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A new species and new records of deep-water Calappidae (Crustacea: Decapoda) from the Indian Ocean with a key to the *Mursia* Desmarest, 1823 species of the region

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Abstract
Deep-water Calappidae collected by German and Russian expeditions to the western Indian Ocean and additional material from several European and American museums were studied. *Calappa japonica* Ortmann, 1892 was recorded from the Red Sea for the first time, where it occurs in unusually deep waters and *C. pustulosa* Alcock, 1896 was recorded for the first time off Madagascar. Eight species of *Mursia* Desmarest, 1823 are known from the Indian Ocean (*M. africana* Galil, 1993, *M. aspera* Alcock, 1899, *M. bicristimana* Alcock and Anderson, 1894, *M. coseli* Crosnier, 1997, *M. cristiata* H. Milne Edwards, 1837, *M. flamma* Galil, 1993, *M. curtispina* Miers, 1886, and *M. minuta* n. sp.). For *M. bicristimana* the status was clarified and a new species described. This description is partly based on a specimen which prior to this study had been erroneously considered a syntype of *M. bicristimana*. New characters and a key are provided to facilitate identification of the Indian Ocean species of *Mursia*. The contrasting geographic distribution patterns of the two genera are discussed with regard to their vertical distribution.

Keywords: *Biogeography,* Calappa, *Calappidae, deep-water fauna, Indian Ocean,* Mursia, *Red Sea*

Introduction

Two genera of box crabs (Calappidae), *Calappa* Weber, 1795 and *Mursia* Desmarest, 1823, are known to occur in deep-water habitats of the Indian Ocean. There are, however, considerable differences in vertical and geographical distribution between the two genera. Even though the recent revisions by Galil (1993, 1997) facilitate the identification and interpretation of the available material, the distribution in particular of deep-water species is still insufficiently known.

In *Calappa* most of the 15 species currently known from the Indian Ocean (Galil 1997; Ng et al. 2002) inhabit shallow water. Only two species, *C. depressa* Miers, 1886 and *C. japonica* Ortmann, 1892, were previously reported below 200 m (Galil 1997; Bellwood 1998). Both species, however, are not restricted to deep-water habitats but

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predominantly inhabit shallow water. However, Türkay (1986) recorded several juvenile specimens of *C.* cf. *pustulosa* Alcock, 1896 from more than 700 m depth in the Red Sea and it was one of the aims of the present study to clarify their identity. This issue is of interest because the deep-water fauna of the Red Sea contains a number of endemic species having close affinity to shallow-water species occurring outside of the region while some populations appear to be conspecifics of widespread Indo-Pacific taxa but occur deeper than in other parts of the range (Türkay 1996). Additional material of adult specimens obtained from the Russian expeditions to the western Indian Ocean enabled the present authors to clarify the status of the Red Sea form considered below as *C. japonica*.

Contrary to the predominantly shallow-water *Calappa*, the deep-water box crabs of *Mursia* are mainly found below 200 m. When revising the genus, Galil (1993) verified the occurrence of four previously known species from the Indian Ocean region and described two new species from the southwestern Indian Ocean, *M. africana* Galil, 1993 and *M. flamma* Galil, 1993. Her work stimulated further study on taxonomy and distribution of deep-water box crabs which resulted in the description of four new species of *Mursia* (Crosnier 1997a, 1997b; Galil and Spiridonov 1998; Galil 2001), one of which, *M. coseli* Crosnier, 1997, occurs in the southwestern Indian Ocean.

At the same time that Galil (1993) published her revision of *Mursia*, an extensive collection of the genus obtained from the 17th cruise of RV *Vitiaz* in both the northwestern and the southwestern Indian Ocean in 1988 was examined by Zarenkov (1994) who adhered to an earlier concept of wide-ranged and highly variable species and thus identified all the material as *M. armata* de Haan, 1837, a species that according to Galil (1993) does not occur in the western Indian Ocean. This motivated us to re-examine the *Vitiaz* material along with other collections from Russian and German deep-sea expeditions to the region and comparative material deposited in several European and American museums. The present study resulted in description of a new species of *Mursia* and conclusions to be drawn regarding the distribution of deep-water calappids in the western Indian Ocean.

Abbreviations

The measurements used are the following: CL, length of carapace measured along midline; CW, maximum width of carapace excluding lateral spines in *Mursia* and width measured immediately anterior to posterolateral lamellae in *Calappa*; LS, lateral spine length; MCW, carapace width including lateral spines in *Mursia*.

Go/1, first gonopod (=first male pleopod); Go/2, second gonopod (=second male pleopod); ov., ovigerous; P1–P5, pereiopods 1–5; St., station.

IORAS, P. P. Shirshov Institute for Oceanology, Russian Academy of Sciences, Moscow; NHM, Natural History Museum, London; MNHN, Muséum National d'Histoire naturelle, Paris; MZUS, Muséum zoologique de l'Université de Strasbourg; SMF, Forschungsinstitut und Museum Senckenberg, Frankfurt am Main; USNM, United States National Museum of Natural History, Washington, DC; ZMB, Zoologisches Museum, Museum für Naturkunde, Berlin; ZMMU, Zoological Museum of the Moscow University, Moscow; ZSI, Zoological Survey of India, Calcutta; ZSM, Zoologische Staatssammlung, München.

Material and methods

The material used in the present study originates from several expeditions to the western Indian Ocean. Of particular importance are the expeditions of the German RV *Meteor* Cruise 5 to the Red Sea and the Gulf of Aden in 1987 (Thiel and Cruise Participants 1987) and the Russian RV *Vitiaz* (new) Cruise 17 to the western Arabian Sea, the Strait of Mozambique, and the islands of the Western Indian Ocean in 1987–88. Further material from some other Russian and German expeditions to the Red Sea and the Gulf of Aden, deposited in the Zoological Museum of the Moscow University, in the P. P. Shirshov Institute for Oceanology, Russian Academy of Sciences (Moscow), and in the Senckenberg Museum, Frankfurt am Main, along with comparative material from several European and American museums was also studied.

The scheme of morphological description basically follows Crosnier (1997a, 1997b) and Galil and Spiridonov (1998). Some new characters not used previously in calappid taxonomy were introduced, e.g. the morphology of the female genital opening. Synonymy of *Calappa* species includes only the papers with comprehensive description and/or illustration of the species under treatment and those containing records from the Indian Ocean.

Systematics

Calappa japonica Ortmann, 1892

(Figure 1A–C)

Calappa japonica Ortmann 1892, p 566, Plate 26, Figure 8; Sakai 1937, p 96, Plate 18, Figure 4; Barnard 1950, p 352, Figure 66n–p; Grindley 1961, p 132; Sankarankutty and Subramanian 1976, p 21; Galil 1997, p 300–303, Figures 10d, 13d, 15, 32; Komai 1999, p 73.

Calappa exanthematosa Alcock and Anderson 1894, p 177; 1895, Plate 15, Figures 1, 1a; Alcock 1896, p 146.

Calappa cf. *pustulosa*: Türkay 1986, p 150–151 [not *Calappa pustulosa* Alcock, 1896].

Material examined

Central Red Sea: RV *Valdivia*, St. VA22/122 TA, in front of Ras el Aswad south of Jeddah, Saudi Arabia, 21°22′N, 39°04′E, depth 383–363 m, 17 April 1978: three juvenile males (SMF 13592, identified as *Calappa* cf. *pustulosa*); RV *Valdivia*, St. VA22/111 TA, 21°28′37″N, 38°15′35″E, depth 740–785 m, 12 April 1979: one juvenile (SMF 13585, identified as *Calappa* cf. *pustulosa*). Southern Red Sea: RV *Akademik Kurchatov*, St. 3097, Cruise 30, 18°38′94N, 40°159′52E, depth 640–615 m, pteropodous mud, 8 January 1980: one female (moult cast) (IORAS unregistered). Gulf of Aden: probably taken by some Russian fisheries research expedition, exact locality unknown: one male, one female (ZMMU Ma 5344–5345), identified as *Calappa* aff. *pustulosa*. Gulf of Oman: Iran, no exact locality, found on the beach, Reza Fatemi coll.: one female (SMF 29501). Japan: exact locality unknown, T. Sakai collection: one female (SMF 22942).

Type locality

Japan, Bay of Tokyo.

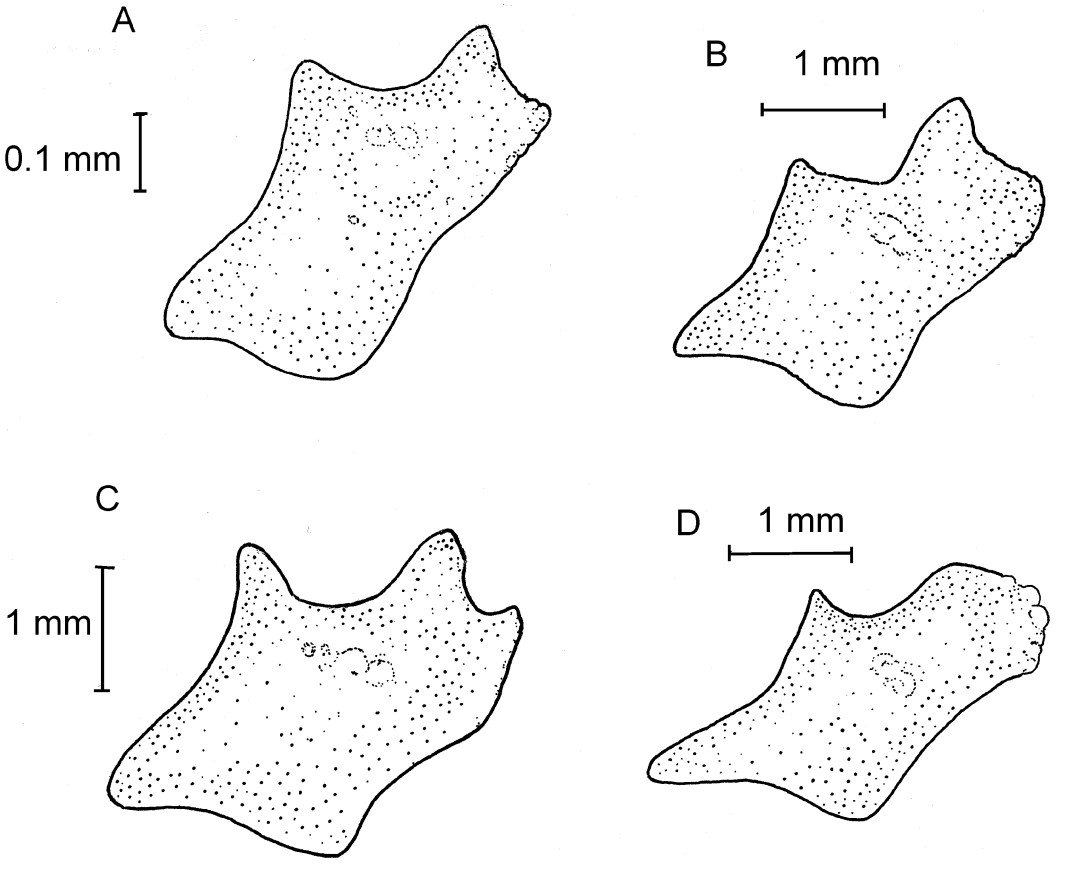

Figure 1. Basal antennal segment of *Calappa*. (A) *C. japonica*, Red Sea, male, CL 13.6 mm (SMF 13592); (B) *C. japonica*, Gulf of Aden, male, CL 46.4 mm (ZMMU Ma 5344); (C) *C. japonica*, Japan, female, CL 53.5 mm (SMF 22942); (D) *C. pustulosa*, Strait of Mozambique, female, CL 54.6 mm (ZMMU Ma 5335).

Type material

Two males and one female syntypes, MZUS 111 (dry) (Komai 1999).

Size (CL × CW)

Juvenile specimens from the Red Sea (SMF 13592): 13.6 × 15.9, 13.3 × 15.4, and 6.9 × 7.4 mm; male from the Gulf of Aden: 46.4 × 61.6 mm; female from the Gulf of Oman: 56.3 × 77.9 mm; specimens from Japan: 53.5 × 70.2 and 96.6 × 133.7 mm.

Habitat

Outside the Red Sea the species is known from 30 to 380 m depth. In the Red Sea it occurs between 363 and 785 m. The habitat in the Red Sea where the IORAS specimen was collected, was observed from the submersible *Pisces* and characterized as "small plateau in front of the steep rift zone covered with pteropodous mud". In the Gulf of Aden the species was collected together with the swimming crab *Charybdis smithii* MacLeay, 1838, known to

inhabit muddy substrates in a depth range from approximately 200 to 300 m (Türkay and Spiridonov 2006).

Distribution

Southern to central Red Sea, Gulf of Aden, Gulf of Oman, Arabian Sea, East to South Africa, Gulf of Bengal, East China Sea, Japan.

Remarks

Sakai (1937) was the first author to synonymize *C. exanthematosa* Alcock and Anderson, 1894 with *C. japonica*. Galil (1997) followed this view. Our specimens from the Gulf of Aden and the Gulf of Oman show no considerable differences to those from Japan with regard to the carapace and cheliped sculpture, the shape of the basal antennal segment, and the morphology of the Go/2. However, the carapace of the juvenile specimens from the Red Sea have a subcircular rather than an elliptical shape and, in general, more distinct tubercles and stronger granulation than those from Japan. The smaller the crabs are, the more these characters are expressed and might lead to confusion with *C. pustulosa*. The tubercle pattern, however, is the same as in adult specimens from the Gulf of Aden and from Japan, and the basal antennal segment is very similar to other specimens of *C. japonica* examined (Figure 1A–C). Thus the specimens from the Red Sea are considered as belonging to *C. japonica* and the differences in carapace shape and granulation are considered to be size-dependent variation.

Calappa pustulosa Alcock, 1896

(Figure 1D)

Calappa pustulosa Alcock 1896, p 147, Plate 6, Figure 1; Sakai 1937, p 97, Plate 18, Figures 2, 3; Sakai 1976, p 134, Plate 41, Figure 1; Dai and Yang 1991, p 106, Text figure 52, Plate 12, Figure 1; Galil 1997, p 311–312, Figures 17e, 20e, 22, 23.

nec *Calappa* cf. *Pustulosa*: Türkay 1986, p 150–151, Plate 1, Figures 4, 5 [=*Calappa japonica*].

Material examined

South-western Indian Ocean: Strait of Mozambique, 25°00.0′S, 35°19.9′E, depth 228 m, shrimp trawl, RV *Vitiaz*, Cruise 17, St. 2635, M. V. Heptner coll.: one female (ZMMU Ma 5355). No exact locality: probably Japan, T. Sakai collection: one male (SMF 22939).

Type locality

Off Ganjam and Orissa coasts, Gulf of Bengal.

Type material

Probably in the ZSI. Number of specimens (syntypes) not known.

Size (CL × CW)

Specimen from the Strait of Mozambique: 54.6 × 60.3 mm; specimen from Japan: 33.7 × 37.1 mm.

Habitat

On sandy or muddy bottom. The present record extends the known depth range which is now from 40 to 228 m.

Distribution

The present record extends the known range to the south-western Indian Ocean, i.e. the Strait of Mozambique. Further distribution range: Maldives, Bay of Bengal, Andaman Sea, Philippines, south China Sea, Japan.

Remarks

Both examined specimens agree well with existing descriptions and illustrations with regard to the carapace and cheliped morphology and the shape of the basal antennal segment (Figure 1D). The tubercles in the large specimen from the Strait of Mozambique are somewhat more smoothed than in most *C. pustulosa*, including our specimen from Japan.

