5 times as long as maximal width, about 1.5 times as long as ischium, with distolateral margin forming blunt angle; carpus noticeably more slender than merus, about 0.6 length of merus, 2.7 times as long as wide; propodus slightly longer than carpus, armed with about 25 stout spiniform setae on ventral margin, most of them organised in two rows, distal-most spiniform setae longer and more robust; dactylus stout, slightly less than 0.3 length of propodus, flexor (= ventral) margin with small tooth-like projection. Fourth pereiopod (Fig. 3C) generally similar to third pereiopod, slightly less robust; coxa lacking both strap-like epipod and setobranch. Fifth pereiopod (Fig. 3D–E) noticeably less stout than third and fourth pereiopods; coxa lacking setobranch; basis and ischium unarmed; merus about 3.2 times as long as maximal width; carpus 0.7 times as long as merus; propodus with a dozen of spiniform setae on distal third, increasing in size and density distally and organised in two more or less distinct rows; distomesial surface of propodus with about seven transverse rows of serrulate setae together forming well-developed cleaning brush; dactylus almost 0.4 length of propodus, similar to that of third and fourth pereiopods.

Pleopods and uropod. Second pleopod with appendix masculina greatly overreaching small appendix interna. Female second pleopod without appendix masculina, appendix interna very long (also on following pleopods). Uropod (Fig. 1D–E) reaching well beyond posterior margin of telson; protopod distally with two small blunt projections separated by shallow furrow; exopod relatively broad, ovate, its distolateral margin with small blunt tooth and slender spiniform seta, latter not reaching posterior margin of exopod; diaeresis broadly sinuous, lacking lateral tooth; endopod ovoid, without specific features.

Colour pattern. Most of carapace and pleon translucent with pale red-wine colour, however, most of it apparently due to the partial visibility of internal organs (possibly ovary); on the other hand, clusters of small red chromatophores clearly visible on anterior flanks of carapace and pleura; mid-dorsal part of carapace and pleon with poorly defined, whitish or colourless longitudinal band stretching from rostrum to (and including) telson; short, whitish streaks and reticulations present on carapace flanks and pleon; all larger appendages, i.e., antennules, antennae, third maxillipeds, all pereiopods and uropods, generally translucent with pale tan-yellow tinge, parts of chelipeds with more intense yellowish colour and hyaline-white distal part of fingers (Fig. 4).

