

New records and new species of the hermit crab genus *Pagurus* Fabricius, 1775 (Crustacea: Decapoda: Anomura: Paguridae) from the Philippines

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Abstract. Although *Pagurus* Fabricius, 1775 is the most species-rich genus in the hermit crab family Paguridae, only two species of the genus, *P. hirtimanus* (Miers, 1880) and *P. spinulentus* (Henderson, 1888), were heretofore known from the Philippines. In this paper, 10 species of the genus, including eight firstly recorded from the Philippines, are reported from the Bohol Sea, based on a collection made during the PANGLAO 2004 Marine Biodiversity Project: *P. conformis* De Haan, 1849, *P. confusus* Komai & Yu, 1999, *P. fungiformis* Komai & Rahayu, 2004, *P. hirtimanus*, *P. kaiensis* McLaughlin, 1997, *P. kulkarnii* Sankolli, 1962, *P. moluccensis* Haig & Ball, 1988, *P. pergranulatus* (Henderson, 1896), *P. spinulentus*, and *P. truncatispinosus*, new species. *Pagurus truncatispinosus*, new species, is compared with *P. carpororaminatus* (Alcock, 1905), *P. cavicularis* Paul'son, 1875, *P. conformis*, *P. spinosior* Komai, Reshmi & Biju Kumar, 2013, and *P. spinulentus*. Detailed descriptions and illustrations are provided for *P. pergranulatus* and *P. spinulentus* because no modern descriptions are available for these two species so far.

Key words. Bohol Sea, *Pagurus truncatispinosus*, new species, PANGLAO 2004 Biodiversity Project

INTRODUCTION

Pagurus Fabricius, 1775 is the most species-rich hermit crab genus in the family Paguridae, represented by about 170 species worldwide (McLaughlin et al., 2010), though its heterogeneity has long been suggested (e.g., Forest & de Saint Laurent, 1968; McLaughlin, 1974, 1997; Komai, 1998, 1999; McLaughlin & Forest, 1999; Olgún & Mantelatto, 2013). The taxonomy of species assigned to the genus has been clarified mainly based on regionally based studies (e.g., McLaughlin, 1974, 1975, 1997; Haig & McLaughlin, 1991; Harvey & McLaughlin, 1991; Ingle, 1993; McLaughlin & Haig, 1993; Sandberg & McLaughlin, 1993; Komai & Imafuku, 1996; Komai, 1998, 1999, 2000a, b, 2003a, b, 2004; Komai & Yu, 1999; McLaughlin & Forest, 1999; de Saint Laurent & McLaughlin, 2000; Komai & Mishima, 2003; Komai & Rahayu, 2004; Komai et al., 2011), though there are still many species to be redescribed in modern standard or to be reassessed. From the Philippines, only two species of the genus have been recorded (Estampador, 1959), i.e., *P. hirtimanus* (Miers, 1880) [as *P. janitor* (Alcock, 1905)] and *P. spinulentus* (Henderson, 1888), in spite of the expected high diversity of the marine fauna in the area.

This study deals with a collection of species of the genus *Pagurus* made during the PANGLAO 2004 Marine Biodiversity Project, which was carried out in the Bohol Sea, the Philippines. This expedition resulted in extensive collection of marine decapod crustaceans (Bouchet et al., 2009), and several taxonomic reports on hermit crabs based upon the collection have been published (McLaughlin & Rahayu, 2007; McLaughlin, 2008; McLaughlin & Lemaitre, 2009; Rahayu & Forest, 2009; Asakura, 2010; Komai, 2013; Komai & Rahayu, 2013a, b, c; Rahayu & Komai, 2013). Herein, the following ten species of *Pagurus* are reported: *P. conformis* De Haan, 1849, *P. confusus* Komai & Yu, 1999, *P. fungiformis* Komai & Rahayu, 2004, *P. hirtimanus*, *P. kaiensis* McLaughlin, 1997, *P. kulkarnii* Sankolli, 1962, *P. moluccensis* Haig & Ball, 1988, *P. pergranulatus* (Henderson, 1896), *P. spinulentus* and *P. truncatispinosus*, new species. Except for *P. hirtimanus* and *P. spinulentus*, the species mentioned above are recorded from the Philippines for the first time. The new species, *P. truncatispinosus*, is compared with *P. carpororaminatus* (Alcock, 1905), *P. cavicularis* Paul'son, 1875, *P. conformis* De Haan, 1849, *P. spinosior* Komai, Reshmi & Biju Kumar, 2013, and *P. spinulentus*. Differentiating characters between the new species and its close relatives are discussed. Detailed descriptions and illustrations are provided for *P. pergranulatus* and *P. spinulentus*, since no modern descriptions are available for these two species.