Mursia africana Galil, 1993
(Figures 2A, B, 3A, B)

Mursia armata: Barnard 1950, p 356, Figure 67g [not *Mursia armata* de Haan, 1837].
Mursia africana Galil 1993, p 352, Figures 1a, 2a, b, 3a, b.
? *Mursia africana*: Ng et al. 2002, p 356–357.

Material examined

South-western Indian Ocean: off Kenya, 01°18′–01°20′N, 41°56′–41°53′E, 177–243 m depth, trawl, 14–15 January 1965, RV *Meteor*, Cruise 1, St. 158: one male, one juvenile (SMF 29497); off Mozambique, 15°05.0′S, 35°15.3′E, depth 210–230 m, shrimp trawl, RV *Vitiaz*, Cruise 17, St. 2635: one male (IORAS uncat.); off Kenya, 03°08′S, 40°20.5′E–03°07′S, 40°21′E, depth 250–255 m, 5 September 1974, A. J. Bruce coll.: one male (holotype, RMNH D 30986).

Type locality

Off Kenya, Western Indian Ocean.

Type material

See under ''Material examined''.

Size (CL × MCW)

Holotype: 30.7 × 56.6 mm, LS = 9.1 mm; specimen from off Mozambique: 30.4 × 53.7 mm, LS = 7.3 mm.

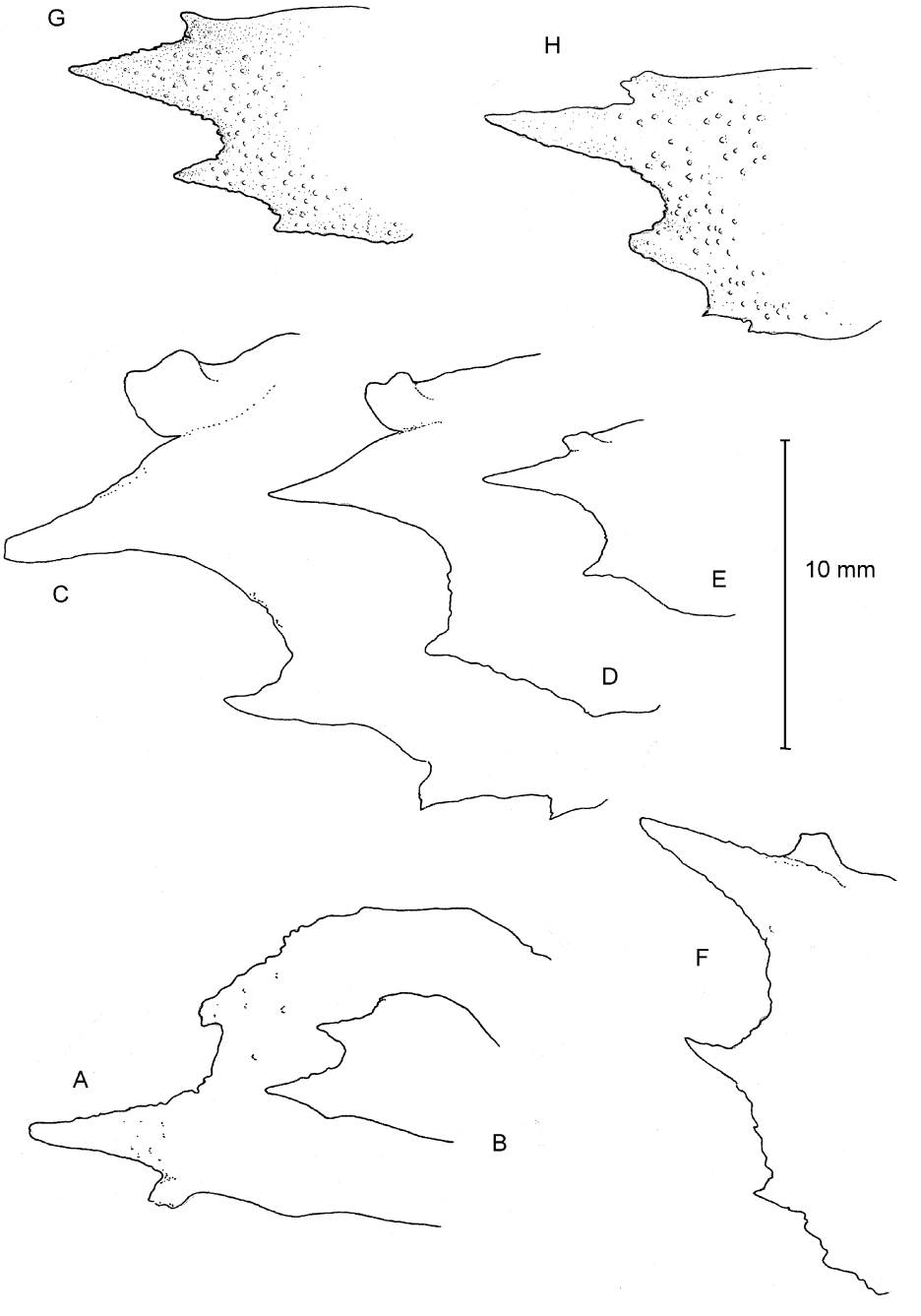

Figure 2. Dorsal view of distal margin of cheliped merus. (A) *Mursia africana*, male, CL 30.4 mm (IORAS, unregistered), left cheliped; (B) *M. africana*, juvenile male, CL 14.7 mm (SMF 29497), left cheliped; (C) *Mursia* aff. *danigoi*, male, CL 52.5 mm (IORAS, unregistered), right cheliped; (D) *Mursia bicristimana*, male, CL 50.0 mm (ZMMU Ma 5353), right cheliped; (E) *M. bicristimana*, female, CL 37.0 mm (SMF 22942), right cheliped; (F) *Mursia flamma*, female, CL 46.3 mm (IORAS, unregistered), right cheliped; (G) *Mursia minuta*, male holotype, CL 17.1 mm (NHM 1907.5.22), right cheliped; (H) *M. minuta*, male, CL 19.5 mm (NHM 1898.8.26.3), right cheliped.

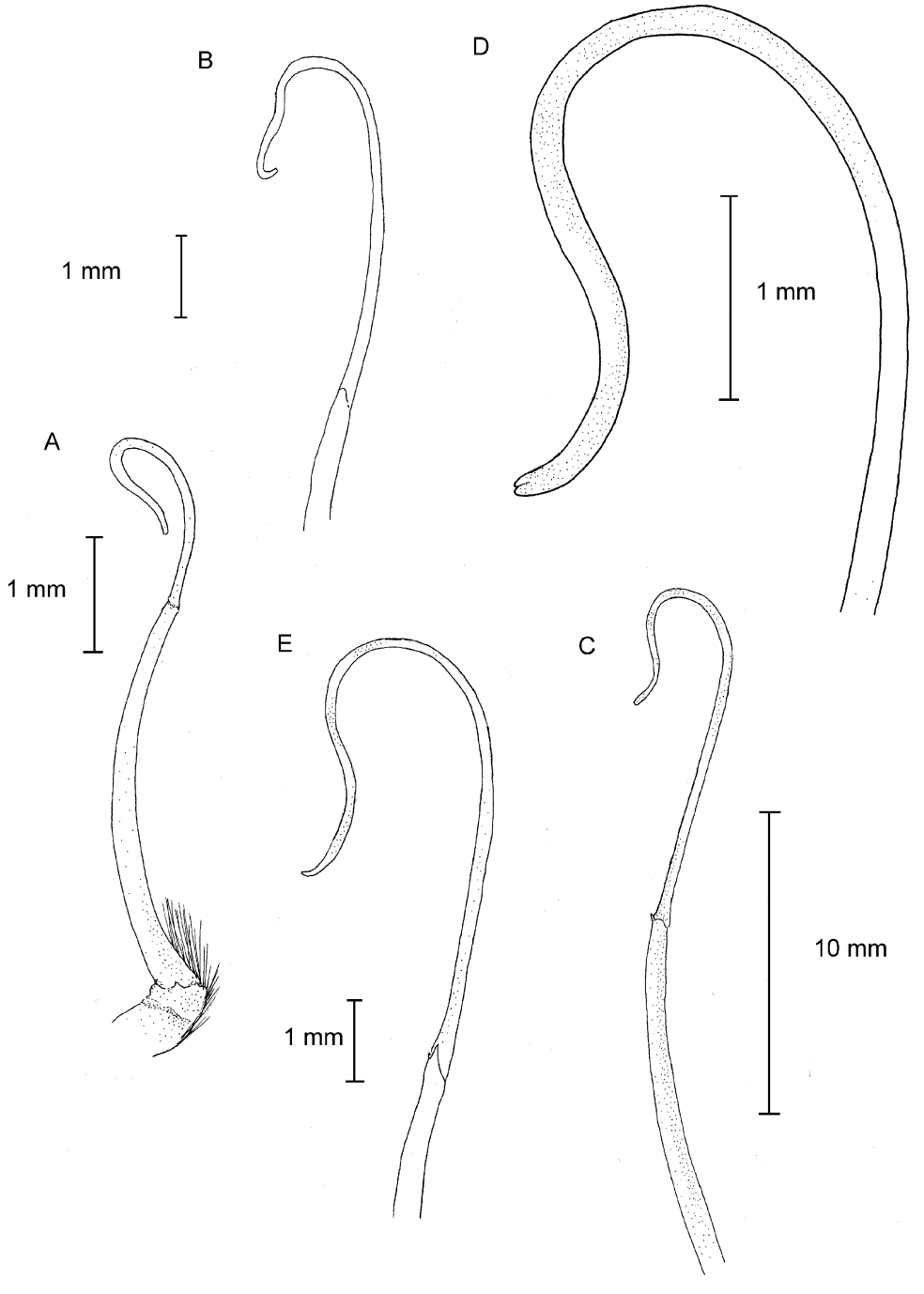

Figure 3. Gonopods 2 (Go/2). (A) *Mursia africana*, left Go/2, abdominal face, juvenile male, CL 14.7 mm (SMF 29497); (B) *M. africana*, left Go/2, abdominal face, CL 30.4 mm (IORAS, unregistered); (C) *Mursia bicristimana*, left Go/2, abdominal face, CL 50.0 mm (ZMMU Ma 5353); (D) *M. bicristimana*, left Go/2, terminal part, same specimen as in (C); (E) *Mursia* aff. *danigoi*, left Go/2, terminal part, abdominal face, CL 52.5 mm (IORAS, unregistered).

Habitat

Trawled at depth range 177–290 m.

Distribution

Along East African coast from Kenya to Mozambique. A record from Thailand by Ng et al. (2002) is questionable, since especially the relative length of the lateral spine is a difficult character to distinguish between *M. africana* and similar species, such as *M. flamma*, and use of the key provided by Galil (1993) might lead to misidentifications (see ''Remarks'').

Remarks

The present specimens agree well with the description of Galil (1993) and the holotype deposited in the RMNH, which has been examined for comparison. Even though *M. africana* is similar to *M. flamma* Galil, 1993, in particular regarding the shape of the Go/2 [compare Figures 3a, b and 10c, d in Galil (1993) and our Figure 3A, B], the two species are distinguished by the following characters: carapace relatively wider and less convex in *M. africana*, lacking the additional tubercle between median and mesial branchial row of tubercles which is present in *M. flamma*; posterior margin of carapace with flattened, nearly effaced lobes in *M. africana* and three sharp teeth in *M. flamma*; the merus of the cheliped bispinose (but with a minute granular tubercle in addition to the two spines) in *M. africana* and trispinose in *M. flamma*. Contrary to the description provided by Galil, the median frontal lobe is more or less triangular in *M. africana*, while it is more rounded and bulbous in *M. flamma*.

The relative length of the lateral spines, a character often used for distinction of the species within the genus, however, is subject to considerable size-related variation. In *M. africana* the LS/CW ratio ranges from 0.35 in small specimens to 0.20 in larger size specimens, while in *M. flamma* it varies from 0.20 to 0.07. Thus, if this character is used for distinction of the two species the size of the actual specimen needs to be taken into account. Otherwise the use of this character might result in misidentifications.

Mursia bicristimana Alcock and Anderson, 1894
(Figures 2D, E, 3C, D, 4A, B, 5A, B, 6A, B, 7A, B, 8A, 9A)

Mursia bicristimana Alcock and Anderson 1894, p 179; 1896, Plate 24, Figure 5; Alcock 1896, p 150–151; 1899, p 23–24, Plate III, Figures 3, 3a, b.

? *Mursia armata bicristimana*: Doflein 1904, p 41, Plate 17, Figure 3, Plate 18, Figure 4.

Mursia bicristimana Lloyd 1907, p 6; Kemp and Sewell 1912, p 29.

? *Mursia bicristimana*: Galil 1993, p 356–357 (part: specimens collected onboard RV *Anton Bruun*).

Mursia armata: Zarenkov 1994, p 100–101 (part: *Vitiaz* St. 2560, 2573, 2825) [not *Mursia armata* de Haan, 1837].

not *Mursia bicristimana*: Laurie 1906, p 355–356; Galil 1993, p 356–357 (part: specimens from Sri Lanka and the Laccadives deposited in the NHM), Figures 1f, 3j, k, 5c, d [=*Mursia minuta* sp. nov.].

Material examined

Gulf of Aden: RV *Meteor* Cruise 5, St. 267, 13°27.5′N, 47°20.5′E–13°27.9′N, 47°21.8′E, depth 359–362 m, beamtrawl, M. Türkay and A. Allspach coll., 13 March 1987: three males, five females (SMF 29499); same data: 104 juveniles (SMF 29500); RV *Ichtyandr*, Haul 60, 14°00.5′N, 48°52′E, depth 250 m, commercial trawl, September 1982, A. Levin coll.: two males (ZMMU Ma 5352). Arabian Sea: South of Socotra Is., RV *Vitiaz* Cruise 17, St. 2560, 12°17.7–12°14.2′N, 53°08.9–53°05.6′E, depth 375–380 m, shrimp trawl, 27 October 1988: two males (IORAS unregistered, identified as *Mursia armata* by N. A. Zarenkov); Error Seamount, RV *Vitiaz*, Cruise 17, St. 2573, 10°19′7–10°16.25′N, 56°07′3–56°07.5′E, depth 408 m, shrimp trawl, 30 October 1988: one male, one female (IORAS unregistered, identified as *Mursia armata* by N. A. Zarenkov); RV *Vitiaz*, Cruise 17, St. 2825, 10°10.5′–10°18.9′N, 56°08.8′–56°06.7′E, depth 395–420 m, M. V. Heptner coll.: one male, four females (ZMMU Ma 5353), two females, one juvenile (IORAS unregistered).

Specimens tentatively assigned to *M. bicristimana*: Nicobar Islands: Deutsche Tiefsee-Expedition, RV *Valdivia*, St. 208, depth 296 m, 7 February 1899: one female (ZMB 13660, identified as *Mursia armata bicristimana* by Doflein). Andaman Sea: International Indian Ocean Expedition, RV *Anton Bruun*, Cruise 1, St. 22B, 10°39′N, 97°06′E, depth 290 m, 24 March 1963: two males, one female (USNM 309672). Philippines: Philippines Expedition, RV *Albatross*, St. 5403, near Capitancillo Island between Leyte and Cebu, 11°10′N, 124°17′15″E, depth 333 m, 16 March 1909: one male, three females (USNM 65407). Philippines Expedition, RV *Albatross*, St. 5408, Camotes Islands, NW of Pacijan Island, 10°40′15″N, 124°15′E, depth 291 m, 18 March 1909: one male (USNM 1006735).