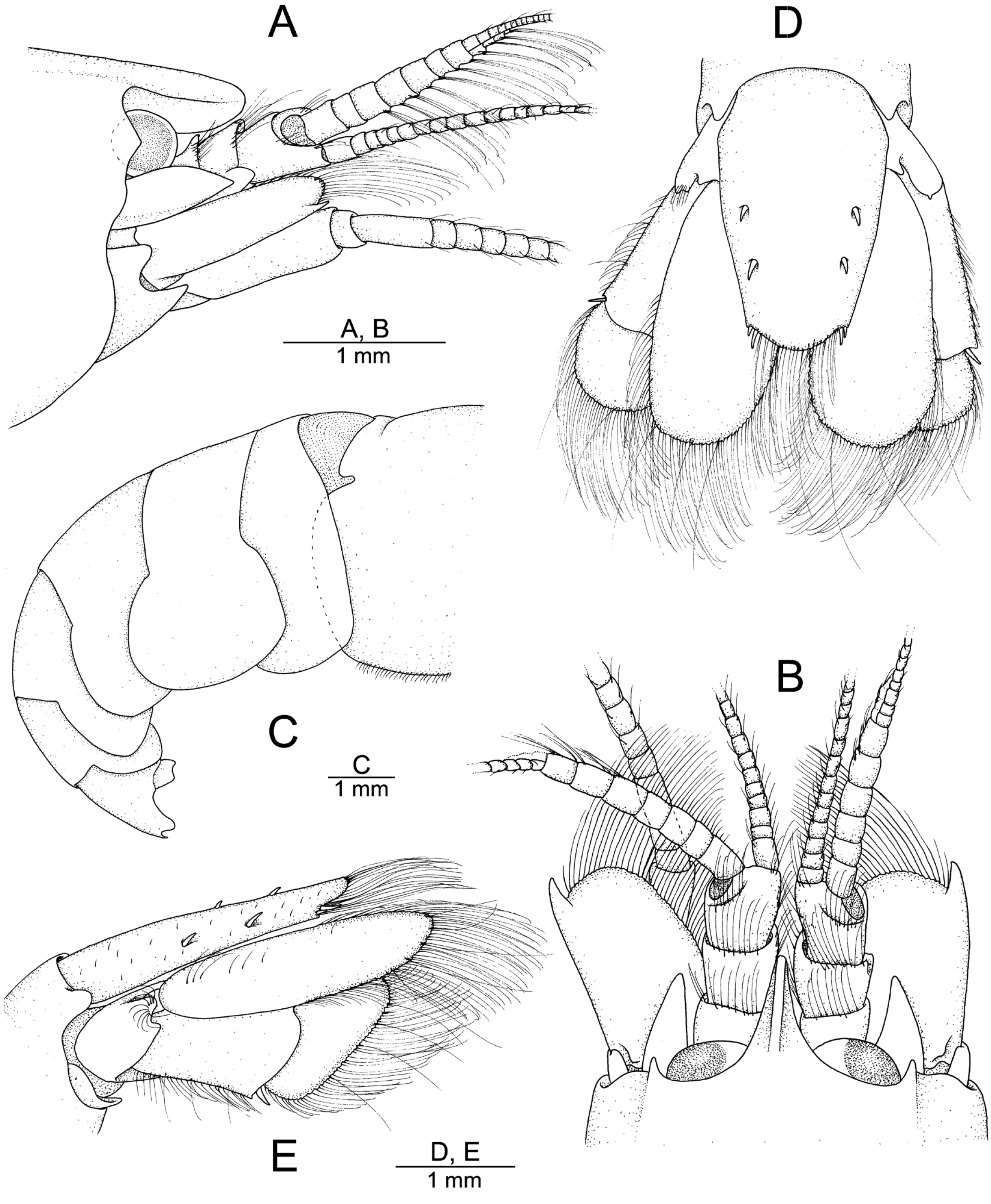

Fig. 1. *Aretopsis sandybrucei* sp. nov., holotype, ♂ (cl 5.31 mm) from Capel Bank, Coral Sea (MNHN-IU-2017-2924). **A**. Anterior part of carapace and right cephalic appendages, lateral view. **B**. Same, dorsal view. **C**. Pleon, lateral view. **D**. Posterior portion of sixth pleonite, telson and uropods, dorsal view **E**. Telson and left uropod, lateral view.