MATERIAL AND METHODS

The PANGLAO 2004 Marine Biodiversity Project was conducted in 2004 jointly by scientists from the Muséum national d'Histoire naturelle, Paris; National Taiwan Ocean

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University; the Lee Kong Chian Natural History Museum (ex Raffles Museum of Biodiversity Research), National University of Singapore (ZRC); University of San Carlos, Cebu; and the National Museum of the Philippines, Manila (NM). The specimens examined are deposited in NM, ZRC, and the Natural History Museum and Institute, Chiba (CBM). The shield length (sl) is measured from the tip of the rostrum to the midpoint of the posterior margin of the shield. General terminology used in the description follows McLaughlin et al. (2007) except for the numbering of the thoracic sternites; terminology for the posterior carapace refers to McLaughlin (2003). Restricted synonymies list major references providing description on morphology and those relevant to local records; reference(s) to primary synonym(s), if available, are also included.

TAXONOMIC ACCOUNT

Family Paguridae

Genus *Pagurus* Fabricius, 1775

Pagurus conformis De Haan, 1849

Restricted synonymy.

Pagurus conformis De Haan, 1849: 204 [type locality: Japan]; Komai, 2004: 322, figs. 1–4; McLaughlin et al., 2007: 254, 255, unnumbered figs.; 2010: 33 (list), fig. 15E.

Eupagurus megalops Stimpson, 1858: 248 [type locality: East China Sea]; 1907: 216.

Pagurus megalops – Miyake, 1978: 84, fig. 31; 1982: 128, pl. 43, fig. 4.

Material examined. 1 male (sl 8.7 mm) (ZRC 2014.0337), PANGLAO 2004, PN1, Balicasag Island, coll. local fisherman, 29 April 2004, tangle nets.

Distribution. Previously known from Japan, Taiwan, and East China Sea, at depths of 5–190 m. Firstly recorded from the Philippines.

Remarks. The present specimen agrees well with the redescription of *P. conformis* by Komai (2004) except for the lack of a ventral median foramen of the carpus of the right cheliped. Komai (2004) believed that the presence of the foramen is diagnostic for *P. conformis*, but the present specimen shows that the character is possibly variable in this species. Similar variation in the presence or absence of the ventral foramen on the carpus of the right cheliped has been reported in *P. cavicarpus* (cf. McLaughlin & Forest, 1999).

Pagurus confusus Komai & Yu, 1999

Restricted synonymy.

Eupagurus obtusifrons – Yokoya, 1933: 85 (in part). Not *Eupagurus obtusifrons* Ortmann, 1892.

Pagurus obtusifrons – Miyake, 1978: 106, pl. 2, fig. 4; 1982: 128, pl. 43, fig. 5; Baba et al., 1986: 203, 204, fig. 151. Not *Pagurus obtusifrons* (Ortmann, 1892).

Pagurus confusus Komai & Yu, 1999: 197, figs. 6–9 [type locality: Tosa Bay, Japan, 140–150 m]; McLaughlin et al., 2007: 280, unnumbered figs.; 2010: 33 (list).

Material examined. 1 male (sl 5.7 mm) (ZRC 2013.0646), Balicasag Island, coll. local fishermen, November 2003 to April 2004, tangle nets; 1 male (sl 10.8 mm), 1 female (sl 8.2 mm), 1 ovigerous female (sl 9.1 mm) (ZRC 2013.0649), Maribohoc Bay, Panglao, 100–300 m, coll. local fishermen, between November 2003 and April 2004, tangle nets; 1 male (sl 5.7 mm) (ZRC 2013.0648), PANGLAO 2004, PN1, Balicasag Island, coll. local fisherman, 28 May 2004; 1 male (sl 4.9 mm) (ZRC 2013.0647), stn T5, W of Baclayon, Bohol Island, 09°35.3'N, 123°52.2'E, 84–87 m, coarse muddy sand, 2 June 2004.

Distribution. Previously known from southern Japan and Taiwan, at depths of 90–262 m. Its range is now extended southward to the Philippines, at depths of 84–300 m.

Remarks. The present specimens agree well with the published accounts of *P. confusus* (cf. Komai & Yu, 1999; McLaughlin et al., 2007).