Type locality

Gulf of Manaar, Sri Lanka. R.I.M.S.S. *Investigator*, St. 151 (13.5 miles north, 64°W of Colombo), depth 142–400 fathoms, brown mud, 4 December 1893 [according to Alcock and Anderson (1894) and Anonymous (1914)].

Type material

In the original description by Alcock and Anderson (1894) there is no mention of the number or sex of the specimens obtained at *Investigator* St. 151. However, since the size (CL × MCW = 21 × 41 mm) is given for only one specimen without indication of further material, this might indicate that the description and original record is based on a single specimen. In this case, that specimen has to be considered a holotype. Its size indicates that it probably is the same as that illustrated by Alcock and Anderson (1896, Plate 24, Figure 5). If not lost or destroyed, this specimen should still be deposited in the ZSI in Calcutta, but all efforts to get any information or the specimen on loan failed. In case that there is more than one specimen in the original sample from *Investigator* St. 151 a lectotype should be selected.

Subsequently a large male (CL × MCW = 47.8 × 88 mm) was reported from *Investigator* St. 204 off Colombo (06°50′20″N, 79°36′20″E, 180–271 fathoms, 18 April 1895) by Anderson (1896). This specimen was mentioned in Alcock's (1896) account of the Calappidae and described and figured in great detail by Alcock (1899, p 23–24, Plate III, Figures 3, 3a, b). This specimen, however, has no type status and most probably it is deposited in the ZSI.

A specimen in the NHM (1898.8.26.3) was considered as a syntype by Galil (1993). Examination of this specimen revealed that it is accompanied by a label carrying the following information "Syntype? or Alcock det. 11°14′30″N, 74°57′15″E, 68–140 fathoms, coll. Indian Museum". Thus, the locality data on the label points to the Laccadive Islands, not to the Gulf of Manaar. Most probably the specimen was collected at *Investigator* St. 246, 15 October 1898, since the coordinates as well as the depth information given on the label agree exactly with the data for that station. It is therefore clear that the specimen was collected at a different locality and four years after the description of *M. bicristimana* was published, consequently this is not a syntype of that species. As will be discussed in detail below, a close examination of the specimen reveals that it belongs to a distinct and yet undescribed species.

Size

The measurements of the presumed type given by Alcock and Anderson (1894) are CL 21 mm, MCW 41 mm; those of the large male mentioned by Alcock (1896, 1899) are CL 47 mm, CW 67 mm. Adult males from the Gulf of Aden measure CL 28.1–48.2, CW 35.5–65.8, LS 4.6–6.2 mm; the females from the same station measure CL 36.1–43.7 mm, CW 45.9–56.5 mm, LS 5.5–6.3 mm (broken in smallest specimen). The male specimen from Error Seamount (ZMMU Ma 5353) measures CL 50.0 mm, CW 65.5 mm, LS 8.0 mm. The female from the Nicobar Islands measures CL 39.9 mm, CW 51.1, LS 9.8; the largest male from the Andaman Sea measures CL 44.2 mm, CW 59.8, LS 8.0.

Habitat

Records range from 250 to 420 m depth. Information on the sediments is scarce. In the case of *Meteor* 5, St. 267 it consisted of fine sand with numerous gastropod and bivalve shells (A. Allspach, personal communication). At *Investigator* St. 360 the sediment was probably fine sand (Lloyd 1907) and at *Investigator* St. 391 it was recorded that the trawl contained a remarkable number of the gastropod *Xenophora pallidula* Reeve, 1842 (Kemp and Sewell 1912).

Distribution

Gulf of Aden, Arabian Sea (off Socotra Is., Error Seamount), Laccadive Sea, Gulf of Manaar. Specimens tentatively assigned to *M. bicristimana*, but probably belonging to very similar but distinct species, have been recorded from the Andaman Sea and the Philippines.

Extended diagnosis (based on Alcock and Anderson and specimens from the Gulf of Aden and the Arabian Sea)

Carapace transversally oval, convex, 1.6–1.7 times broader than long (including lateral spines) and 1.25–1.35 times broader than long not counting lateral spines. Dorsal surface finely granular with one median and six radial rows of tubercles (protuberances according to Crosnier 1997a, 1997b) and one additional tubercle in each anterolateral region. Front wider than orbit, trilobate, median lobe broadly triangular, projecting well beyond rounded lateral lobes. Supraorbital margin unifissured. Inner suborbital tooth subtriangular with external edge straight or slightly convex, separated from outer orbital margin by U-shaped hiatus opening into oblique subhepatic canal. Anterolateral margin arched, with 11

acuminate granular denticles decreasing in size posteriorly. Lateral spines of moderate length, measuring from about one-tenth of CW in adult specimens from the Gulf of Aden to about one-third of CW in small juveniles, directed horizontally and slightly anterolaterally. Posterior margin with lateral lobes sharply triangular, median lobe small to indistinct.

Merus of cheliped bispinose, distal spine shorter than lateral spine of carapace. Upper margin of palm bearing a row of seven triangular teeth increasing in size up to sixth, last tooth smaller than the previous one. Outer surface bearing a continuous generally smooth ridge above lower margin with low sharp tooth proximally and finely granulated depression in distal half. Above this ridge seven granular tubercles forming three indistinct longitudinal rows. Area between the ridge and the rows of tubercles almost smooth. Lower margin serrated, but without well-developed teeth.

Ambulatory legs laterally compressed. Length to width ratio in meri varies from 3.4 in P2 to 3.1 in P5. Propodi with length to width ratio varying from 3.1 in P2 to 2.5 in P5, sharply keeled dorsally.

Crest on tergite 2 of abdomen trilobate, lateral lobes rounded, median subrectangular with almost straight or slightly convex posterior border, not projecting considerably beyond laterals. Penultimate segment of male abdomen subquadrate with sinuous margins. Ultimate segment (telson) forming equilateral triangle with slightly concave lateral margins.

Go/1 elongate, curved and tapering distally towards spinulose tip. Spinules forming terminal field around opening and extending in a thickening row along mesial face. Go/2 much longer than Go/1 with hook-shaped terminal tube, tip not reaching half distance to junction with basal part; junction mesially with pair of stiff bristles.

Female genital sternite and two previous sterna partly included in sterno-abdominal cavity densely beset with minute spinules similar to those on Go/1. Genital opening covered with spheroid cap, shifted close to anterior edge of sternite, posteriorly bordered by smooth elevated thickened cuticle, mesially bordered by subtriangular smooth area with median eminence.

Size-related variation

Within the material from the Gulf of Aden and the Arabian Sea the relative length of the lateral carapace spines decreases with size. Small specimens have lateral spines of about one-third of CW, while those of adult specimens do not exceed about one-tenth of CW. The expression of the median lobe on the posterior margin of the carapace is also variable. While small, but usually well discernible in adult males, it is very indistinct in females, and in juveniles this lobe cannot be recognized at all.

Coloration

Alcock and Anderson (1894) describe the coloration of *M. bicristimana* as ''salmon pink''. When obtaining the second specimen, Anderson (1896, p 103) made the following notes regarding the colour in life: ''upper surface of leg and carapace pale bluish white studded with orange red granules, lower surface white, inner surface of merus of cheliped deep orange''. All specimens studied by the authors had been stored in alcohol for extended periods and their colour was pale cream with a slightly darker carapace. In some specimens an orange spot on the inner surface of the palm near the junction with the movable finger was still visible.

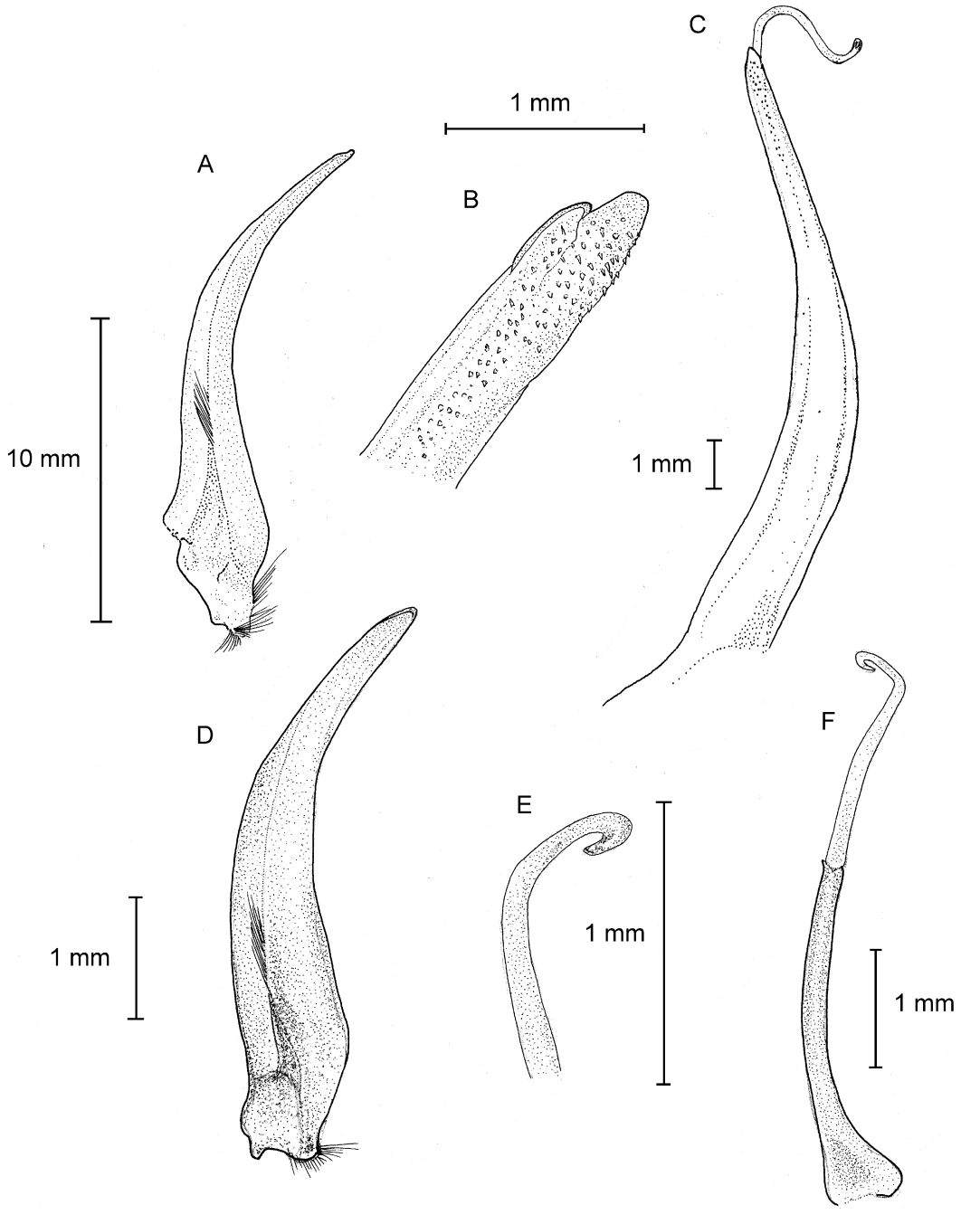

Figure 4. Gonopods 1 and 2 (Go/1 and 2). (A) *Mursia bicristimana*, left Go/1, CL 50.0 mm (ZMMU Ma 5353); (B) *M. bicristimana*, left Go/1, proximal part, same specimen as in (A); (C) *M. bicristimana*, right Go/2 inserted in Go/1, CL 48.4 mm (SMF 22942); (D) *Mursia minuta*, left Go/1, holotype, CL 17.1 mm (NHM 1907.5.22); (E) *M. minuta*, left Go/2, terminal part, same specimen as in (D); (F) *M. minuta*, left Go/2, same specimen as in (D).

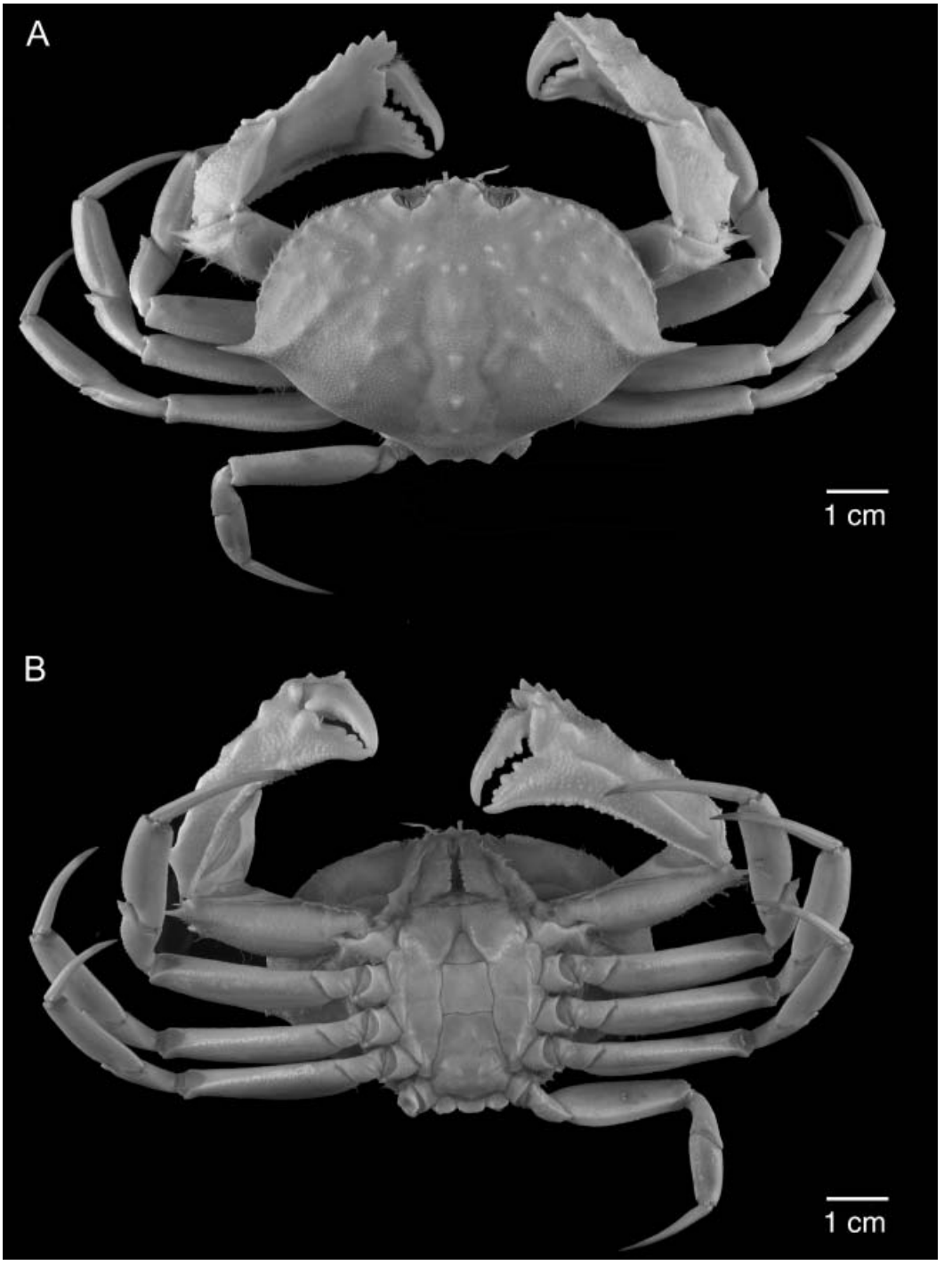

Figure 5. *Mursia bicristimana*, male, Gulf of Aden, CL 48.4 mm (SMF 22942). (A) Dorsal view; (B) ventral view.