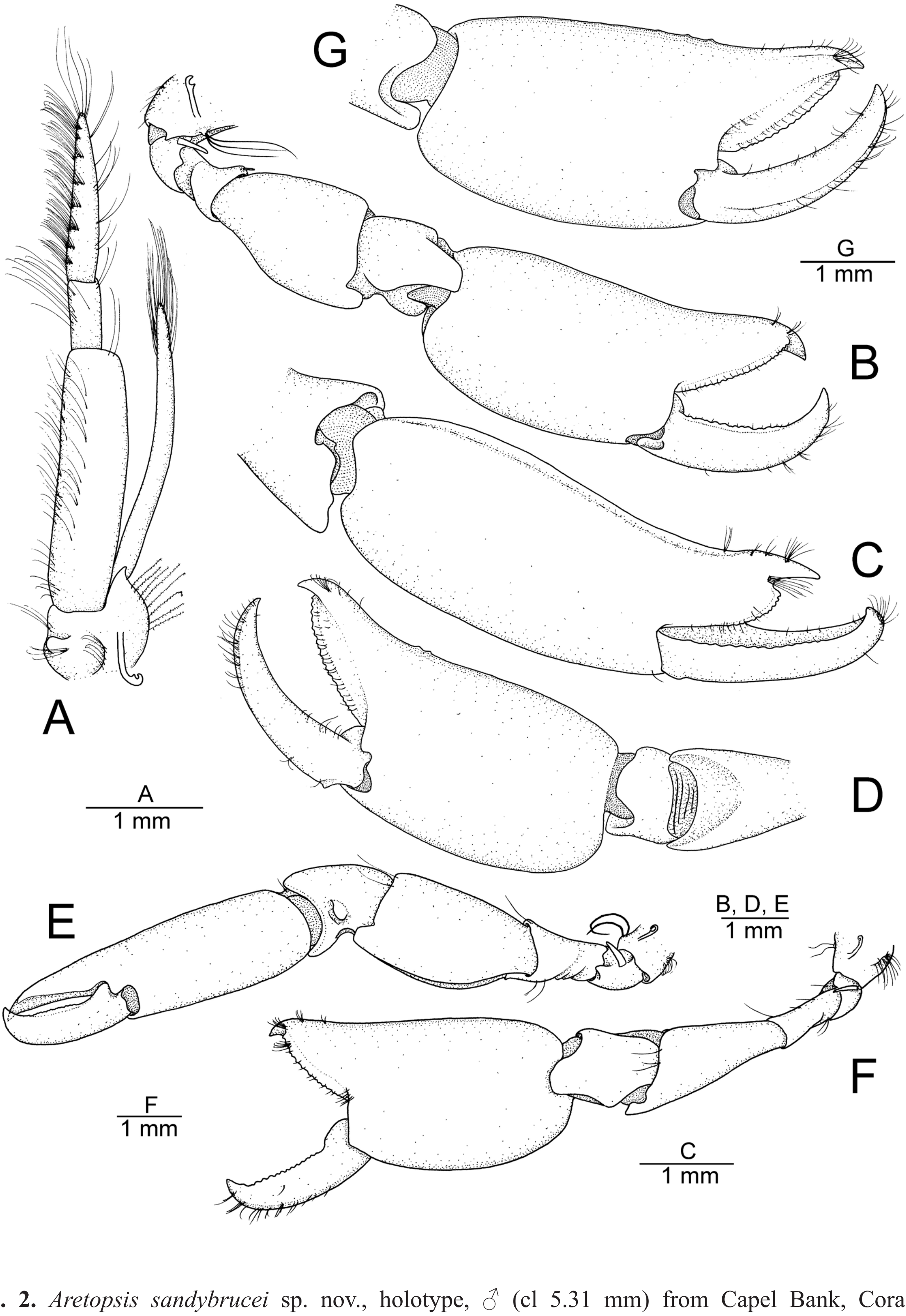

Fig. 2. *Aretopsis sandybrucei* sp. nov., holotype, ♂ (cl 5.31 mm) from Capel Bank, Coral Sea (MNHN-IU-2017-2924). **A**. Third maxilliped, lateral view. **B**. Right (major) cheliped, lateral view. **C**. Same, distal portion of carpus and chela, dorsolateral view. **D**. Same, distal portion of merus, carpus and chela, mesial view. **E**. Left (minor) cheliped, dorsolateral view. **F**. Same, chela fingers open, lateral view. **G**. Same, chela, mesial view.

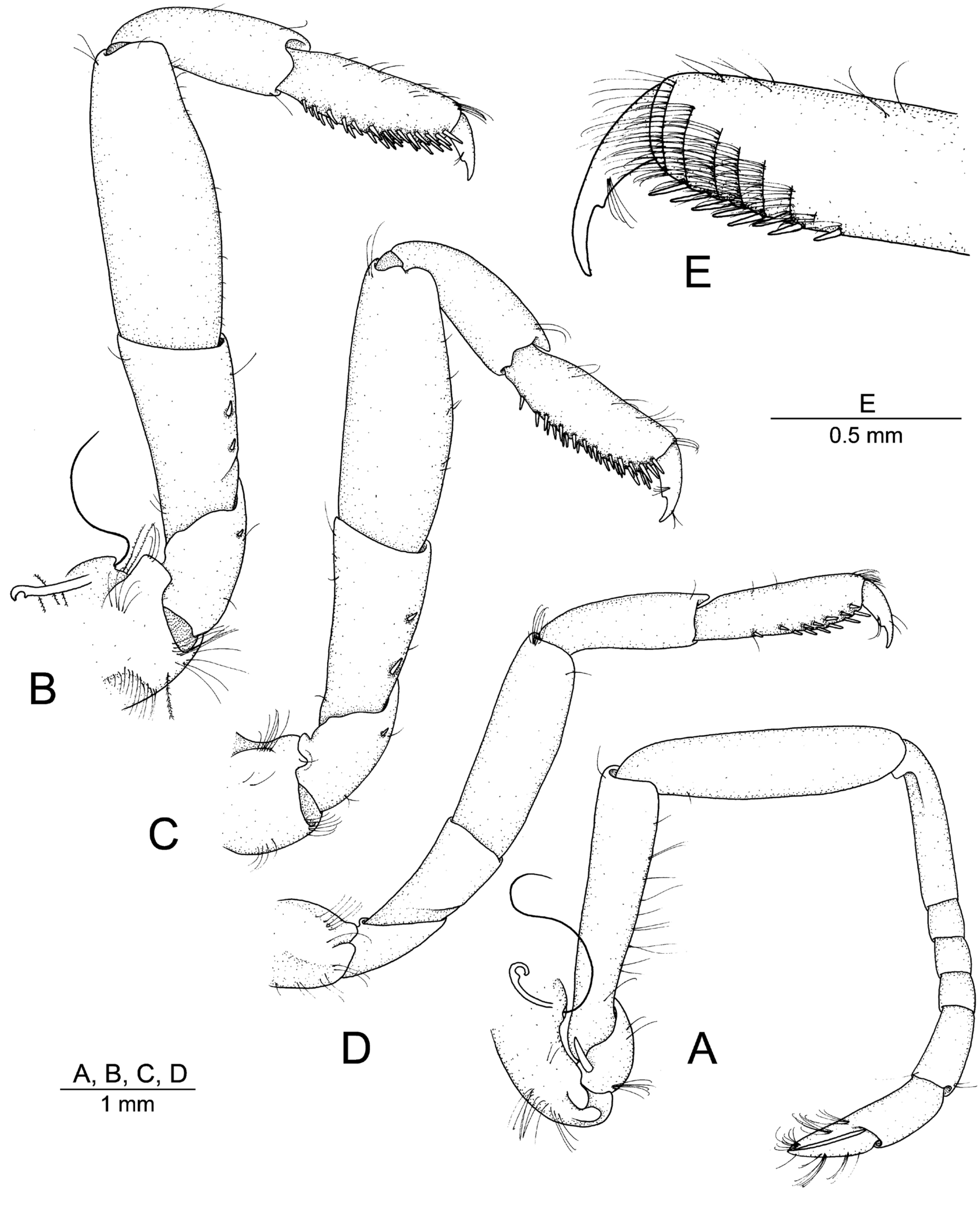

Fig. 3. *Aretopsis sandybrucei* sp. nov., holotype, ♂ (cl 5.31 mm) from Capel Bank, Coral Sea (MNHN-IU-2017-2924). **A**. Second pereiopod, lateral view. **B**. Third pereiopod, lateral view. **C**. Fourth pereiopod, lateral view. **D**. Fifth pereiopod, lateral view. **E**. Same, distal portion of propodus and dactylus, mesial view.