Pagurus fungiformis Komai & Rahayu, 2004 (Fig. 1A)

Pagurus fungiformis Komai & Rahayu, 2004: 191, figs. 1B, 6–9 [type locality: Bitung, Sulawesi, Indonesia, intertidal]; McLaughlin et al., 2010: 33 (list).

Material examined. 5 males (sl 1.9–2.9 mm), 1 ovigerous female (sl 2.3 mm), (ZRC 2013.0645), PANGLAO 2004, stn M51, Mayacabac, Panglao Island, 09°36.8'N, 123°52.2'E, sand and sea grass, intertidal, 30 June 2004.

Distribution. Previously known from Indonesian localities (Sulawesi and Ambon), intertidal. Now from the Philippines.

Remarks. The present material agrees well with the type description of *P. fungiformis* by Komai & Rahayu (2004). As has been discussed by the original authors, this species is similar to *P. moluccensis* in the general morphology and the coloration in life (cf. Fig. 1A, C), but it is readily recognisable by the unique, characteristic armature of the palms of both chelae, consisting of closely set, low, rounded tubercles with multi-denticulate margins.

Pagurus hirtimanus Miers, 1880

Restricted synonymy.

Pagurus hirtimanus White, 1847: 60 (nomen nudum).

Pagurus hirtimanus Miers, 1880: 375, 376 [type locality: Philippines and Fiji]; Gordan, 1956: 330 (bibliography); Lewinsohn, 1969: 62; Haig & Ball, 1988: 186; Minemizu, 2000: 154, unnumbered figs.; McLaughlin et al., 2010: 33 (list), fig. 15G; Humann & Deloach, 2010: 163, unnumbered fig.; Poupin & Juncker, 2010: 5, 236, 237, fig. a; Poupin et al., 2013: 47, fig. 25A, B.

Eupagurus japonicus? – Miers, 1880: 375, pl. 14, figs. 6, 7. Not *Pagurus japonicus* (Stimpson, 1858).

Eupagurus hirtimanus – De Man, 1888: 426.

Eupagurus janitor Alcock, 1905a: 832, pl. 68, figs. 2, 4 [type locality: Hululu, Malé Atoll, Maldives]; 1905b: 125, 132, pl. 11, fig. 6; Estampador, 1937: 505; 1959; Yap-Chiongco, 1938: 208, pl. 2, fig. 1.

Pagurus janitor – Gordan, 1956: 331 (bibliography).

Not *Eupagurus hirtimanus* – Terao, 1913: 369 = *Pagurus pectinatus* (Stimpson, 1858).

Material examined. 1 male (sl 2.0 mm) (ZRC 2013.0633), PANGLAO 2004, stn B8, Napaling, Panglao Island, 09°37.1'N, 123°46.1'E, 3 m, reef platform, 7 June 2004; 1 ovigerous female (sl 8.0 mm) (ZRC 2013.0636), stn B10, Momo Beach, Panglao Island, 09°36.5'N, 123°45.6'E, 3–14 m, reef wall with small caves, 10 June 2004; 1 ovigerous female (sl 5.6 mm) (ZRC 2013.0637), stn B23, Black Forest, Balicasag Island, 09°31.1'N, 123°41.3'E, 20–25 m, rubble on sand, 25 June 2004; 1 male (sl 4.6 mm) (ZRC 2013.0641), stn B39, Abatan River, Bohol Island, 09°45.2'N, 123°56.0'E, 0–2 m, sand, consolidated cliff, 26 June 2004; 1 male (sl 9.4 mm), 2 females (sl 9.1, 8.4 mm) (ZRC 2013.0630), stn M1, Alona Beach, Panglao Island, 09°32.9'N, 123°46.6'E, 0–1 m, May to July 2004; 1 male (sl 3.9 mm), 1 female (sl 8.7 mm) (ZRC 2013.0631), stn

M2, W end of Alona Beach, Panglao Island, 09°32.8'N, 123°45.9'E, reef flat with sea grass bed, 0–2 m, 30 May 2004; 1 male (sl 3.2 mm) (ZRC 2013.0639), stn M3, Danao, Panglao Island, 09°32.5'N, 123°44.7'E, 0–2.5 m, reef, 31 May 2004; 3 males (sl 4.1–5.9 mm) (ZRC 2013.0632), stn M7, Momo Beach, Panglao Island, 09°36.1'N, 123°45.2'E, 0–3 m, reef platform with sea grass, 1 June 2004; 1 male (sl 4.0 mm) (ZRC 2013.0642), stn M10, Bingag/Tabalong, Panglao Island, 0–3 m, 09°37.8'N, 123°48.4'E, rocky area with sea grass, 5 June 2004; 1 ovigerous female (sl 10.1 mm) (ZRC 2013.0638), stn M22, Napaling, 09°37.2'N, 123°46.4'E, 0–3 m, coral platform, 15 June 2004; 5 males (sl 3.3–5.3 mm), 1 female (sl 5.2 mm) (ZRC 2013.0635), stn M40, Looc, Panglao Island, 09°35.7'N, 123°44.7'E, 0–3 m, fringe mangrove, sea grass beds and hard bottom, 22–28