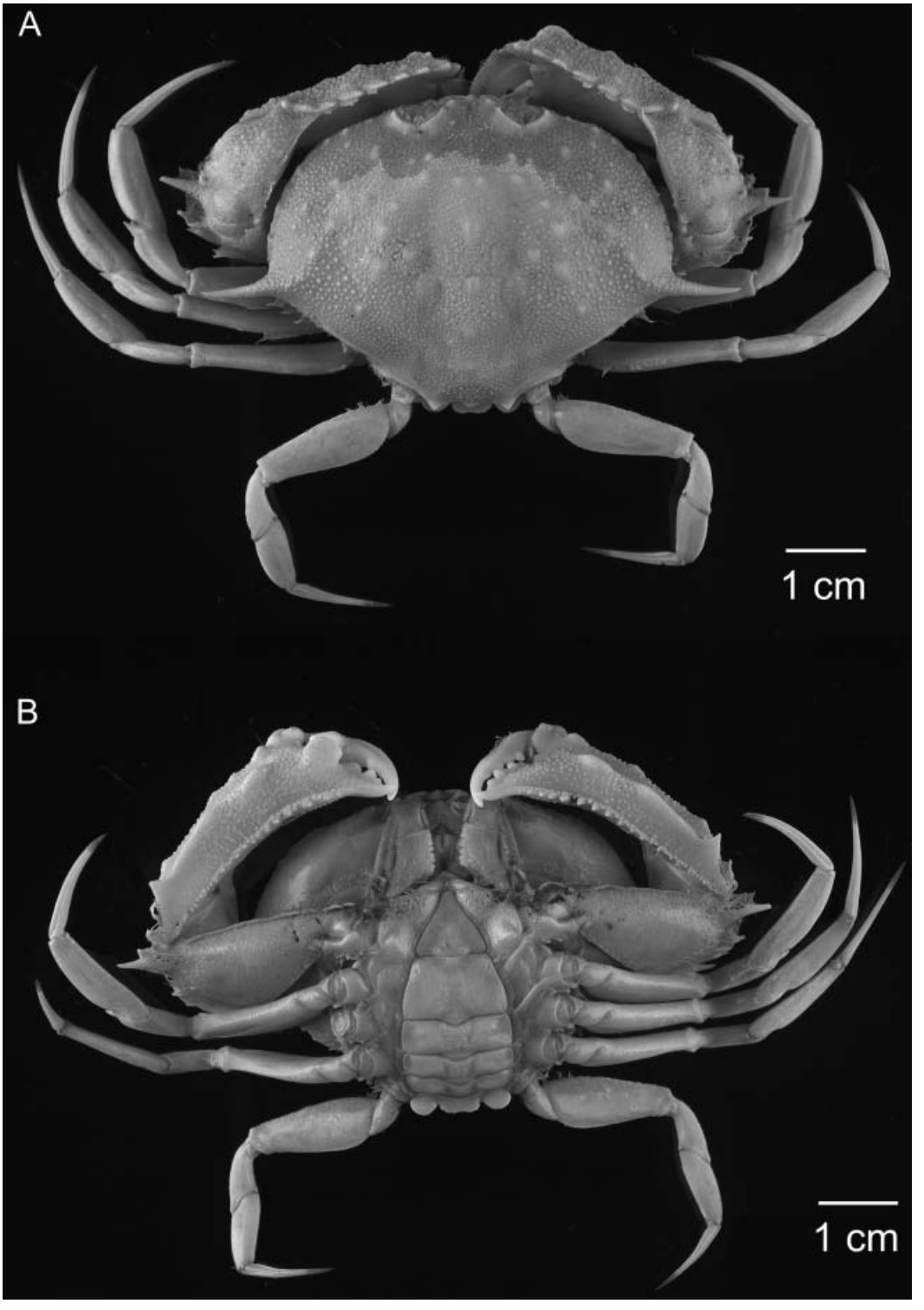

Figure 6. *Mursia bicristimana*, female, Nicobar Islands, CL 39.9 mm (ZMB 13660). (A) Dorsal view; (B) ventral view.

Affinities

Mursia bicristimana resembles *M. africana*, *M. flamma*, *M. coseli*, and *M. danigoi* in carapace morphology and tubercle pattern on the carapace, median lobe of front projecting beyond laterals, unifissured supraorbital margin, and Go/2 morphology. It is, however, distinguished from all above species by the outer surface of the palm bearing a continuous, indistinctly trilobed, mostly smooth ridge composed of three fused lobes above the lower margin. In *M. africana* and *M. flamma* all three of these lobes are widely separated. In *M. coseli* the lobes are separated from each other by granular depressions forming a wave-like ridge. In *M. danigoi* a subsidiary tubercle partly fills the gap between the proximal and the median lobe while the distal lobe is widely separated. Further distinguishing characters and their respective character states in the different species are given in Table I.

Remarks

The identity of *M. bicristimana* is difficult to clarify because of the inaccessibility of the type specimen (or specimens) in the ZSI. As already discussed above, the specimen from NHM certainly is not a type of *M. bicristimana* and, due to some considerable morphological differences such as the number of spines on the cheliped merus (four spines versus two in *bicristimana*), it cannot even be considered conspecific with the specimen described and figured by Alcock and Anderson (1894, 1896). The diagnosis given by Galil (1993) and in particular the characteristic shape of the Go/2 of the specimen thus do not refer to *M. bicristimana sensu* Alcock and Anderson, but to a yet undescribed taxon.

Lloyd (1907) reported *M. bicristimana* from the western Gulf of Aden (RIMSS *Investigator* St. 360, 13°36′N, 47°32′E, 130 fathoms, probably fine sand) and Kemp and Sewell (1912) mention a record from the Laccadive Sea (RIMSS *Investigator* St. 391, 9°14′10″N, 75°45′E, 237 fathoms). In both cases the material is probably housed in the collections of the ZSI and was not available for examination. It is, however, probable that the specimens are conspecific with the other material from the northwestern Indian Ocean and is therefore assigned to *M. bicristimana*.

The specimens from the Andaman Sea listed by Galil (1993) under the same species, however, do not have the characteristic Go/2 and apparently are not conspecific with the new taxon mentioned above. These specimens appear to be conspecific with a specimen from the Nicobar Islands collected by the Deutsche Tiefsee-Expedition and identified as *Mursia armata bicristimana* by Doflein (1904). The specimens from the Andaman Sea and the Nicobars as well as those from the Gulf of Aden and the Arabian Sea agree with *M. bicristimana sensu* Alcock and Anderson in most characters including the characteristic ridge above the lower margin of the palm, the morphology of the front and the posterior border. There are, however, important differences between the material from the northwestern and the eastern Indian Ocean. In specimens from the Nicobars and the Andaman Sea the carapace bears a well-developed additional tubercle between median and first radial row of tubercles (Figure 6A). In specimens from the Gulf of Aden, this additional tubercle is hardly visible (Figure 5A). The lateral spines of the carapace in adult specimens from the Andaman Sea and the Nicobars reach about 0.15–0.18 times CW, while the Gulf of Aden specimens have somewhat shorter spines reaching only about 0.10 times CW in adult specimens. Similarly, the distal spine on the cheliped merus in specimens from the Eastern Indian Ocean is between one-quarter and one-third of the length of the merus excluding the spine, while it is somewhat shorter in specimens from the Gulf of Aden reaching only about one-fifth of the merus length.

Comparing both forms with the figure in Alcock (1899), it appears that the specimens from the Gulf of Aden are more similar to the one depicted there, since the carapace is quite smooth and the merus of the cheliped is clearly bispinose. Thus, the specimens from the Gulf of Aden would be true *M. bicristimana* (providing, that the specimen depicted in Alcock 1899 is the same species as that described by Alcock and Anderson 1894), while those from the Andaman Sea are similar, but differ in several characters and might belong to a distinct species. Since, however, direct comparison with the type material was not possible the identity of true *M. bicristimana* is still not completely clarified, therefore no further taxonomic and nomenclatural actions were taken. The specimens from the Nicobars and the Andaman Sea are therefore preliminarily assigned to *M. bicristimana*.

Furthermore, five specimens from the USNM collected by the RV *Albatross* in the Philippines and identified as *M. bicristimana* have been examined. The specimens, ranging in CW from 20.2 to 40.6 mm, agree with *M. bicristimana* by possessing the characteristic

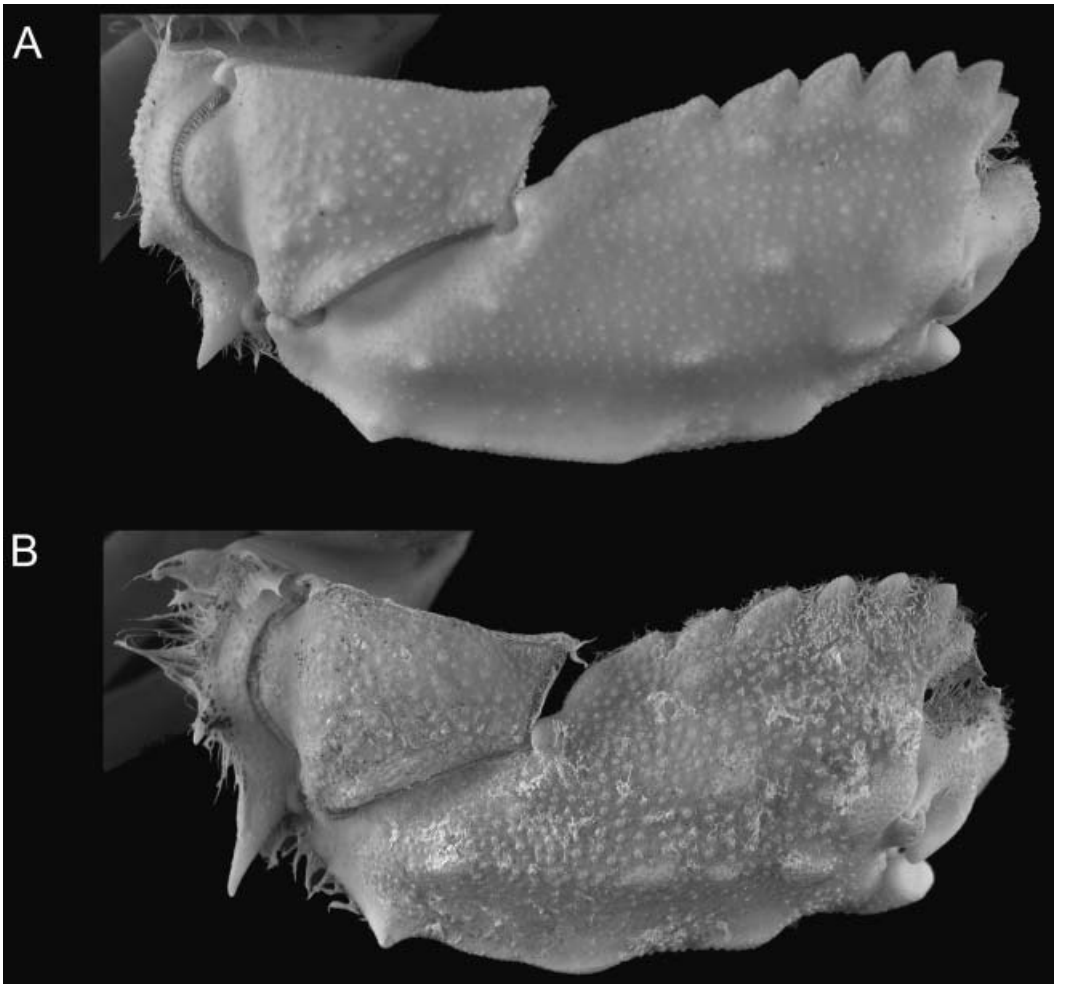

Figure 7. Cheliped palm of *Mursia bicristimana*. (A) Male, Gulf of Aden, CL 48.4 mm (SMF 22942); (B) female, Nicobar Islands, CL 39.9 mm (ZMB 13660).

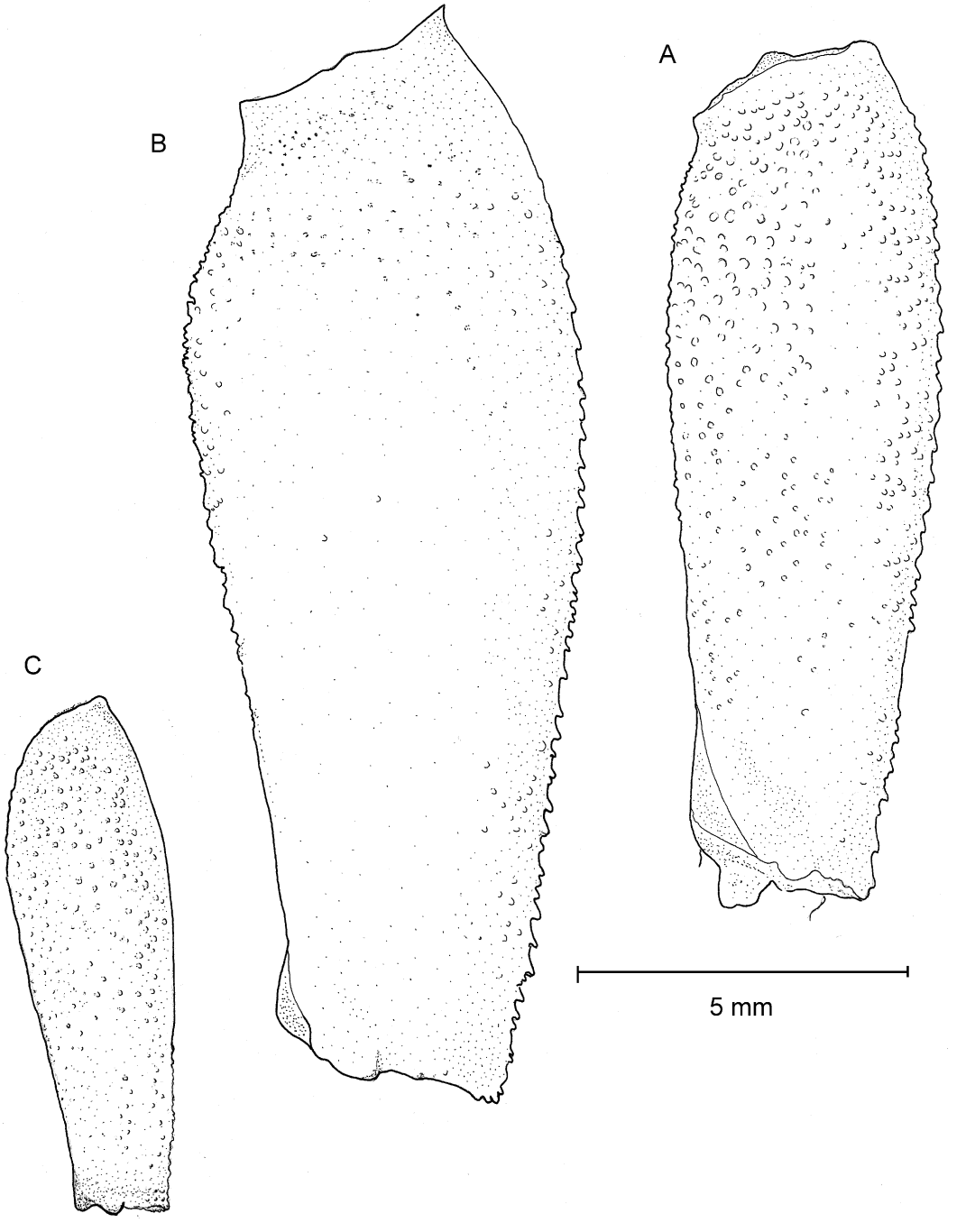

Figure 8. Merus of left last ambulatory leg, posterior view. (A) *Mursia bicristimana*, CL 48.4 mm, (SMF 22942); (B) *Mursia* aff. *danigoi*, CL 52.5 mm (IORAS, unregistered); (C) *Mursia minuta*, male, CL 19.5 mm (NHM 1898.8.26.3).