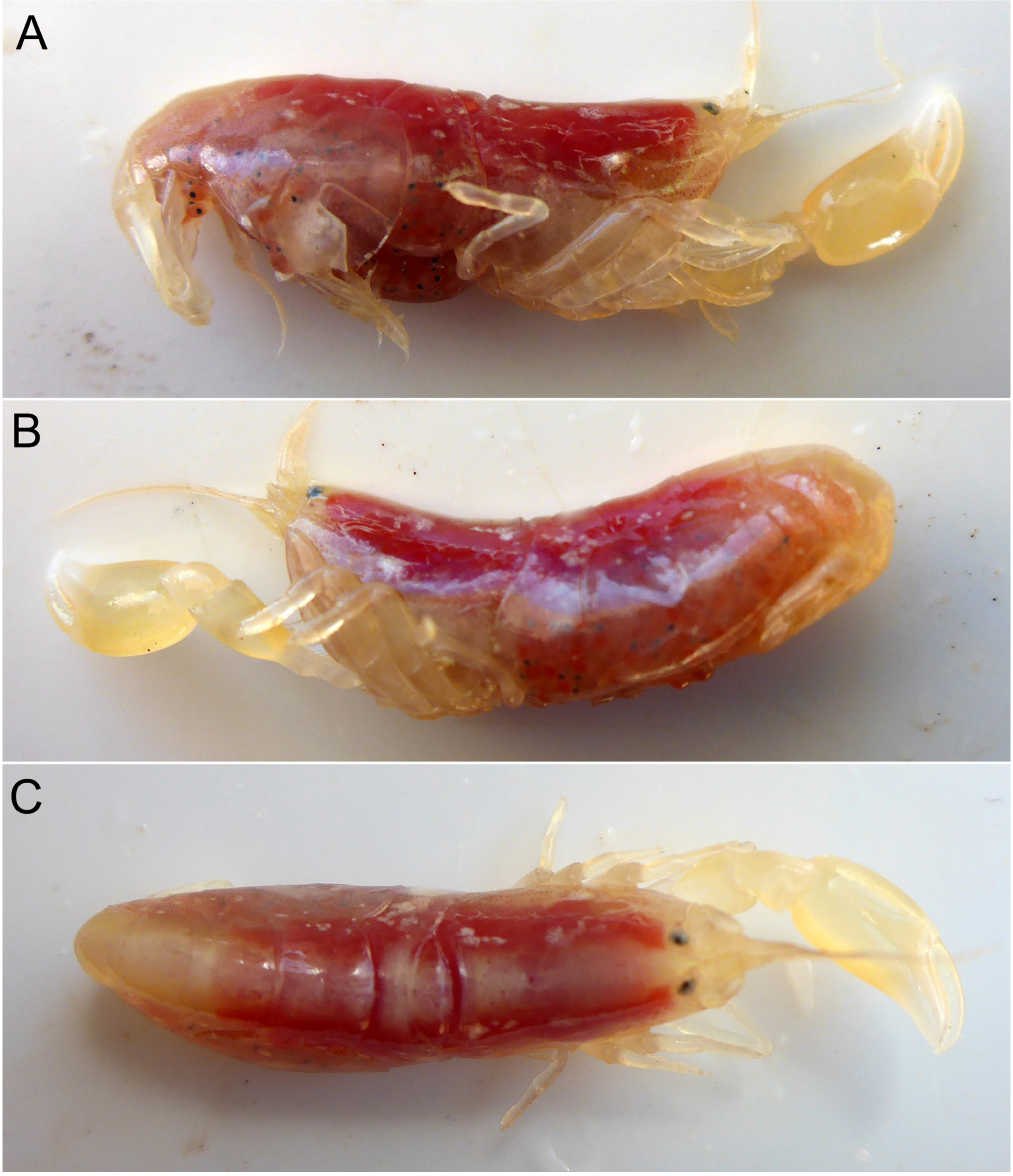

Fig. 4. *Aretopsis sandybrucei* sp. nov., paratype, ovigerous ♀ (cl 6.58 mm) from Argo Bank, Coral Sea (MNHN-IU-2017-2770), shrimp missing right (minor) cheliped, photographed shortly after collection. **A**. Right lateral view. **B**. Left lateral view. **C**. Dorsal view. Photographs by Dr. Sarah Samadi.