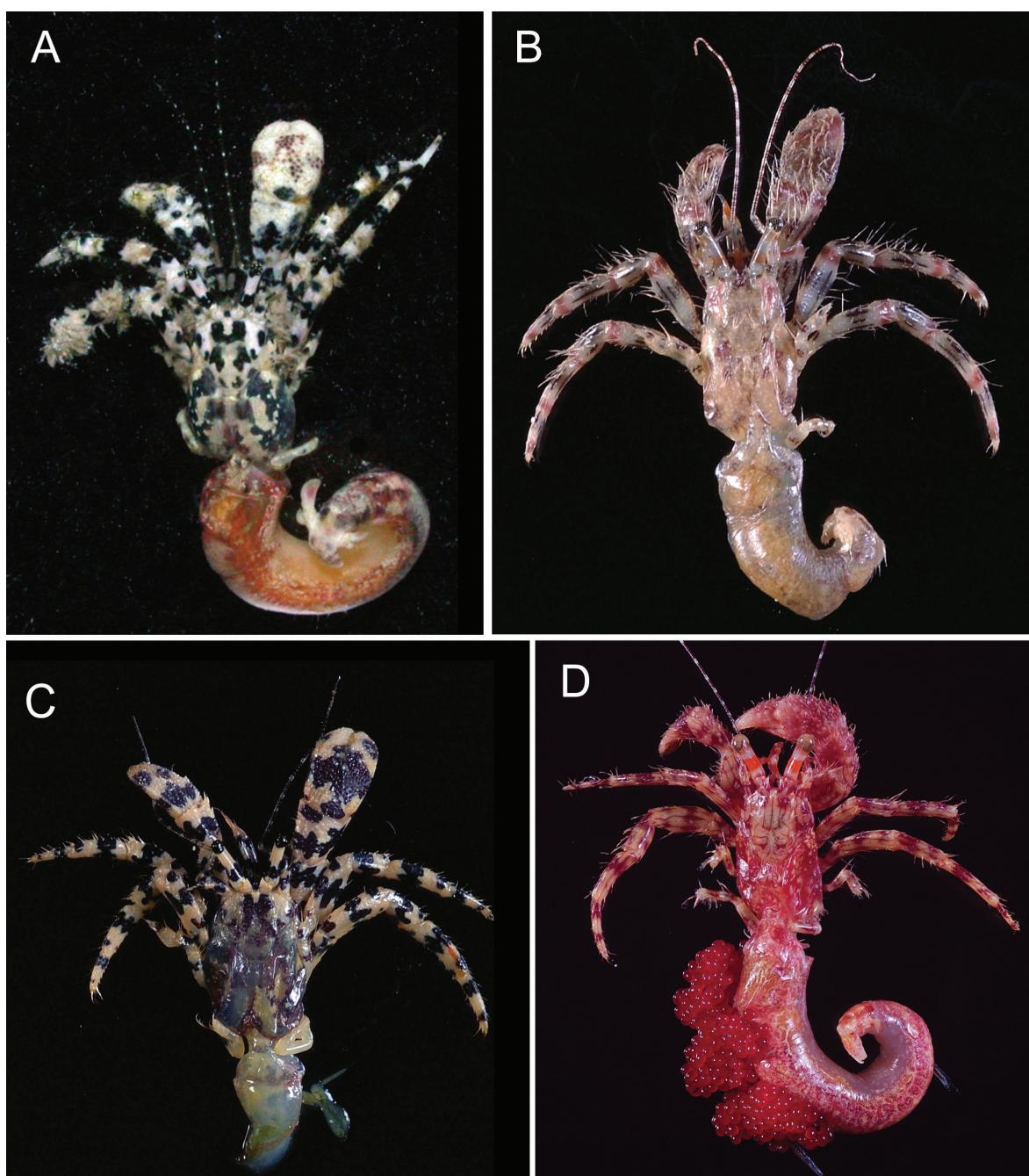


Fig. 1. A, *Pagurus fungiformis* Komai & Rahayu, 2004, male (sl 2.7 mm), PANGLAO 2004, stn M51, Mayacabac, Panglao Island, ZRC 2013.0645; B, *Pagurus kulkarnii* Sankolli, 1962, male (sl mm), PANGLAO 2004, stn R66, Sungcolan inlet, Panglao Island, ZRC 2014.0300; C, *Pagurus moluccensis* Haig & Ball, 1988, male (sl 3.2 mm), PANGLAO 2004, stn M2, west end of Alona Beach, Panglao Island, ZRC 2013.0644; D, *Pagurus pergranulatus* (Henderson, 1896), PANGLAO 2004, stn R16, Black Forest, Balicasag Island, ovigerous female (sl 6.0 mm), ZRC 2014.0301.

June 2004; 4 males (sl 3.2–11.1 mm) (ZRC 2013.6043), stn M58, Balicasag Island, 09°31.3'N, 123°41.0'E, intertidal, 4 July 2004; 2 ovigerous females (sl 10.7, 12.5 mm) (ZRC 2013.0634), stn N4, Alona reef, 09°32.9'N, 123°46.9'E, 15–20 m, 10 June 2004, bated traps; 2 males (sl 11.1, 13.2 mm) (ZRC 2013.0640), stn R3, Alona reef, 09°33.0'N, 123°46.5'E, 5–24 m, base of reef slope, May to July 2004.

Distribution. Widely distributed in the Indo-West Pacific: from Red Sea and eastern Africa to Fiji, north to southern Japan and south to Queensland, Australia; intertidal to 25 m.

Remarks. The name “*Pagurus hirtimanus*” was firstly mentioned by White (1847) in his list of crustaceans in the collection of the British Museum (Natural History). However, the name was unavailable because White (1847) did not give a description. The author of this name has been attributed to Miers (1880), who provided a description of *P. hirtimanus* for the first time, although Miers (1880) questionably referred the species to *P. japonicus* (Stimpson, 1858) (as *Eupagurus*).