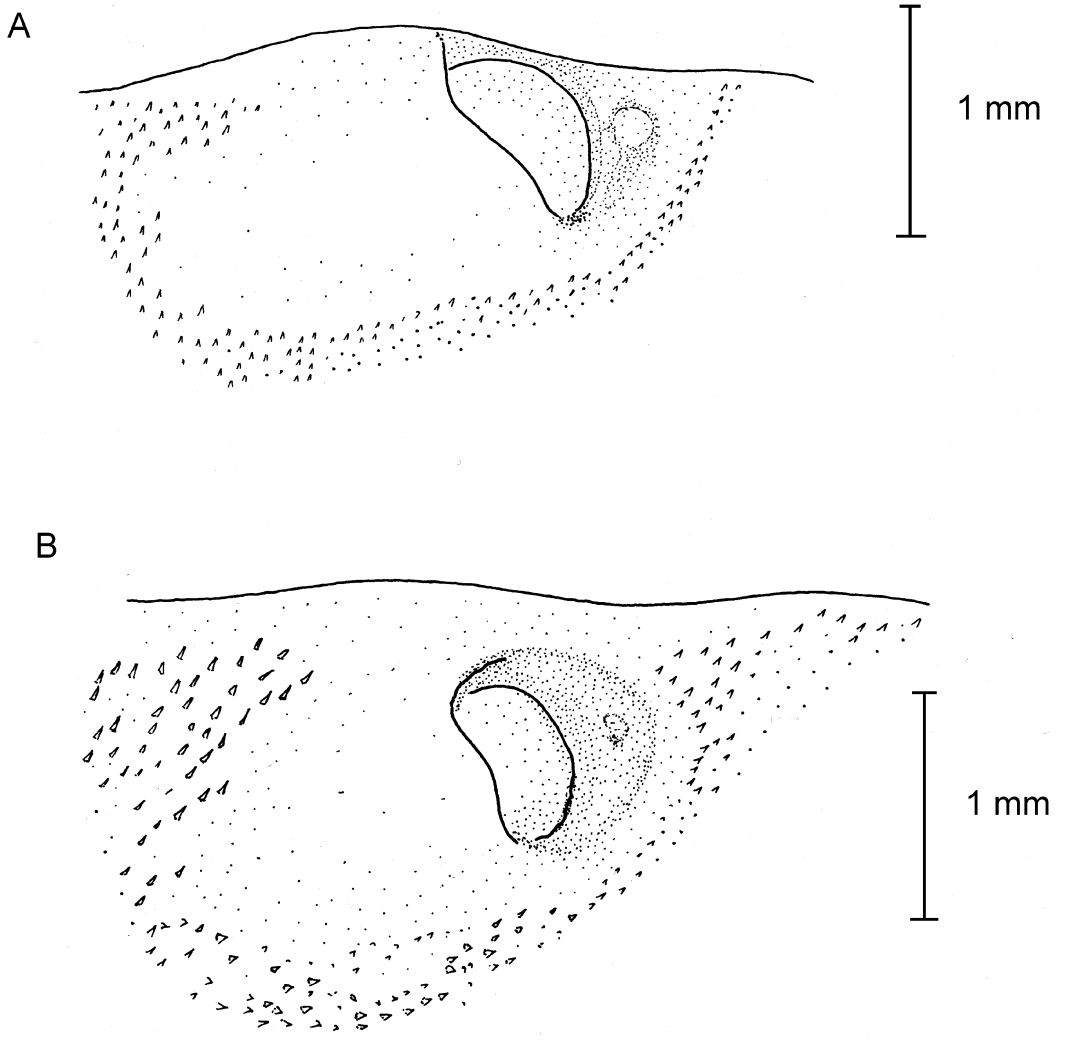

Figure 9. Female genital opening. (A) *Mursia bicristimana*, right genital opening, CL 37.0 mm (SMF 22942); (B) *Mursia flamma*, right genital opening, CL 46.3 mm (IORAS, unregistered).

ridge above the lower margin of the palm and by having a bispinose cheliped merus. They do, however, differ from *M. bicristimana* as described above, by having a smoother and less granular carapace, relatively longer lateral spines (0.21–0.24 times CW) and longer distal spines on the cheliped merus (one-third to almost half the length of the merus excluding the spine). Furthermore, the meri of the last pereiopods are more slender and have a less granular surface and upper margin in specimens from the Philippines than in specimens of similar size from the Gulf of Aden. For example, the largest specimen from the Philippines (CW 40.6 mm) has a length/width ratio of 3.5 for the merus of the last pereiopod, while the same ratio in a specimen from the Gulf of Aden (CW 34.4 mm) is only 3.2, even though the specimen is smaller and the legs of smaller specimens tend to be more slender in both forms. As for the specimens from the Andaman Sea, they are tentatively assigned to *M. bicristimana* for the time being although they may represent a distinct taxon.

Mursia minuta n. sp.

(Figures 2G, H, 4E, F, 8C, 10A–D, 11A, B, 12A, B)

Mursia bicristimana: Laurie 1906, p 355–356; Galil 1993, p 356–357 (part: specimens deposited in the NHM), Figures 1f, 3j, k, 5c, d [not *Mursia bicristimana* Alcock and Anderson, 1894].

Material examined

Holotype: Sri Lanka, Gulf of Manaar, Herdman coll.: one male (NHM 1907.5.22). Paratype: Sri Lanka, Gulf of Manaar, Herdman coll.: 1 ov. female (NHM 1934.1.16.23).

Non-type material. Laccadives: RIMSS *Investigator* St. 246, 11°14′30″N, 74°57′15″E, 68–148 fathoms (126–275 m), 15 October 1898: one male (NHM 1898.8.26.3). Gulf of Aden: 13°22.4′N, 46°42.9′E, RV *Akademik Petrovsky*, Cruise 14, St. 35, depth 87 m, Sigsbee trawl, D. L. Ivanov and B. V. Mezhov coll., 26 November 1983: one male (moult cast) (ZMMU Ma 5351); 15°52′N, 52°23′E, RV *Akademik Kovalevsky*, St. 657, depth 83 m, muddy sand, beam trawl, V. V. Murina coll., 11 September 1966: two males (ZMMU Ma 3902) (freshly moulted; identified as *Mursia armata bicristimana* by N. A. Zarenkov).

Type locality

Gulf of Manaar, Sri Lanka.

Etymology

The epithet "*minuta*" (Latin for "small") refers to the body size of the species which is much smaller than most other species within *Mursia*.

Size

Maximum carapace length does not exceed 20 mm, carapace width excluding lateral spine not more than 25 mm in the material examined. Exact size data are as follows. Holotype: CL=17.1, CW=21.7, MCW=28.0, P3=29.9 mm. Female paratype: CL=16.8, CW=20.4, MCW=25.4 mm (tips of lateral spines broken). Male from the Laccadive Islands: CL=19.5; CW=24.1; MCW=32.4; P3=36.6. Male from the Gulf of Aden (*Akademik Petrovsky* St. 35): CL=17.0 mm, CW=26.0 mm, MCW=27.4, SL 3.5 mm. Male from *Akademik Kovalevsky* St. 657: CL=13.0, CW=16.9, MCW=20.5.

Habitat and vertical range

For the type specimens from the Gulf of Manaar no ecological data are available, but due to the fact that the material originates from a study of the pearl oyster banks it can be assumed that they probably originate from relatively shallow waters. The specimen from the Laccadives (NHM 1898.8.26.3) is from a station with sandy/stony bottom and a depth range of 124–271 m. The specimens from the Gulf of Aden have been collected on muddy sand at depths of 83 and 87 m.

Distribution

Gulf of Aden, Laccadive Islands, Gulf of Manaar.

Description (based on holotype)

Carapace transversally oval, convex, ca 1.65 times broader than long (counting lateral spines) and ca 1.25 times broader than long not counting lateral spines. Dorsal surface coarsely granular excepting frontal and orbital region, which is finely granulated. A longitudinal row of four blunt tubercles (protuberances according to Crosnier 1997a, 1997b) along the midline, two closely set tubercles anterior to it on mesogastric region.

Branchial regions with two converging radial rows of four blunt tubercles each, the external one sinuous and meeting base of lateral spine. A mesial additional row of three less-marked tubercles present between median row and mesial branchial row, with anterior tubercle being rather well-developed and others hardly discernible. Second additional row consisting of two tubercles present between two branchial rows. Each hepatic region with a row of four tubercles, increasing in size anteriorly. Two additional tubercles on each side of gastric region (anterior being smaller than posterior) and one in each anterolateral region.

Front of about the same width as orbit, depressed, trilobate, median lobe broadly triangular, pointed; lateral lobes rounded, somewhat elevated, less produced than median. Supraorbital margin parabolic, with a single fissure but some grooving in place of second

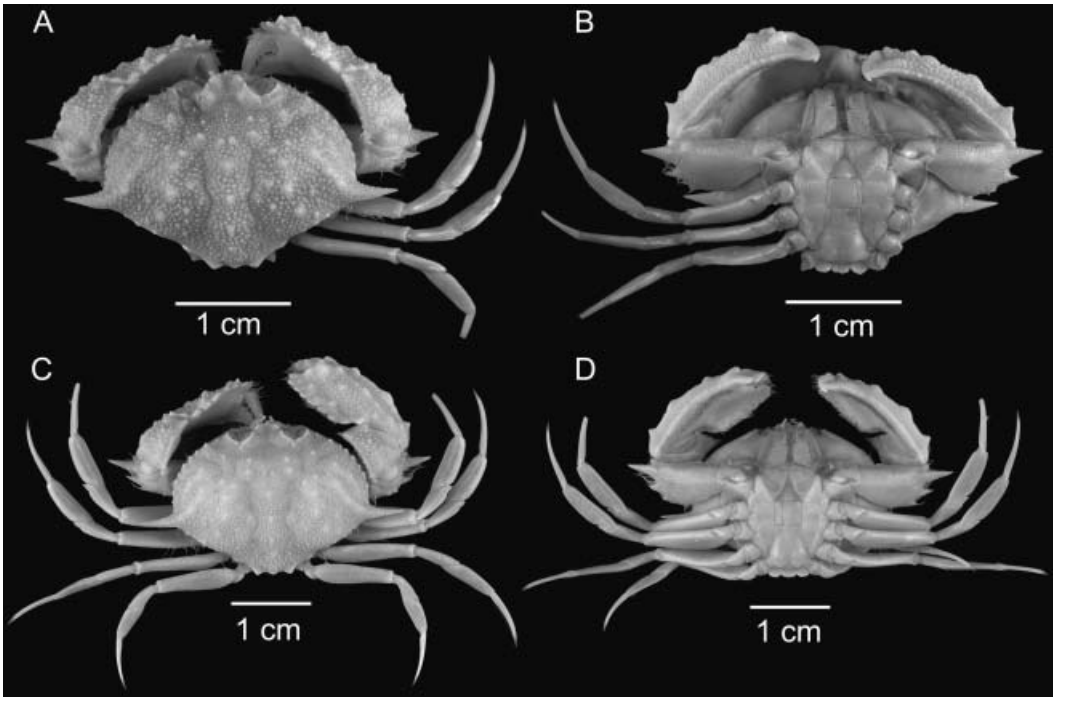

Figure 10. *Mursia minuta* sp. nov. (A, B) Male holotype, CL 17.1 mm (NHM 1907.5.22), dorsal and ventral views, respectively; (C, D) male from Laccadive Islands, CL 19.5 mm (NHM 1898.8.26.3), dorsal and ventral views, respectively.

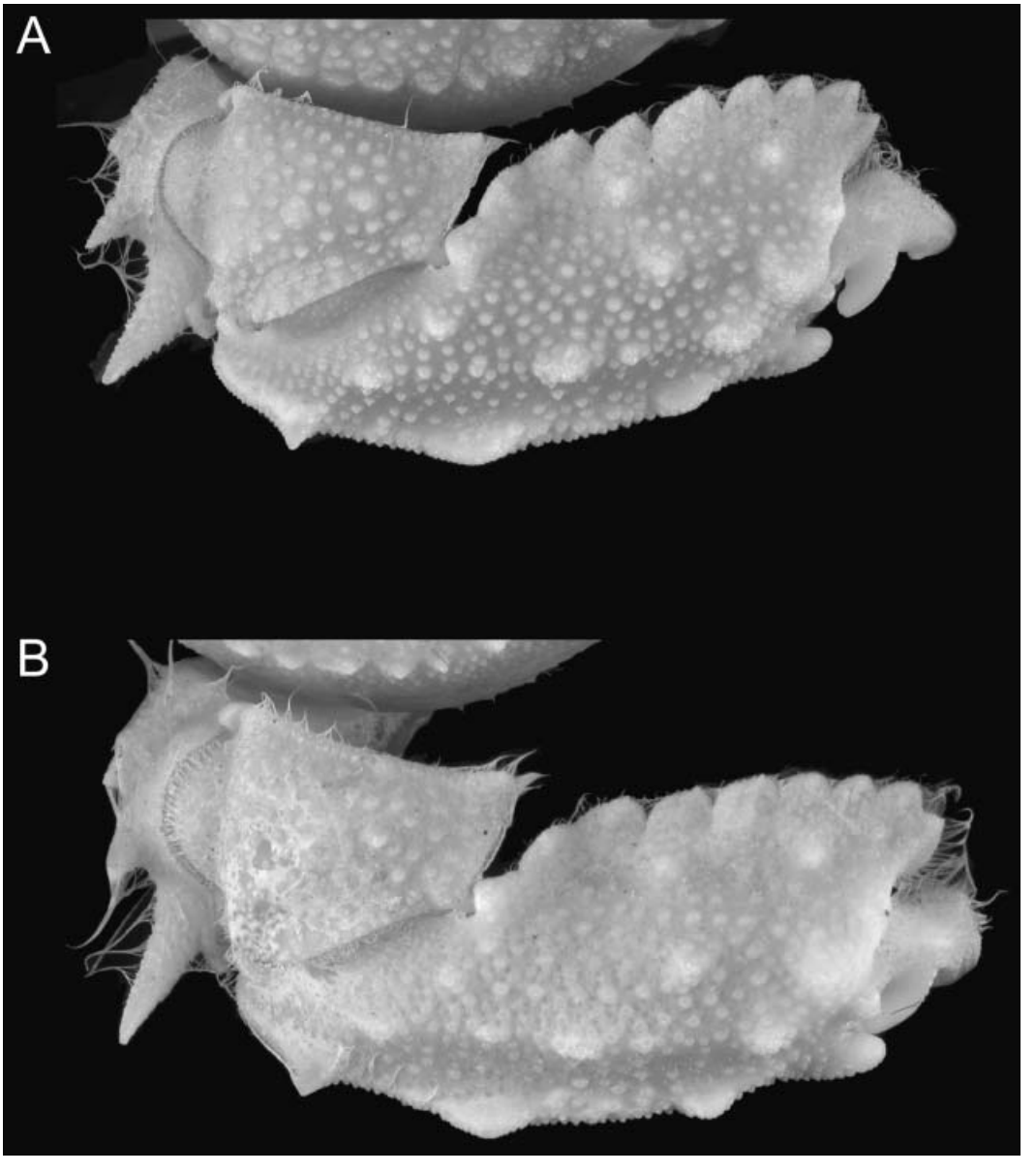

Figure 11. *Mursia minuta* sp. nov., right cheliped. (A) Male holotype, CL 17.1 mm (NHM 1907.5.22); (B) male from Laccadive Islands, CL 19.5 mm (NHM 1898.8.26.3).

fissure. Inner suborbital tooth sub-triangular, with outer margin straight and inner margin convex, separated from outer orbital margin by V-shaped hiatus opening into oblique subhepatic canal. Subhepatic region markedly granular. Anterolateral margin arched, carrying nine acuminate granular denticles with largest in middle part of arch and two to three additional granules anteriorly.