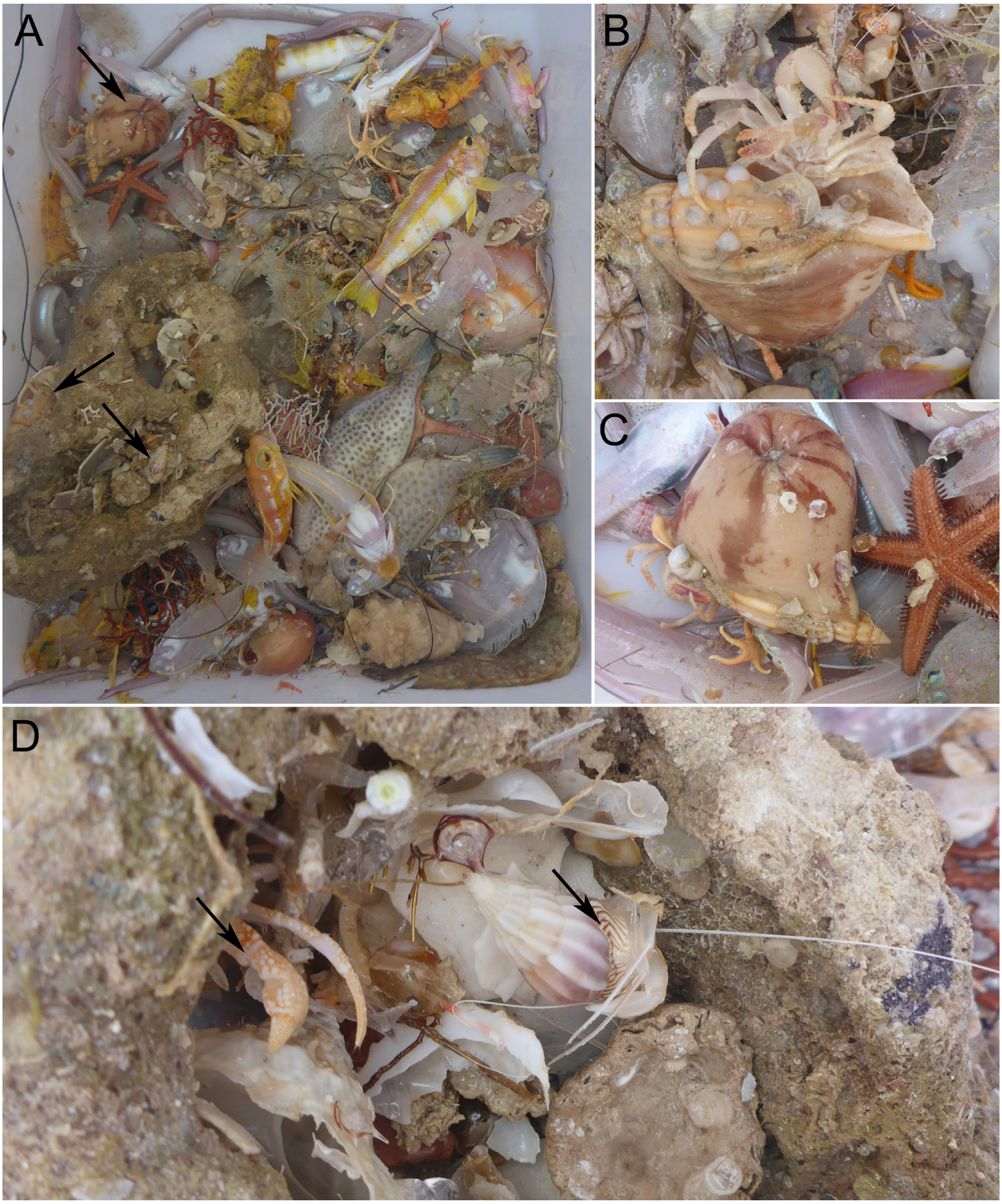

Fig. 5. Bottom trawl haul contents of KANADEEP Sta. CP4958 (Argo Bank), collection locality of one of the paratypes of *Aretopsis sandybrucei* sp. nov. **A**. General view of haul contents, with black arrows pointing to several hermit crabs (Paguridae). **B**–**C**. Hermit crab, possibly *Diacanthurus* sp. (Paguridae), carrying a large gastropod shell also harbouring a sea anemone. **D**. Two hermit crabs of the family Paguridae. Photographs by Dr Sarah Samadi.

Distribution

Presently known only from three deep-water banks (Capel, Nova and Argo) of the Chesterfield Plateau, Coral Sea (part of New Caledonia's Exclusive Economic Zone), between New Caledonia and Queensland, Australia.

Ecology

The three specimens of *A. sandybrucei* sp. nov. were collected by a Warén dredge (DW stations) or a bottom trawl (CP stations) over deep reef bottoms, at a depth range of 280–550 m. No associations were noted in the field. However, several animals from Argo Bank (stn. CP4958) were photographed immediately after pulling up and emptying the trawl into a bin, among them a female paratype of *A. sandybrucei* sp. nov. (Fig. 4) and at least two species of deep-water hermit crabs of the family Paguridae (Fig. 5), including possibly a species of *Diacanthurus* McLaughlin & Forest, 1997 (T. Komai, pers. comm. to AA).