Terao (1913) recorded *P. hirtimanus* from Hokkaido, northern Japan (as *Eupagurus*). Komai & Ueshima (in press) re-examined the specimens studied by Terao (1913) and confirmed that they represent *P. pectinatus* (Stimpson, 1858), a species distributed in cold waters of the western North Pacific (Komai, 2000a).

Pagurus kaiensis McLaughlin, 1997

Pagurus kaiensis McLaughlin, 1997: 526, figs. 25a–l, 42e–f [type locality: Kai Islands, Indonesia, 205–212 m]; McLaughlin et al., 2010: 33 (list).

Material examined. 1 male (sl 7.3 mm) (ZRC 2013.0650), PANGLAO 2004, stn P3, Balicasag Island, 09°31.1'N, 123°41.5'E, ca. 100 m, 31 May 2004, tangle nets from local fishermen, 8 June 2004; 1 female (sl 3.9 mm) (ZRC 2013.0652), stn T35, between Libaong and Pamilacan, 9°31.8'N 123°50.4'E, 172–182 m, 3 July 2004; 1 male (sl 3.0 mm) (ZRC 2013.1119), stn T37, Cervera shoal, West Pamilacan Island, 09°28.2'N, 123°50.7'E, 132–190 m, sand on echinoderm bed, 4 July 2004; 1 male (sl 8.0 mm) (ZRC 2013.0651), Balicasag Island, coll. local fishermen, 2 March 2004, tangle nets.

Distribution. Heretofore known only from Kai Islands, Indonesia, at depths of 210–268 m. Newly recorded from the Philippines, at shallower depths, 100–190 m.

Remarks. The present material agrees well with the original description of *P. kaiensis* by McLaughlin (1997).

Pagurus kulkarnii Sankolli, 1962 (Fig. 1B)

Restricted synonymy.

Pagurus kulkarnii Sankolli, 1962: 136, figs. 1, 2 [type locality: Bombay, India, intertidal]; Tirmizi & Siddiqui, 1982: 89, figs. 44, 45; Rahayu, 1996: 350; McLaughlin, 2002: 446; McLaughlin et al., 2007: 258, unnumbered figs.; 2010: 33 (list); Moradmand & Sari, 2007a: 30, fig. 2H; 2007b: 112, figs. 1, 2; Naderloo et al., 2012: 69 (list); Naderloo & Türkay, 2012: 28.

Not *Pagurus kulkarnii* – Morgan, 1987: 182; 1990: 27; Davie, 2002: 84. = *Pagurus hedleyi* Grant & McCulloch, 1906.