Lateral spines moderately long and stout, comprising ca 0.15 of CW, nearly straight, directed horizontally with markedly granular surface. Posterolateral margin sinuous, granular, with some granules in anterior half larger than others. Posterior margin

moderately granular, trilobate: both median and lateral lobes low, triangular, similar in size. Thoracic sternum and visible parts of sterna with moderate development of even granulation, those parts of sterna within sterno-abdominal cavity smooth.

Third maxillipeds elongate; exopod bearing longitudinal fringe of hair along complete length. Endopod ischia not closing in midline, leaving a narrow triangular gap; inner margins bearing rows of rounded teeth decreasing in size distally; merus with distolateral corner forming rounded process.

Chelipeds equal in size, evenly covered with granules similar to those on carapace excepting part of lower surface of merus and inner surface of palm. Distal margin of merus bearing three laterally directed rather stout spines; distal spine largest reaching distinctly more than half length of lateral spine of carapace and ca 0.4 of maximal merus length (excluding spines); following spine reaching about half length of distal spine, and third spine being smallest. Proximally to third spine is a small spinule or sharpened tubercle. In holotype, this tubercle is more developed in left cheliped, almost indistinguishable in right one. Carpus with three tubercles on outer surface, hardly distinguishable from background granulation, anterodistal corner triangular. Upper margin of palm bearing a row of two rather blunt proximal teeth and seven subtriangular teeth. Outer surface in lower part bearing a granular ridge with three distinct elevations, proximal triangular and sharp, median and distal rounded, subequal in size. Depressions between elevations are markedly granular. Above this ridge eight granular tubercles form three indistinct longitudinal rows: lower and median ones with three, and upper with two tubercles each. Lower surface granular, lower margin with coarse granules and six to eight denticles in anterior half. Inner surface nearly smooth in upper part, sparsely granular in lower part, with angled fringe of hair along lower margin and base of fixed finger. Fixed finger slightly deflexed, cutting edge bearing a row of irregular rounded teeth in left cheliped, and a large crushing tooth in right one. Movable finger with granular outer face and typical molariform proximal process in major cheliped; inner surface with milled ridge extending for most of length and becoming less clear distally.

Ambulatory legs laterally compressed, P3 being longest (but not much longer than P2). Length to width ratio in meri varies from 3.35 in P2 to 3.08 in P3 and 3.06 in P4. Upper surface and lower margin of meri granular, distal margin unarmed; in last pair of legs granulation extends to most of posterior face excepting lower distal corner. Upper surface of carpi with three granular carinae, median one ending in a terminal spine; distal margin with well-developed spines decreasing in size from P2 to P4. Propodi with length/width ratio comprising ca 3.7 in P2–P4, sharply keeled dorsally, in P2 and P3 keels serrated and preceded by a sparse row of granules at anterior surface of article; anterior and posterior surfaces with usual grooves. Dactyli longer than propodi, slender and slightly curved.

Abdominal terga smooth. Crest on tergite 2 of abdomen trilobate, lateral lobes rounded, median subrectangular with almost straight margin, not projecting considerably beyond laterals. Abdominal terga 3–5 fused. Penultimate segment subquadrate with sinuous lateral borders; ultimate segment (telson) forming equilateral triangle with slightly concave lateral margins. Go/1 tubular, evenly curved. Go/2 somewhat longer than Go/1, with distal part corkscrew-shaped.

Female characters and variation. Female sterna sparsely and finely granulated. Female abdomen smooth, terga separate: third tergite being broader than second and slightly

broader than fourth and fifth. Genital opening covered with spheroid cap, shifted close to anterior edge of sternite, posteriorly bordered by smooth somewhat elevated cuticle, mesially bordered by subtriangular smooth area with median eminence.

Egg mass extends laterally somewhat beyond coxa of anterior ambulatory legs. Eggs small, measuring ca 0.3–0.4 mm in diameter.

The male from the Laccadive Islands is similar to the holotype, with somewhat less coarse granulation on the carapace. Only the anterior tubercle in the mesial additional row between the median and the mesial branchial row of tubercles is recognizable. The meri of P5 (missing in the holotype and the paratype) lack a distinct spine distally and are sparsely granular over most of posterior surface; carpi lack anterior carina. Length to width ratio in meri varies from 3.40 in P2 to 3.26 in P3, 3.22 in P5, and 3.16 in P4. Propodi length/width ratio varies from 3.0 in P2, 3.72 in P3, 4 in P4 to 2.9 in P5.

Affinities

The present species is closest to *Mursia australiensis* Campbell, 1971, known from Australia, New Caledonia and, until recently with some reservation, from Japan (Campbell 1971; Galil 1993). A male specimen from Sagami Bay, Japan (Haberer coll., ZMB, unregistered), examined by us clearly belongs to that species, thus confirming the occurrence of *M. australiensis* in Japan.

Similarity between the two species includes general outline, carapace and cheliped granulation, and the Go/2 having a rather short and relatively stout curved terminal part. Within the genus this type of gonopod morphology is shared only by the above two species and *Mursia trispinosa* Parisi, 1914 (see Galil 1993, Figure 10h, i).

Mursia minuta n. sp. can be distinguished from *M. australiensis* by the lobes near the lower margin of the cheliped manus forming a granular ridge with three elevations, while in *M. australiensis* the three lobes are widely separated and do not form a ridge-like structure. The median lobe of the crest on the second abdominal tergite is broadly subrectangular with an almost straight margin in *M. minuta*, while it is rounded and much narrower in *M. australiensis*. The Go/2 in *M. minuta* is somewhat spiralled while it is sinuous in *M. australiensis*.

Mursia trispinosa is distinguished from *M. minuta* n. sp. by the three isolated large and pointed teeth near the lower margin of the cheliped palm and the strongly denticulated lower margin of the palm. Furthermore, in *M. trispinosa* the posterior margin of the carapace is bilobed, and the Go/2 is crochet-shaped.

Remarks

The specimen from the Laccadives was considered erroneously a syntype of *M. bicristimana* Alcock and Anderson, 1894 by Galil (1993). For details see "Remarks" on that species.

Mursia coseli Crosnier, 1997

(Figure 13A)

Mursia coseli Crosnier 1997b, p 750–755, Figures 1, 2, 3A–E, 4A.

Mursia armata: Zarenkov 1994, p 99–102 (part: only *Vitiaz* stations 2603 and 2804) [not *Mursia armata* de Haan, 1837].

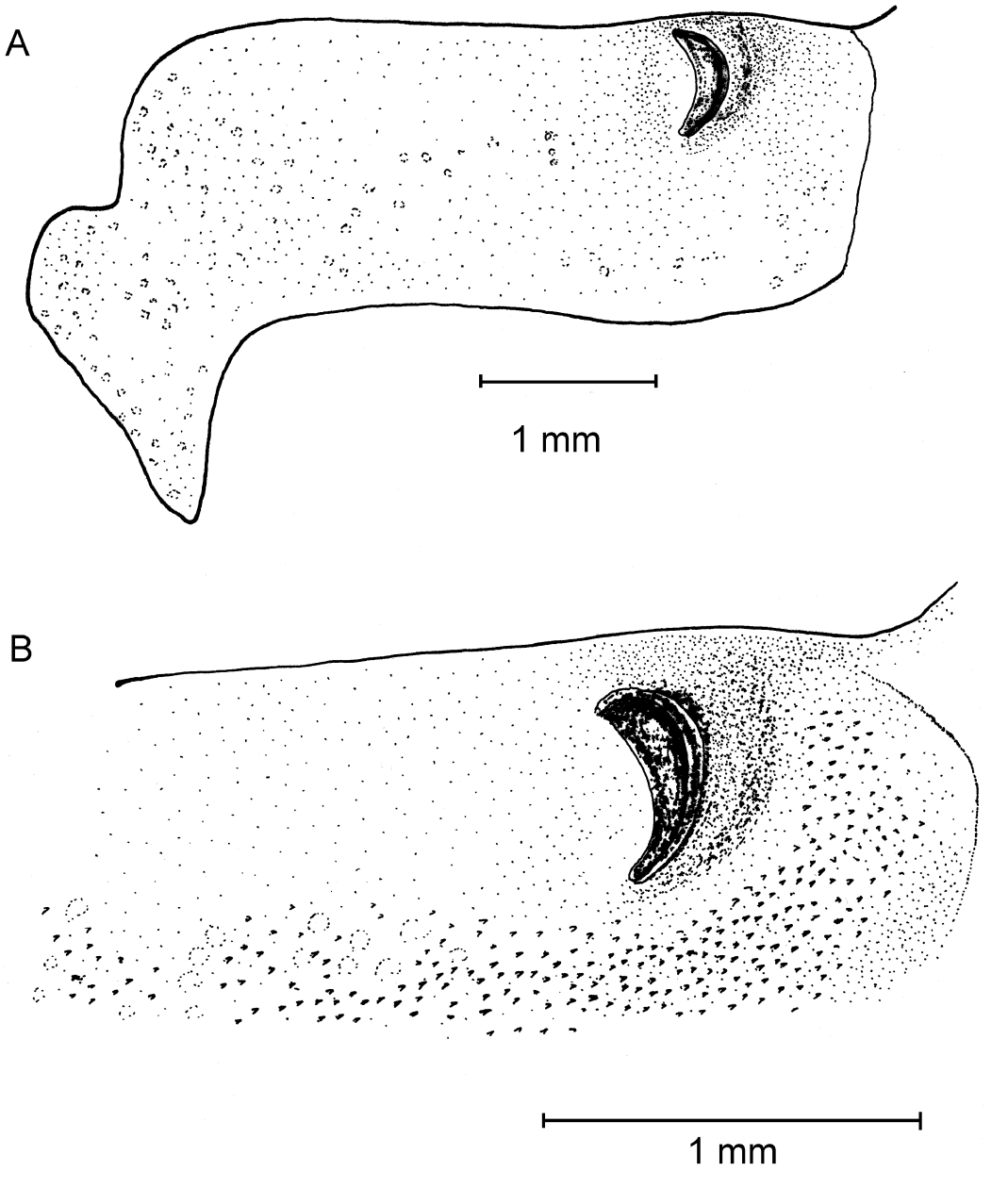

Figure 12. *Mursia minuta* sp. nov., female paratype, CL 16.8 mm (NHM 1934.1.16.23). (A) Female genital sternite; (B) female genital opening.

Material examined

Southwestern Indian Ocean: off Madagascar, RV *Vitiaz*, Cruise 17, St. 2603, 11°06′S, 48°18.6′E, depth 380 m, 12 November 1988: two males (one in ZMMU Ma 4858, one in IORAS, unregistered; originally identified as *Mursia armata* by N. A. Zarenkov, then re-identified by A. Crosnier); off Madagascar, RV *Vauban*, 12°39.8′S, 48°15.2′E, 375–385 m, 14 April 1971, A. Crosnier coll.: one male (holotype; MNHN B. 25584); same data as

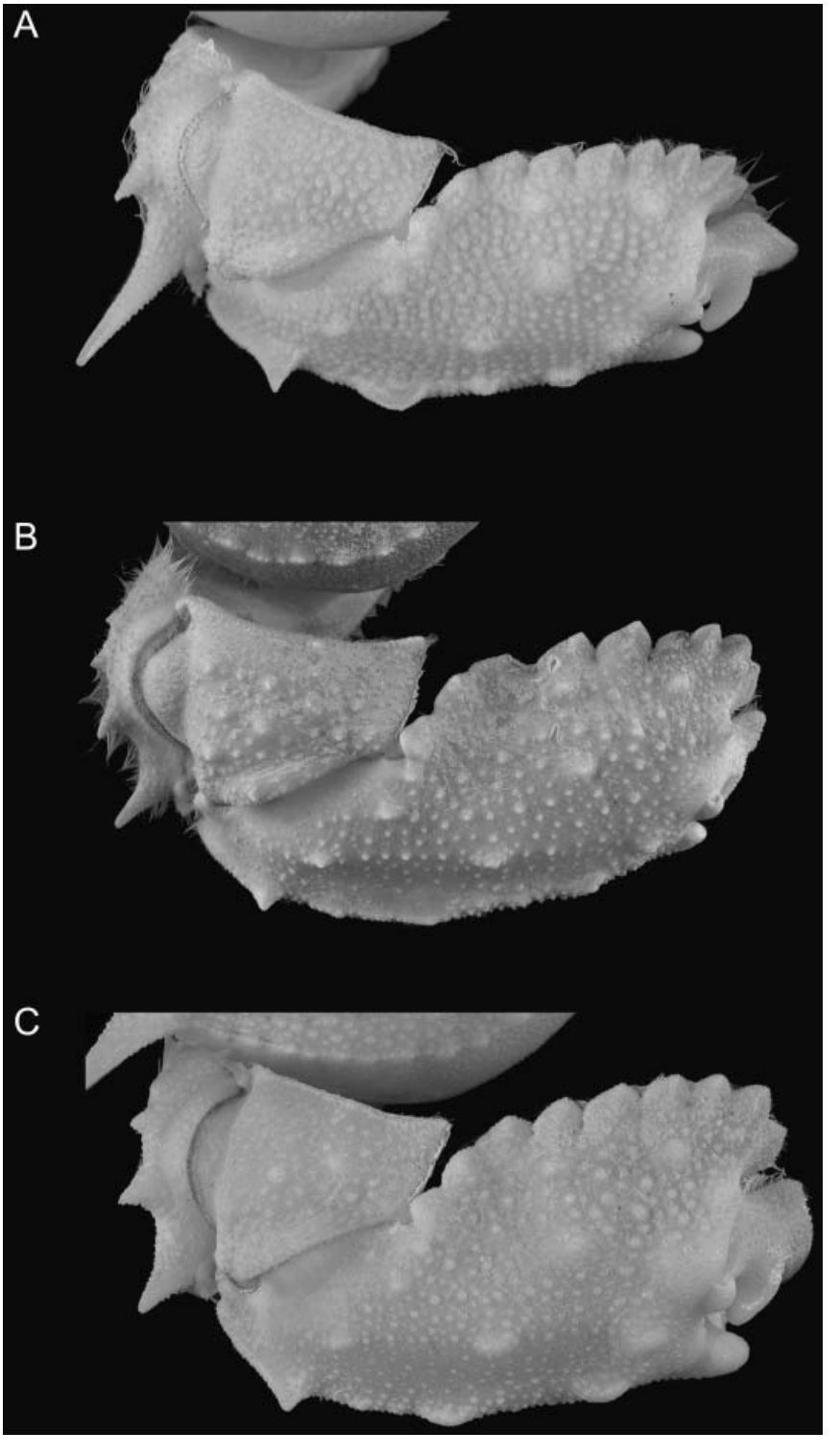

Figure 13. Cheliped palm. (A) *Mursia coseli*, male holotype, CL 21.6 mm (MNHN B.25584); (B) *M.* aff. *danigoi*, CL 52.5 mm (IORAS, unregistered); (C) *Mursia danigoi*, male paratype, 26.8 mm (MNHN B.22371).