Remarks

Aretopsis sandybrucei sp. nov. can easily be distinguished from its two congeners, *A. amabilis* and *A. manazuruensis*, by the proportions of the articles of the three last pereiopods (walking legs) and the development of the secondary (= accessory) unguis on the flexor margin of their dactyli. In *A. sandybrucei* sp. nov., the third, fourth and fifth pereiopods are generally much stouter than their homologues in *A. amabilis* and *A. manazuruensis.* This stoutness can easily be observed and measured on the merus of the third pereiopod, which is noticeably swollen and is at most 2.7 times as long as maximal width of *A. sandybrucei* sp. nov. (Fig. 3B) vs not swollen and at least 4.0 times as long as maximal width in *A. amabilis* (cf. De Man 1911: pl. 4 fig. 14f; Banner & Banner 1973: fig. 12k; confirmed on comparative material from Lizard Island, MTQ-W33075), and slightly swollen and about 3.2 times as long as maximal width in *A. manazuruensis* (cf. Suzuki 1971: fig. 12.4). Secondly, in *A. sandybrucei* sp. nov., the flexor margin of the dactylus of the third to fifth pereiopods bears a very small, i.e., only slightly projecting, secondary unguis (Fig. 3A), which contrasts to a much better developed, i.e., clearly more projecting, secondary unguis on the dactylus of these appendages in the other two species (cf. Bruce 1969: fig. 2c; Suzuki 1971: fig. 12.6a; Banner & Banner 1973: fig. 12k). In addition, in *A. sandybrucei* sp. nov., the basis of the third and fourth pereiopods is armed with a minute spiniform seta, which does not seem to be the case of *A. amabilis* based on De Man's (1910, 1911) description and illustrations (verified on comparative material, MTQ-W33075), and is also absent in *A. manazuruensis* according to Suzuki (1971: figs 12.4, 5). Another small difference between *A. sandybrucei* sp. nov., *A. manazuruensis* and *A. amabilis* lies in the antepenultimate article of the third maxilliped, in which the distodorsal margin is ending bluntly in the former two species (Fig. 2A; Suzuki 1971: fig. 11.3), but has a distinct rounded projection in the latter species (Bruce 1969: fig. 3f).

A direct comparison of the chelipeds between the species of *Aretopsis* is rather difficult because of the variation in the shape and armature of the major chela reported for *A. amabilis* (Bruce 1969; Nomura 1986) and the very limited material presently available for *A. manazuruensis*, known only from the female holotype (Suzuki 1971), and *A. sandybrucei* sp. nov., known from the male holotype and two female paratypes. However, none of the specimens of the new species has the fingers largely gaping and armed with prominent teeth, as illustrated for several adult specimens of both sexes of *A. amabilis* (cf. Ramadan 1936: pl. 2, fig. 12, as *A. aegyptiaca*; Bruce 1969: figs 14a–b, e–f; Banner & Banner 1973: fig. 12c; Nomura 1986: fig. 3a–c; Marin 2010: figs 1, 4). Both *A. amabilis* and *A. sandybrucei* sp. nov. can be separated from *A. manazuruensis* by the very unequal and asymmetrical chelipeds, which were described by Suzuki (1971) as "symmetrical in size", with only the left cheliped illustrated in the habitus drawing (idem: fig. 10), in addition to two figures showing the proximal articles of the right cheliped (idem: fig. 12.2) and the chela of what appears to be the left cheliped (contrary to Suzuki's figure legend), judging from the position of a strong carpal process present on the lateral surface only (idem: fig. 12.3).

The cheliped merus of *A. sandybrucei* sp. nov. is ventrally unarmed and distoventrally bears a rectangular projection (Fig. 2B, D), whereas the cheliped merus of at least some specimens of *A. amabilis* is ventrally armed with spiniform setae and distoventrally bears a prominent tooth (De Man 1911: pl. 4, fig. 14d; Marin 2010: fig. 2d; comparative material, MTQ-W33075). Bruce (1969: fig. 4) did not illustrate these spiniform setae, but in the text mentioned that "the merus is provided with one or two long slender spines". Miyake & Miya (1967) stated that the "outer lower margin of the merus is indented and bristled", possibly referring to the spiniform setae (unclear in their fig. 3d). On the other hand, they were neither illustrated nor described for the material of *A. amabilis* reported by Ramadan (1936) or Banner & Banner (1973), and therefore, it is not quite clear whether they are present in all specimens so far reported as *A. amabilis*.

Another cheliped feature that may add to the distinction between *A. sandybrucei* sp. nov., *A. manazuruensis* and *A. amabilis* is the presence (in the first two species) or absence (in the last species) of a slender spiniform seta on the distodorsal margin of the ischium (cf. Fig. 2A; Bruce 1969: fig. 4a; Suzuki 1971: fig. 12.2; Banner & Banner 1973: fig. 12d–e). As for the spiniform setae on the merus, the absence of this seta in *A. amabilis* may be simply due to the lack of detailed observation of the base of the cheliped and/or inaccurate figures (or with all setae simply omitted for clarity), although it was confirmed to be absent in both specimens from Lizard Island.

The colour pattern of *A. sandybrucei* sp. nov. (Fig. 4) is generally similar to that reported for *A. amabilis* (Vannini *et al*. 1993: fig. 1 (bottom); Marin 2010: figs 3–4) and *A. manazuruensis* (Suzuki 1971: fig. 10). However, the new species is clearly different from *A. amabilis* and *A. manazuruensi*s in having a generally less contrasting, somewhat duller colour pattern, including the more translucent and homogenously coloured pale yellow chelae (although with distally white fingers) and tail fan.