Material examined. 1 male (sl 3.6 mm) (ZRC 2014.0300), PANGLAO 2004, stn R66, Sungcolan inlet, Panglao Island, 09°38.3'N, 123°50.3'E, 1–3 m, channel between lagoon and sea, 28 June 2004.

Distribution. Iran, Pakistan, India, Thailand, Singapore, Taiwan, intertidal and herein recorded from the Philippines, at depths of 1–3 m.

Remarks. The present specimen agrees well with the previous accounts of *P. kulkarnii* (e.g., Sankolli, 1962; Tirmizi & Siddiqui, 1982; McLaughlin, 2002; McLaughlin et al., 2007) in both morphology and fresh coloration (Fig. 1B).

Pagurus moluccensis Haig & Ball, 1988 (Fig. 1C)

Pagurus moluccensis Haig & Ball, 1988: 187, figs. 14, 15 [type locality: north side of Banda Besar, Indonesia, intertidal]; Komai & Rahayu, 2004: 184, figs. 1A, 2–5; McLaughlin et al., 2010: 33 (list).

Material examined. 1 male (sl 3.2 mm) (ZRC 2013.0644), PANGLAO 2004, stn M2, west end of Alona Beach, Panglao Island, 09°32.8'N, 123°45.9'E, 0–2 m, reef flat with sea grass bed, 30 May 2004.

Distribution. Previously known from Indonesia, intertidal. Now recorded from the Philippines.

Remarks. The present specimen agrees well with the redescription of *P. moluccensis* given by Komai & Rahayu (2004).

Pagurus pergranulatus (Henderson, 1896) (Figs. 1D, 2–5)

Eupagurus pergranulatus Henderson, 1896: 520 [type locality: off east coast of Ceylon (Sri Lanka), 28 fathoms]; Alcock & Anderson, 1897: pl. 31, fig. 1; Alcock, 1905b: 125, pl. 11, fig. 1. *Pagurus pergranulatus* – Gordan, 1956: 333 (bibliography); Haig & Ball, 1988: 190; Rahayu, 1996: 350; McLaughlin, 1997: 526 (key); Davie, 2002: 84; McLaughlin et al., 2010: 34 (list).

Material examined. 1 ovigerous female (sl 6.0 mm) (ZRC 2014.0301), PANGLAO 2004, stn R16, Black Forest, Balicasag Island, 09°31.1'N, 123°41.3'E, 6–22 m, edge of reef platform and slope, 4 June 2004.

Description. Eleven pairs of biserial gills.

Shield (Fig. 2A) approximately as long as broad; anterior margins between rostrum and lateral projections gently concave; anterolateral margins sloping; posterior margin roundly truncate; dorsal surface slightly convex transversely, with longitudinal row of tufts of moderately long setae on either side of midline; paragastric grooves faint. Rostrum acutely triangular, extending as far as level of lateral projections. Lateral projections roundly triangular, with small submarginal spine. Posterior carapace (not figured), measured along midline, distinctly shorter than shield; carapace lateral lobe moderately narrow, sclerotised but not strongly calcified;

cardiac sulci parallel, reaching to midlength of posterior carapace; sulci cardiobrachiales also parallel, slightly falling short of midlength of posterior carapace; median area consisting of posteromedian and posterolateral plates not calcified but weakly sclerotised, with several paired tufts of stiff setae; branchiostegite membranous, with scattered tufts of short to moderately long, stiff setae.

Ocular peduncles (including corneas) (Fig. 2A) moderately stout, about 0.8 times as long as shield; slightly inflated basally; cornea slightly dilated, its width about 0.4 of peduncular length; dorsal surface with longitudinal row of tufts of moderately short setae mesially. Ocular acicles narrowly subtriangular with rounded tips, separated basally by width of more than one acicle, with minute submarginal spine distally (left) or spine missing (right); dorsal surface shallowly concave. Interocular lobe partially overhung by rostrum, medially concave.

Antennular peduncles (Fig. 2A), when fully extended, slightly falling short of distal corneal margins. Ultimate segment about 1.3 times as long as penultimate segment, slightly widened distally in lateral view, with 1 short seta at dorsolateral distal angle. Basal segment with distolateral margin produced in rounded lobe; statocyst lobe weakly inflated, with prominent spine distally; ventromesial distal angle not produced, bearing tuft of long stiff setae.