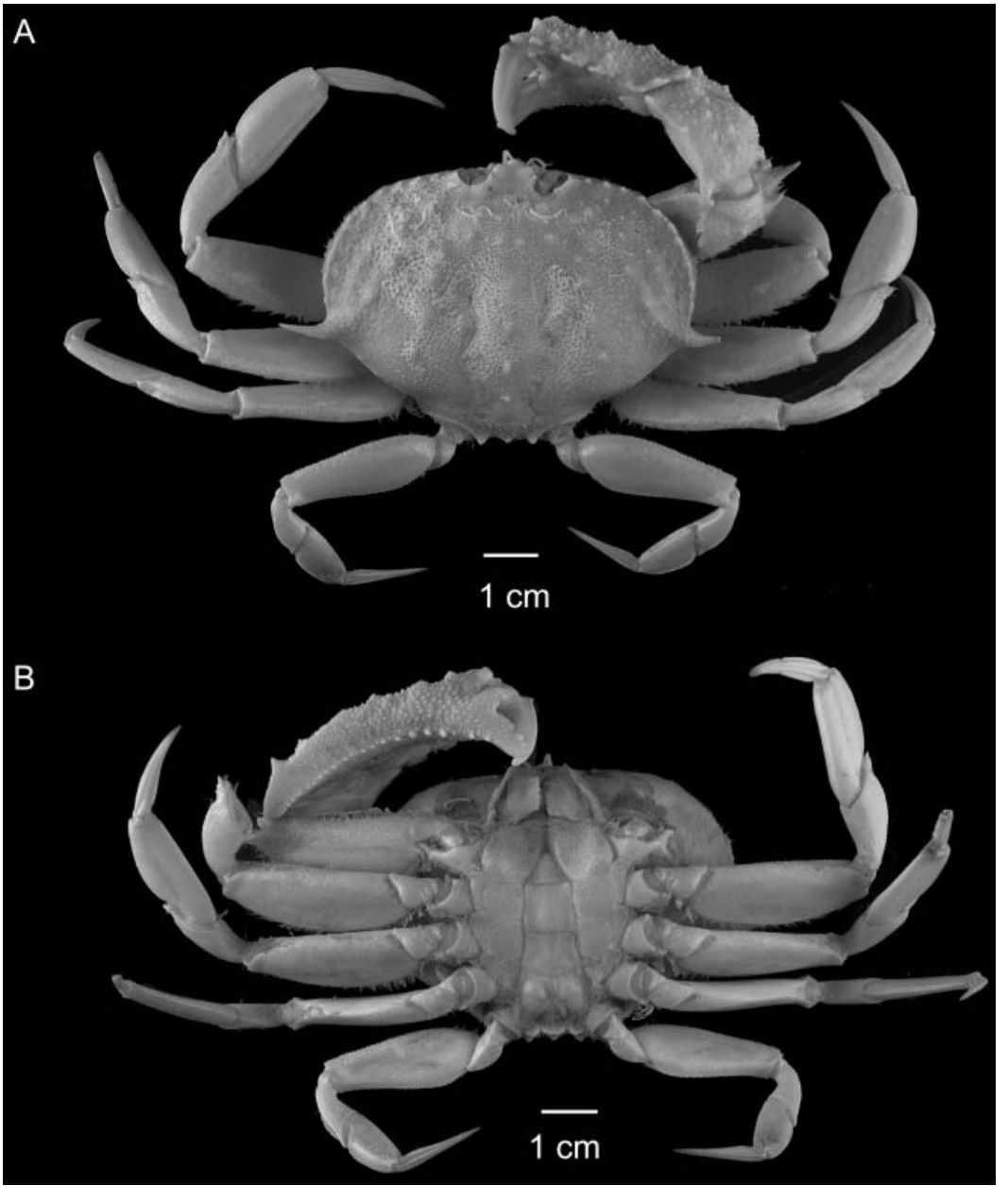

Figure 14. *Mursia* aff. *danigoi*, CL 52.5 mm (IORAS, unregistered). (A) Dorsal view; (B) ventral view.

holotype: one female (paratype; MNHN B. 25585); same data as holotype, MNHN B. 24478: one male, eight females (small specimens).

Type locality

Off Madagascar.

Type material

Holotype and 17 paratypes in the MNHN (Crosnier 1997b).

Size

Holotype: CL 21.6 mm, CW 25.6 mm, MCW 37.3 mm. Paratype: MNHN B. 25585: CL 23.3 mm, CW 27.1 mm, MCW 34.1. Male ZMMU Ma 4858: CL 21.5 mm, CW 25.3, MCW 35.8 mm.

Habitat

Known from 245 to 460 m.

Distribution

Known only from off Madagascar.

Mursia* sp. aff. *danigoi Galil, 1993

(Figures 2C, 3E, 8B, 13B, 14A, B)

? *Mursia danigoi* Galil 1993, p 360, Figures 1e, 3g–i, 5a, b; Tan et al. 2000, p 142, Figure 1a.

Material examined

Saya de Malha Bank, 11°06′S, 62°14′E, RV *Vitiaz*, Cruise 17, St. 2804, depth 230–235 m, shrimp trawl: one male (IORAS unregistered, previously identified as *Mursia armata* by N. A. Zarenkov).

Comparative material of *M. danigoi*: Philippines, 13°58.0′N, 120°13.7′E, MUSORSTOM 1, St. 58, 143–178 m, 26 March 1976: one female (paratype; MNHN B. 22371); 14°00.5′N, 120°16.5′E, MUSORSTOM 2, St. CP 59, 186–190 m, 28 November 1980: one male (MNHN B. 22366).

Size

The specimen from Saya de Malha measures CL=52.5 mm, CW=65.8 mm, LS=9.4 mm (one spine partly broken off). The holotype of *M. danigoi* measures CL=45 mm, CW=55 mm, MCW=71 mm.

Coloration

Even though the specimen has been stored in alcohol for an extended period and has lost most of its coloration, there are orange markings present in the pterygostomial region anterior to the base of the chelipeds, on the upper face of the cheliped merus, and on the inner surface of the cheliped palm near the base of the movable finger. In the specimen from Taiwan assigned to *M. danigoi* by Tan et al. (2000) there is a vertical red patch on the base of the cheliped movable finger as well as on the inner

surface of the palm and there are four minute dots on each side of the distal margin of the buccal cavity. According to the colour photograph of the above authors, the background colour of the carapace is orange. A pattern of dark red patches extends posteriorly up to the epibranchial regions while carapace and cheliped tubercles are whitish (Tan et al. 2000).

Habitat and vertical range

The specimen from Saya de Malha was collected at a depth of 230–235 m. *Mursia danigoi* from the Western Pacific was collected at a depth of 143–204 m.

Distribution

The examined specimen originates from Saya de Malha Bank in the western Indian ocean, while *M. danigoi* is known from the Philippines and Taiwan.

Remarks

The present specimen is close to *M. danigoi* and *M. coseli* in having a quadrispinose cheliped merus and a trilobate posterior margin of the carapace. According to Crosnier (1997b), the distinguishing characters between the two species include a more uneven granulation of the carapace in *M. coseli* and the length/width ratio of the P5 merus being 2.6–2.8 in *M. danigoi* versus 3.3 in *M. coseli*. The specimen from Saya de Malha shows the character state as described for *M. danigoi* in having a length/width ratio of the merus of the fifth pereiopod of 2.6.

It differs, however, from both species in having the anterior part of the anterolateral margin of the carapace unevenly curved, the lobes near the lower margin of the cheliped merus being incompletely fused forming a ridge-like structure and the Go/2 having a shorter recurved terminal part, not reaching the junction with proximal part. Since, however, only a single specimen is available and the extent of individual variation of these characters is unknown we refrain from describing a new taxon.

Mursia cristiata H. Milne-Edwards, 1837

Mursia cristiata H. Milne Edwards 1837 (1 July), p 109–110; Holthuis 1993, p 603–606, Figure 1a–c; Galil 1993, p 357–358, Figures 4a, 5e, f, 6a, c.

Mursia cristimanus de Haan 1837 (16 August), p 70; Barnard 1950, p 354, Figure 67a–f; Macpherson 1983, p 18, Figures 8, 9a–f.

Mursia cristimana: de Haan 1837 (16 August), p 70, Plate E; Krauss 1843, p 52; Doflein 1904, p 38–39, Plate 16, Figures 5–12, Plate 18, Figure 1.

Material examined

South Africa: Off Cape Town, Dr Isaeff coll., 15 December 1888: two females, one ov. female (ZMMU Ma 916); same locality, same collector: one male, one ov. female (ZSM 408/3); Francis Bay, RV *Valdivia*, St. 100: two males (ZSM 408/2). South Atlantic: St. Helena Island, Salmin coll.: one female, one ov. female (ZSM 408/1).

Type locality

"Cap de Bonne Espérance" (Cape of Good Hope), South Africa.

Type material

Mursia cristiata: Daniele Guinot from the MNHN kindly checked the collections in Paris and found three lots, each containing one specimen, labelled "Cap de Bonne Espérance" in the dry collection. Two of the specimens (MNHN-B. 97 and MNHN-B. 4096) were collected by Pierre-Antoine Delalande and the third one (MNHN-B. 96) was collected by Jules Verreaux. According to D. Guinot (personal communication) the two specimens collected by Delalande can be considered syntypes of *M. cristiata*, while the third specimen (collected by Verreaux) might have been collected later and should not be considered a type. From the two syntypes D. Guinot and Regis Cléva selected the male specimen (MNHN-B 4096) of approximately 35 mm CL as the lectotype. The other syntype, a specimen of similar size (MNHN-B 97), is selected as paralectotype. *Mursia cristimanus*: lectotype (selected by Holthuis 1993): RMNH D 38213: one male (dry), Cape of Good Hope, South Africa, H. B. van Horstok coll. 1826–1833, and RMNH D 38153 (mouthparts of RMNH D 38213). Paralectotypes (selected by Holthuis 1993): RMNH D 38152: two males (dry), Cape of Good Hope, South Africa, H. B. van Horstok coll. 1826–1833.

Size

Lectotype of *M. cristiata* (CL × MCW): 35 × 45 mm with one spine being slightly broken; lectotype of *M. cristimanus*: CL 27.5, CW 30.0, MCW 34.8 mm (Galil 1993). Examined specimens (CL × CW): males: 18 × 18.5 (LS 2.5)–30 × 33.5 (LS 3.0); ov. females: 20.0 × 21.5 (LS 2.0)–21.2 × 20.0 (LS 1.5).

Habitat and vertical range

Known from 10 to more than 300 m depth.

Distribution

South Africa from Natal to Namibia. St Helena Island in the South Atlantic. The latter record by Doflein (1901) was questioned by Manning and Holthuis (1981) but confirmed by our examination of the original material in the ZSM.

Remarks

Full synonymy and a more detailed discussion of the nomenclatorial problems are given by Holthuis (1993, p 603ff).

Mursia flamma Galil, 1993
(Figures 2F, 9B)

? *Mursia armata curtispina*: Doflein 1904, p 40, Plate 17, Figure 2, Plate 18, Figure 3 [? not *Mursia curtispina* Miers, 1886].

Mursia flamma Galil 1993, p 362–363, Figures 7a, 9a, b, 10c, d; Crosnier 1997b, p 755–756 (discussion of differences to *Mursia coseli*), Figures 3F, 5B.

Mursia armata: Zarenkov 1994, p 99–102 (part: only *Vitiaz* stations 2603, 2622, 2633, 2644, and 2635) [not *Mursia armata* de Haan, 1837].

Material

Strait of Mozambique: RV *Vitiaz* Cruise 17, St. 2622, 21°12.8′S, 35°41.8′E, depth 490–500 m, shrimp trawl: one female (IORAS, unregistered); RV *Vitiaz* Cruise 17 St. 2633, 25°25.8′S, 33°54.8′E, depth 420–430 m, shrimp trawl, 24 November 1988: one male (IORAS, unregistered); RV *Vitiaz* Cruise 17, St. 2635, 25°05′S, 35°15.3′E, depth 210–230 m, shrimp trawl, 25 November 1988: two females (IORAS, unregistered). Off Madagascar: RV *Vitiaz* Cruise 17, St. 2603, 11°06′S, 48°18.6′E, depth 380 m, 12 November 1988: one male (IORAS unregistered). RV *Vitiaz* Cruise 17, St. 2644, 22°19.5′S, 43°06.1′E, depth 330 m, shrimp trawl: one female juvenile (IORAS, unregistered). RV *Professor Mesyatsev* FAO-VNIRO Cruise, off Mozambique (?), exact locality unknown, B. G. Ivanov coll.: one male, one female (ZMMU Ma 5354). Specimens recorded as *M. armata curtispina* by Doflein 1904. Indonesia: RV *Valdivia* St. 199, 0°15.5′N, 98°04′E, S. of Nias Island, depth 470 m: one male, one female (ZMB 13662).

Type locality

Madagascar.

Type material

Male holotype (MNHN B24371) and numerous paratypes deposited in the MNHN; one paratype in the South African Museum (Galil 1993).

Size

The holotype measures CL=57.9 mm, CW=68.2 mm, MCW=76.6 mm. The female specimens from the Straits of Mozambique (ZMMU 2635) measure, CL=47.4 mm, CW=56.8 mm, MCW=64.3 mm and CL=46.5, CW=55.6, MCW=64.8 mm.

Habitat

The overwhelming majority of records are from a depth range of 300–510 m. The shallowest station where we recorded the species had a depth of 210–230 m. Galil (1993), however, indicates it from St. 3 of *Mascareignes* III Cruise (22°27.3′S, 43°07′E) at a depth of 35 m.

Distribution

Off Madagascar and along east African coast from Natal to Tanzania; West of Sumatra, Indonesia.

Remarks

An important character not mentioned in the original description of the species, but seen both in the photographs of type specimens (Galil 1993, Figure 7; Crosnier 1997b, Figure 5B) and in our material, is an extra pair of tubercles located between the inner

Table I. Character states of selected species of *Mursia* from the Indian Ocean.