Aretopsis sandybrucei sp. nov. is also ecologically separated from its shallow-water congeners, presently being known from a depth range of 280–550 m, i.e., 230 m below the deepest record of *A. amabilis*, represented by a specimen dredged at 50 m off Ujung Pandang, Sulawesi, Indonesia (Banner & Banner 1985). However, most records of *A. amabilis* and the single record of *A. manazuruensis*, are from the lower intertidal or shallow subtidal depths ranging from 1 to 10 m, often on coral reefs and adjacent habitats (De Man 1910; Miyake & Miya 1967; Bruce 1969; Banner & Banner 1973; Marin 2010, 2014; present study). The host (or hosts, if multiple) of *A. sandybrucei* sp. nov. are currently unknown, although the general similarity of the new species to other species of the genus, including the colour pattern, suggests that it may be a deep-water hermit crab of the family Paguridae, possibly *Diacanthurus* sp. (see above and Fig. 5). Noteworthy, this pagurid carried a shell almost fully occupied by a large sea anemone (Fig. 5B–C), which is also commonly observed in many shallow-water hosts (*Dardanus* and *Aniculus*) of *A. amabilis*.

Discussion

As mentioned above, *A. amabilis* probably is a protandric hermaphrodite, based on the presence of an appendix masculina on the second pleopod of females, including ovigerous ones (Miyake & Miya 1967; Banner & Banner 1968, 1973; Nomura 1986). However, Bruce (1969) did not observe an appendix masculina on the female second pleopod in his material of *A. amabilis* from the Seychelles, illustrating a well-developed one for a male (idem: fig. 2d). Similarly, Suzuki (1971) did not illustrate an appendix in the ovigerous female holotype of *A. manazuruensis* (idem: fig. 12.8) and it also absent in both ovigerous female paratypes of *A. sandybrucei* sp. nov., indicating that not all of these populations might be hermaphroditic.

The current taxonomic concept of *A. amabilis* and *A. manazuruensis* is far from satisfactory (Chace 1988) and we feel that further work with both taxa will be needed. The first species appears to be variable in several characters (De Man 1910, 1911; Miyake & Miya 1967; Bruce 1969; Banner & Banner 1973; Chace 1988), including (1) the general shape of the chelipeds, including armature of the major chela fingers; (2) the presence or absence of slender spiniform setae on the cheliped meri; (3) the presence or absence of an appendix masculina in females [all discussed above]; (4) the development of a small exopod-like lobe on the basis of the first (cheliped) and second pereiopods; (5) the armature of the ischium of the third and fourth pereiopods; (6) the shape of the posterior margin of the telson; and (7) the presence or absence of a palp on the mandible [all discussed below].

With regard to the small exopod-like lobe on the basis of the first two pereiopods, this structure seems to be absent in the specimens of *A. amabilis* from Indonesia, Australia and the Seychelles, at least based on the accounts of De Man (1910, 1911), Banner & Banner (1973) and Bruce (1969), respectively, but is present in the material from southern Japan (Miyake & Miya 1967: fig. 2d), as well as in the comparative material from Lizard Island. Since a small exopod-like lobe is also present on the basis of the first and second pereiopods in *A. manazuruensis* (Suzuki 1971: fig. 12.2) and in *A. sandybrucei* sp. nov. (Figs 2B, D, 3A), its presence may be ancestral within the genus *Aretopsis*. In fact, a small exopod or exopod-like lobe is also present in several other genera more or less closely related to *Aretopsis,* together forming the so-called athanoid clade or AP clade in Anker *et al*. (2006). The phylogenetic position of the AP clade within the Alpheidae (Anker *et al*. 2006) suggests that the exopod-like structure on the first two pereiopods may be a "neoformation" rather than a highly reduced exopod, i.e., "rudimentary exopod" of Miyake & Miya (1967). Whatever the case may be, it is one of the synapomorphies of the athanoid clade (Anker *et al*. 2006).

De Man (1911) and Miyake & Miya (1967) reported that the ischium of the third, fourth and fifth pereiopods of *A. amabilis* is armed with a spiniform seta, which is also the case in the material from Lizard Island. The specimens from the Seychelles (Bruce 1969) and Australia (Banner & Banner 1973) were apparently lacking spiniform setae on the ischia of the walking legs. However, it cannot be excluded that these spiniform setae were simply very small and overlooked by the latter authors. In *A. sandybrucei* sp. nov., these spiniform setae are present on the ischia of the third and fourth pereiopods, but are absent on the ischium of the fifth pereiopod (Fig. 3B–C–D), just like in *A. manazuruensis* (Suzuki 1971: fig. 12.4–5–6). Banner & Banner (1973) pointed out to a difference in the shape of the posterior margin of the telson, which was illustrated as truncate in the Indonesian type specimen of *A. amabilis* (De Man 1911: pl. 4, fig. 14c), almost straight in the Japanese specimens of Miyake & Miya (1967: fig. 2l), and slightly convex in the Australian material of Banner & Banner (1973: fig. 12l) and the Japanese material of Nomura (1986: fig. 2d).