Antennal peduncles (Fig. 2A) overreaching corneal bases but not reaching distal corneal margins, with supernumerary segmentation. Fifth segment with few setae laterally. Fourth segment with 1 prominent subdistal tuft of stiff setae mesially. Third segment unarmed on ventromesial distal angle, with several tufts of long stiff setae mesially. Second segment with dorsolateral distal angle slightly overreaching midlength of fourth segment, terminating in bifid spine; dorsomesial distal angle with small spine; mesial and lateral faces with short to long stiff setae. First segment with subterminal spinule on lateral face; ventrodistal margin with cluster of spinules just lateral to excretory pore. Antennal acicle overreaching base of cornea but not reaching distal corneal margin, gently arcuate, terminating in small spine obscured by long stiff setae; dorsomesial margin with several tufts of long stiff setae. Antennal flagellum about 3 times as long as shield; each article with 1 or 2 minute setae on distal margin.

Mouthparts not dissected. Third maxilliped (Fig. 2B) moderately slender; dactylus shorter than propodus; carpus unarmed on dorsodistal margin; merus unarmed on dorsodistal and ventral margins; ischium with crista dentata consisting of narrowly spaced, moderately small, blunt to subacute corneous teeth, and with 3 moderately strong accessory teeth (Fig. 2C); basis-ischium fusion incomplete; basis with 2 denticles on mesial margin; exopod reaching distal margin of merus.

Chelipeds grossly unequal. Right cheliped (Figs. 3A–D) with chela 1.5 times longer than greatest width at base of dactylus, generally suboval in outline in dorsal view. Dactylus subequal in length to palm and slightly overlapped by fixed

finger, slightly curved ventrally; dorsal surface with sparse, short feathered setae and prominent median row of broad-based, closely set spines or spine-like tubercles; dorsomesial margin with closely set, moderately large tubercles decreasing in size distally; space between dorsal midline and dorsomesial margin with small, low tubercles each bearing central or subdistal, slender, proximally directed and curved capsule; ventral surface with row of low, moderately large protuberances adjacent to mesial margin and tufts of moderately short stiff setae arranged in longitudinal rows; cutting edge with row of broad calcareous teeth and adjacent row of tufts of stiff setae, terminating in large calcareous claw. Palm distinctly longer than carpus; dorsomesial margin delimited by single row of moderately large, stout spines, dorsomesial distal angle somewhat produced with few small spines; dorsolateral margin delimited by small, sharp, forwardly directed spines extending onto fixed finger and decreasing in size and sharpness distally; dorsal surface convex, with numerous, small, scattered capsulate spines and row of moderately small, acute spines on proximal half of midline; vast majority of capsulate spines bifid terminally, flanking base of each capsule, sometimes bearing tuft of short to moderately long feathered setae (Fig. 3E, F); capsules similar to those on dactylus; mesial face with scattered, very low, small protuberances and tufts of short stiff setae; ventrolateral surface with scattered, very low, minute to small protuberances and sparse very short setae; ventral surface gently convex, with some low protuberances accompanied by tufts of long setae. Cutting edge of fixed finger with row of low calcareous teeth, terminating in large calcareous claw. Carpus slightly shorter than merus; dorsomesial margin delimited by row of large sharp spines accompanied by tufts of long stiff setae; dorsal surface with scattered, small to moderately large spines and tufts of short to long stiff setae, dorsodistal margin with row of small spines; dorsolateral margin delimited by row of small spines; lateral surface with some very low, small protuberances, all accompanied by tufts of short stiff setae, ventrolateral margin with 1 small distal spine; mesial surface shallowly concave medially, with some low protuberances, all accompanied by tufts of long stiff setae; ventral surface with distal margin strongly raised, fringed with long stiff setae. Merus unarmed on dorsodistal margin; dorsal surface glabrous; lateral surface nearly glabrous except for few tufts of short setae, ventrolateral margin with row of small sharp spines and some small, low tubercles proximally; mesial surface with sparse tufts of short setae, ventromesial margin slightly elevated, with row of closely spaced small spines or tubercles; ventral surface with some low, blister-like protuberances and tufts of moderately long setae. Ischium with tufts of short setae on all surfaces; ventromesial margin with few denticles.