Character	*M. bicristimana* sensu Alcock and Anderson	*M. bicristimana* (Gulf of Aden)	*M. bicristimana* (Andaman Sea)	*M. minuta*	*M. africana*	*M. flamma*	*M. coseli*	*M. danigoi*	*M.* sp. aff. *danigoi*
Frontal median lobe	Triangular	Sharply triangular	Triangular	Sharply triangular	Triangular	Rounded	Rounded, only slightly projecting	Triangular	Rounded
Posterior margin	Trilobate, lateral lobes triangular, median lobe indistinct	Trilobate, median lobe small to indistinct	Trilobate, median lobe small to indistinct	Trilobate, median lobe broadly triangular and similar in size to laterals	Indistinctly trilobate, with hardly recognizable flattened lobes	Tridentate, with three sharply triangular teeth	Trilobate with prominent lateral teeth and indistinct median lobe	Trilobate, median lobe prominent, but smaller than triangular laterals	Trilobate, median lobe prominent, but smaller than triangular laterals
Merus of cheliped	Bispinose	Bispinose	Trispinose, proximal spine small to indistinct	Quadrispinose	Bispinose, but sometimes with an additional sharpened proximal tubercle	Trispinose	Quadrispinose, but fourth spine very small, sometimes indistinct	Quadrispinose, but fourth spine very small, sometimes indistinct	Quadrispinose, fourth spine small, but distinct
Outer face of palm	Closely and sharply granular	Moderately granular	Moderately granular	Coarsely granular	Coarsely granular	Moderately to coarsely granular	Coarsely granular	Moderately granular	Moderately granular
Lowest row of tubercles on outer face of palm	Unevenly trilobed continuous ridge	Almost completely fused, forming nearly smooth ridge	Almost completely fused, forming nearly smooth ridge	Incompletely fused lobes forming partly granular ridge	Three widely separated teeth (lobes)	Three widely separated teeth (lobes)	Four teeth or lobes, separated	Three teeth or lobes, separated	Incompletely fused lobes forming gran ular ridge
Gonopod 2	Unknown	Tip by far not reaching half distance to junction with basal part	Tip by far not reaching half distance to junction with basal part	Tip relatively short and coiled (corkscrew-shaped)	Tip reaching half distance to junction with basal part	Tip reaching half distance to junction with basal part	Tip nearly reaching junction with basal part	Tip nearly reaching junction with basal part	Tip nearly reaching junction with basal part

branchial and median rows of tubercles on the carapace. They may be indistinct in juvenile specimens. Contrary to the description given by Galil, the frontal median lobes of *M. flamma* are rounded, not triangular. The female genital opening and surrounding cuticular field are similar to those in *M. bicristimana*, but are located a greater distance from the sternite edge and the mesial eminence is much less pronounced and more regularly shaped than in *M. bicristimana*.

Examination of the specimens collected by the Deutsche Tiefsee-Expedition off Nias Island, west of Sumatra and published by Doflein (1904) as *Mursia armata curtispina* Miers, 1886, revealed that these specimens correspond better with the description of *M. flamma* Galil, 1993 than with that of *M. curtispina*. In particular, the surface and anterolateral border of the carapace are more coarsely granulated than in *M. curtispina*, and the patterns are identical to those of *M. flamma* from East Africa. The median tooth on the posterior margin is not as small as in *M. curtispina* and the teeth forming the lowest row of tubercles on the outer face of the palm are more elevated and sharper than in *M. curtispina*. Furthermore, the Go/1 of the male from Nias agrees well with that of *M. flamma* from East Africa. Since, however, *M. curtispina* had been described on the basis of a single female specimen, comparison of that character is not possible.

Poore (2004) reported *M. curtispina* to occur in Australia (Western Australia, Northern Territories, Queensland, and New South Wales). However, the lateral spine of the figured specimen (Poore 2004, Figure 97b) is about a quarter of the maximal carapace width. In that character this specimen is different from *M. flamma* and thus it is possible that *M. curtispina* or a similar taxon occurs in the easternmost part of the Indian Ocean off the Western Australian coast.

Key to the Indian Ocean species of *Mursia*

1. Posterior margin of carapace arcuate, entire; suborbital tooth subquadrate; front pointed . . . . . *M. cristiata*
– Posterior margin bi- or trilobate; suborbital tooth triangular; front trilobate . . 2

2. Lateral carapace spines minute, less than 0.05 carapace width; lateral frontal lobes more prominent than median; outer surface of cheliped palm covered with acuminate granules and tubercles; upper and lower margins of pereiopodal meri with conical tubercles . . . . . *M. aspera* Alcock, 1899
– Lateral carapace spines more than 0.05 carapace width; lateral frontal lobes less prominent than median; outer surface of cheliped palm more or less coarsely granular with rows of large lobes or teeth; upper and lower margins of pereiopodal meri granular, but lacking conical tubercles 3

3. Lowest row of tubercles on outer face of cheliped palm consisting of three widely separated teeth or lobes 4
– Lowest row of tubercles on outer face of cheliped either consisting of four teeth or lobes or of fused teeth forming a more or less continuous ridge 6

4. Posterior margin of carapace indistinctly trilobate with hardly recognizable flattened median lobe; merus of cheliped bispinose, sometimes with an additional sharpened proximal tubercle . . . . . *M. africana*
– Posterior margin of carapace distinctly trilobate with sharply triangular lateral teeth; merus of cheliped trispinose 5

5. Upper margin of pereiopodal meri and carpi distinctly granular; lateral carapace spines 0.07–0.20 times carapace width (depending on size) . . . . *M. flamma*
– Upper margin of pereiopodal meri and carpi minutely granular; lateral carapace spines about 0.20–0.25 times carapace width . . . . . *M. curtispina*

6. Merus of cheliped bispinose or trispinose with proximal spine very small or indistinct 7
– Merus of cheliped quadrispinose, but fourth spine can be small or even indistinct 9

7. Merus of cheliped bispinose 8
– Merus of cheliped trispinose, but with very small and sometimes almost indistinct third spine . . . . . *M. bicristimana* (specimens from the Andamans)

8. Outer face of palm closely and sharply granular; lowest row of tubercles on outer face of palm forming an unevenly trilobed continuous ridge. . . . . *M. bicristimana sensu* Alcock and Anderson
– Outer face of palm moderately granular; lowest row of tubercles on outer face of palm almost completely fused, forming a nearly smooth ridge . . . . . *M. bicristimana* (specimens from the Gulf of Aden)

9. Tip of Go/2 short and coiled (corkscrew-shaped); posterior border of carapace with median lobe broadly triangular and similar in size to laterals *M. minuta* n. sp.
– Tip of Go/2 not coiled, nearly reaching junction with basal part; posterior border of carapace with median lobe smaller than laterals 10

10. Length/width ratio of the merus of fifth pereiopod >3; posterior border of carapace with indistinct median lobe . . . . . *M. coseli*
– Length/width ratio of the merus of fifth pereiopod <3; posterior border of carapace with prominent median lobe 11

11. Outer surface of palm bearing four separate teeth. . . . . *M. danigoi*⋆
– Outer surface of palm bearing incompletely fused lobes forming granular ridge above lower margin . . . . . *M.* sp. aff. *danigoi*

⋆*M. danigoi* has not been recorded from the Indian Ocean, but is included in the key due to its similarity to the specimen from Saya de Malha identified as *M.* sp. aff. *danigoi*.

Discussion

Traditional views of deep-water biodiversity and zoogeography assume that species diversity is low and that most species are widely distributed, this being attributed to the lack of distributional barriers and uniformity of environmental conditions (Ekman 1935, 1953). This concept of a species-poor, more or less homogeneous deep-water fauna within broad latitudinal ranges is to some extent based upon a scarcity of available material and fragmental faunistic knowledge. Limited understanding of species diversity in deep water has limited incorporation of deep-sea organisms into zoogeographic analyses.

With regard to the Calappidae and the Indian Ocean region, prior to the revisionary works by Galil (1993, 1997), six species from *Calappa* and *Mursia* were known to occur below 200 m depth. In *Calappa*, two species, *C. japonica* and *C. depressa* Miers, 1886, were known from deep-water localities within the region. New collections and intensive taxonomic research that included Galil's (1997) revision have not led to increased numbers of deep-water species being reported from the region, except for a new record of *C. pustulosa*

from Madagascar in the present paper. All three of the species recorded from the shelf break in the Indian Ocean are widespread with distributional ranges including the western Indian Ocean as well as the western Pacific.

The presence of *C. japonica* in the Red Sea, where it inhabits unusually deep water of up to 785 m depth, is of particular interest. There are no clear signs of morphological differentiation between the Red Sea and Indian Ocean populations. In many other decapod taxa the populations in the deep Red Sea are considered to be distinct subspecies, vicariant species, or species without a clear affinity to the Indian Ocean congeners (Türkay 1986, 1996; Spiridonov and Türkay 2001, 2007; Türkay and Spiridonov 2006). These varied levels of evolutionary differentiation are probably the result of multiple isolation events caused by sea-level changes and current reversals in the Straits of Bab al-Mandeb since the Miocene (Klausewitz 1983a, 1983b, 1989; Türkay 1986). Thus it can be concluded that *C. japonica* either has invaded the Red Sea very recently, probably during the holocene transgression following the last Ice Age, or the observed morphological homogeneity of *C. japonica* indicates a slow evolutionary change of morphological characters within that species, or even within the genus *Calappa*.

Mursia in contrast shows a very different pattern of diversity and distribution in deep waters of the Indian Ocean. Four species (*M. aspera* Alcock, 1899, *M. bicristimana*, *M. cristiata*, and *M. curtispina* Miers, 1886) were known from deep waters throughout the Indian Ocean prior to the work by Galil (1993), which described two additional species, *M. africana* and *M. flamma*. Subsequently, Crosnier (1997b) described *M. coseli*. Moreover, in the present paper one species *M. minuta* n. sp. is described from more shallow waters, and a second (*M.* sp. aff. *danigoi*) is reported from the central Indian Ocean. In *M. bicristimana* regional variation in several important characters was observed and could indicate more than one taxon is included under the current concept of that species. Thus, within the last decade, the number of species of *Mursia* known to occur in the Indian Ocean has doubled and probably will further increase in the future. Several of these species have more or less restricted geographical ranges within the Indian Ocean (Figure 15). Contrary to the situation in the genus *Calappa*, there is a comparatively high diversity of species with more restricted distributional ranges in *Mursia*. This agrees well with data from other recent taxonomic revisions and biogeographical analyses of tropical deep-water decapod fauna, which indicate that species numbers are considerably higher and distribution ranges often much more restricted than previously thought (Manning and Holthuis 1981; Macpherson and Baba 1993; Guinot and Richer de Forges 1995; Lemaitre 1996, 1999; Spiridonov and Zhadan 1999; Spiridonov and Türkay 2001; Türkay and Spiridonov 2006).

Ecologically, both genera are similar in inhabiting soft sediments (Sakai 1976), but there are considerable differences regarding their bathymetric ranges. While the species of *Mursia* are almost completely restricted to the shelf break and upper continental slope with a bathymetric distribution centred around 300 m, most species of *Calappa* inhabit shallow shelf regions (Bellwood 1998) and even those occurring deeper usually range into relatively shallow waters.

Mursia and *Calappa* belong to different clades of calappid crabs, and palaeontological data indicate that they diverged not later than the Oligocene and by that time might have already had different depth preferences (Bellwood 1998). Apparently *Mursia* is adapted to living in relatively cold deep waters, while *Calappa* is a mainly shelf-inhabiting group adapted to warm shallow waters (Galil 1997). The unusual occurrence of *C. japonica* at a depth of more than 700 m in the Red Sea can be easily explained by the extraordinary

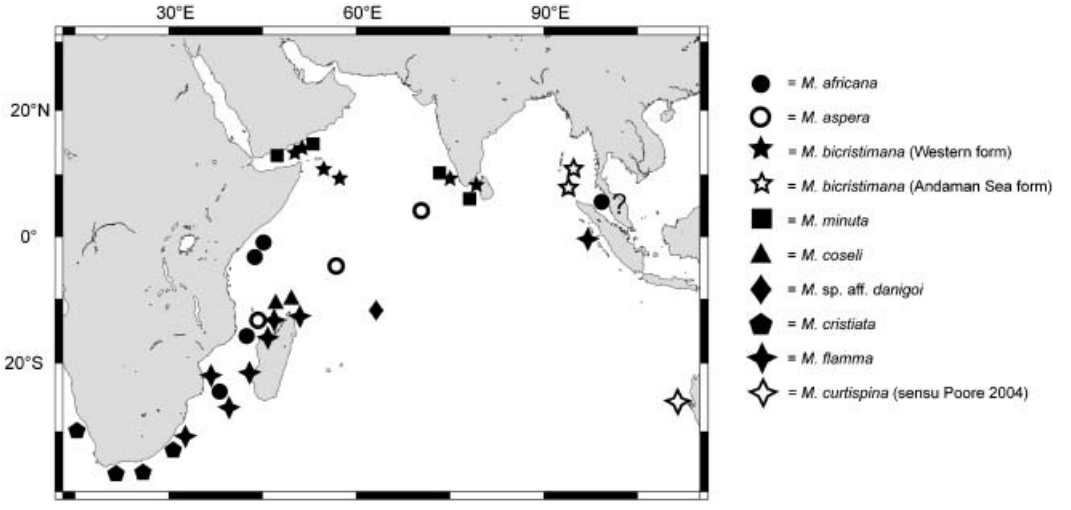

Figure 15. Distribution of *Mursia* species in the Indian Ocean.

temperature characteristics of the Red Sea with a homoiothermic water column, measuring 21.5–22.0°C from 200 m down to the greatest depths (Siedler 1969; Morcos 1970).

We suppose that the observed differences in geographical distribution patterns are closely related to the differences in vertical distribution between the two genera. Other studies of decapod distribution also indicate that shallow-water shelf taxa are generally more widely distributed in the Indo-Pacific than upper slope taxa (Spiridonov and Zhadan 1999).

A possible explanation for this somewhat surprising pattern might be the more patchy distribution of suitable habitats along the continental slope and shelf break. The mosaic distribution and variety of habitats in that zone stand in sharp contrast to the environmental conditions on the shelf and in the abyssal plains, which are usually areas of sediment accumulation. The slope, however, is mainly an area of denudation, but where possible mosaic accumulation of sediments takes place and generates a high habitat heterogeneity (Zenkevich 1977). Zenkevich's generalizations derived from the observations of the great deep-sea expeditions of the mid-20th century and were recently confirmed by direct observations using submersibles (Roux 1994).

In the case of *Mursia*, being restricted to soft sediment substrates and a relatively narrow vertical range, the mosaic set of habitats results in a fragmental distribution along the slope. As in other brachyuran decapods the larvae of *Mursia* are probably planktonic with a high ability for dispersal, but the fragmentary distribution of suitable habitats and the strong vertical gradient leads to elimination of a high proportion of larvae if there are no mechanisms of retention.

Continental slopes and seamounts usually form a complicated pattern of meso- and macroscale eddies. It is generally accepted that local circulation systems developing over seamounts provide retention of the larvae of seamount-dwelling demersal organisms, in particular fishes, even though these eddies are not stationary. To achieve retention it is sufficient if these eddies are stable over periods as long as the duration of larval pelagic life (Parin et al. 1985). This was also demonstrated using a simulation model incorporating turbulent diffusion (Rudyakov and Tseitlin 1985). The eddies usually associated with boundary currents over continental slopes may similarly contribute to the restriction of larval dispersal of continental slope species, but case studies do not exist.

In the northern Indian Ocean there may be other oceanographic mechanisms restricting larval dispersal, in particular the seasonal current reversal related to the monsoon (Wyrtki 1973; Neiman et al. 1997). Larvae released in the transitional season probably have better chances to settle close to the parental habitats and not to be transported to areas where settling is impossible. Moreover, seasonal reproduction appears to be a rather common phenomenon in the north-western Indian Ocean in several animal taxa including brachyuran crabs (Zarenkov 1971; Daniel and Chakrapany 1983; Couwelaar et al. 1998; Türkay and Spiridonov 2006) and might be an adaptation to the above-mentioned oceanographic phenomena.

Both mosaic distribution of habitats and oceanographic phenomena might result in a considerable restriction of gene flow and consequently in increased species diversity and restricted species distribution in shelf break and upper slope taxa.

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