Suzuki (1971) did not include the number of strap-like epipods in the gill-exopod formula of *A. manazuruensis*. The structures that this author called "mastigobranchs" obviously are lobe-like epipods of the first and second maxillipeds. However, from the number of setobranchs in the gill-exopod formula and from Suzuki's description and illustrations, it can tentatively be deducted that the strap-like epipods are present on the third maxilliped and the first two pereiopods only, i.e., not on the third pereiopod, which would explain Chace's (1988: p. 59–60) statement "pereopods typically with strap-like epipods on 2 or 3 anterior pairs" in the generic diagnosis of *Aretopsis*. However, in *A. sandybrucei* sp. nov., a well-developed strap-like epipod is present on the coxa of the third pereiopod, despite the absence of a setobranch on the fourth (Fig. 3B–C). Therefore, the number of strap-like epipods in *A. manazuruensis* remains somewhat unclear.

Chace (1988) made several interesting observations while comparing his single specimen of *A. amabilis* from Negros Island, Philippines (USNM 213482), with *A. manazuruensis* of Suzuki (1971). Firstly

Chace (1988: p. 60) stated: “The specimen from Sagami Bay described by Suzuki [= *A. manazuruensis*] superficially resembles the type species so closely – even to the color pattern and the association with hermit crabs – that its specific identity might be questioned, especially if the symmetrical first chelipeds of the unique holotype could possibly have resulted from regeneration”. This hypothesis was supported by Nomura (1986), who reported *A. amabilis* from the northern-most locality in Japan (Kushimoto), suggesting that the holotype of *A. manazuruensis* may be an “abnormally deformed individual, judging from the form of its first pereiopods”. In addition, the description of *A. manazuruensis* by Suzuki (1971) seems to contain some errors, for instance, in the count of the pleurobranchs, two on the first pereiopod, and none on the fourth pereiopod, which would be a highly unusual branchial formula for an alpheid shrimp. The same may be true for the posterior margin of the telson, which according to Suzuki’s description and figure (Suzuki 1971: fig. 11.7) is armed with only two spines (one at each distolateral angle, instead of the usual two). It is more likely that Suzuki (1971) simply overlooked the minute lateral spiniform seta. Thus, the most plausible explanation for *A. manazuruensis* is an abnormal specimen of *A. amabilis* with regenerated chelipeds, combined with some inaccuracies in Suzuki’s (1971) description and illustrations. The synonymy of *A. manazuruensis* with *A. amabilis* is also supported by the fact that no specimen matching the diagnostic features of *A. manazuruensis* has been collected in central Japan, a well-sampled area, in over 50 years.

In contrast to all of the above, after his first intuition on *A. manazuruensis*, Chace (1988: p. 60) continued: “Examination of the first specimen of *Aretopsis* to be recorded from the Philippines, however, revealed no palp on the mandible, in contrast with the prominent one illustrated by Suzuki. If *A. manazuruensis* does prove to differ in consistently having one, rather than two, pairs of posterolateral telson spines, symmetrical first chelipeds, and a slightly different branchial formula, in addition to the mandibular palp, perhaps a distinct genus should be proposed for it.” However, this statement contrasts with the observations of Bruce (1969), who provided detailed figures of all mouthparts of a specimen of *A. amabilis* from the Seychelles, illustrating a well-developed palp on the mandible (idem: fig. 3a). The absence or presence of a mandibular palp in the same species would be highly unusual for a caridean shrimp. Therefore, the identity of Chace’s (1988) specimen from Negros Island, which in fact was identified by Banner & Banner in 1983, remains somewhat questionable and will need to be confirmed. Anker (2001) briefly re-examined Chace’s specimen, without focusing specifically on its mandibles or other mouthparts, stating in his diagnosis of *Aretopsis*: “mandible with two-segmented palp”. Since the mandible definitively has a palp in *A. amabilis* sensu Bruce (1969), *A. manazuruensis* of Suzuki (1970) and *A. sandybrucei* sp. nov. (see above), as well as in related athanoid genera, its presence in *Aretopsis* seems to be ancestral. Of course, it cannot be excluded that Chace (1988) simply accidentally detached the mandibular palp while dissecting the mouthparts of his Philippine specimen.

In summary, most of the present evidence suggests that *A. manazuruensis* is a junior synonym of *A. amabilis*. Small differences in the antepenultimate article of the third maxilliped, the armature of the ischia of the third to fifth pereiopods, and the development of the appendix masculina in females, may be taxonomically important to some extent, but are presently difficult to evaluate; in addition, at least the latter two features seem to be variable among specimens assigned to *A. amabilis* (see above). Since *A. amabilis* is also variable in a number of other morphological characters and therefore needs a comprehensive revision, preferably involving molecular analyses, a formal synonymisation of *A. manazuruensis* at this stage would be premature. Indeed, if this analysis shows that two or multiple species are involved in what could well be *A. amabilis* species complex, Suzuki’s (1971) name *A. manazuruensis* would be potentially available for one of them. However, such an analysis is well beyond the scope of the present study.

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