Left cheliped (Fig. 4A–C) slightly overreaching base of dactylus of right cheliped, moderately compressed laterally. Chela elongate subovate in dorsal view, 2.7 times longer than greatest width at base of dactylus. Dactylus distinctly longer than palm, nearly straight with ventrally curved tip; dorsal surface sloping mesially, unarmed but with sparse tufts of short feathered setae; all surfaces with tufts of moderately short to long stiff setae; cutting edge with row

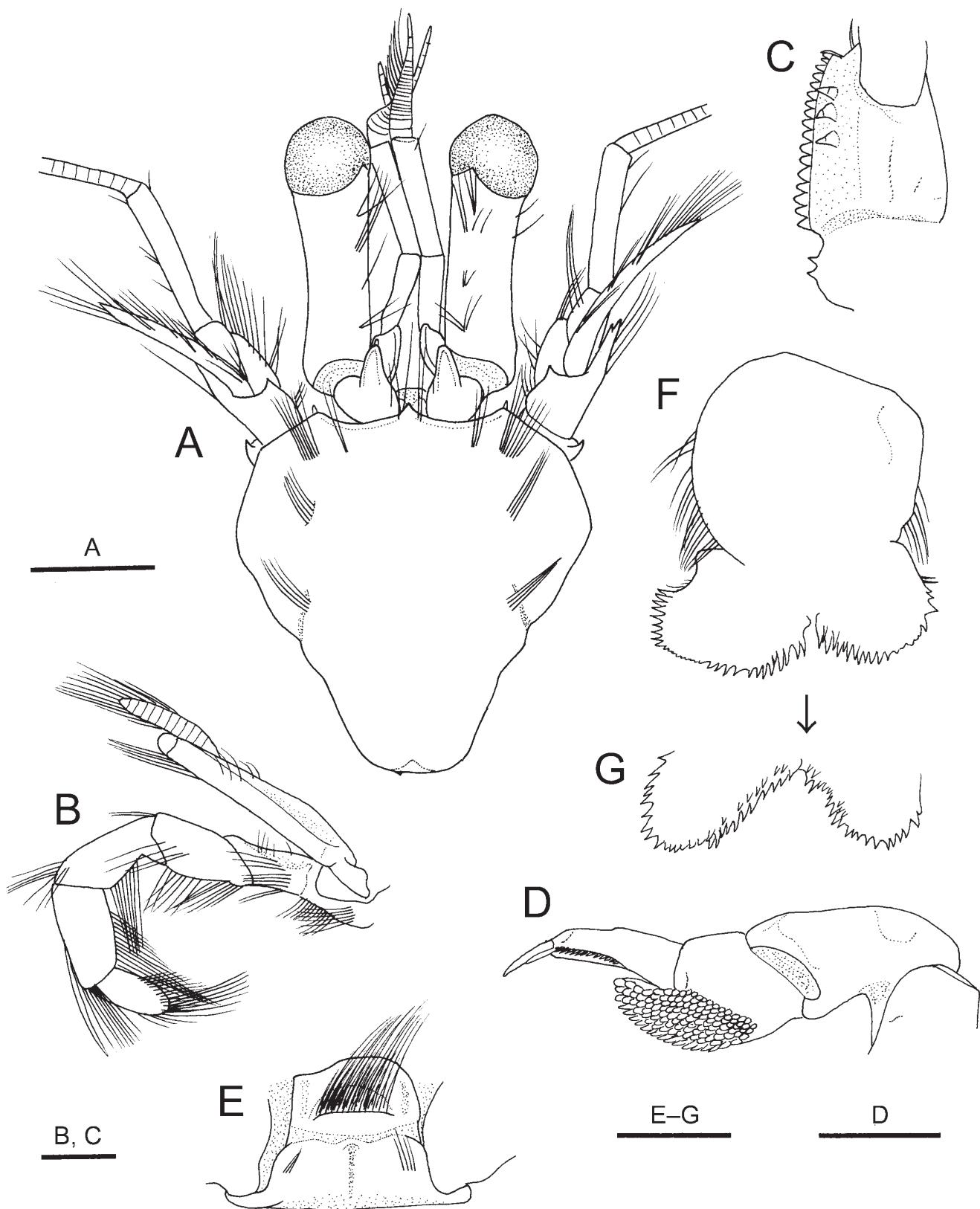


Fig. 2. *Pagurus pergranulatus* (Henderson, 1896), PANGLAO 2004, stn R16, Black Forest, Balicasag Island, ovigerous female (sl 6.0 mm), ZRC 2014.0301. A, shield and cephalic appendages, dorsal view; B, left third maxilliped, lateral view; C, same, ischium, ventral view (setae omitted); D, left fourth pereopod, lateral view (setae omitted); E, thoracic sternite 6, ventral view; F, telson, dorsal view; G, same, terminal margins, posterodorsal view. Scale bars = 2 mm for A; 1 mm for B-G.

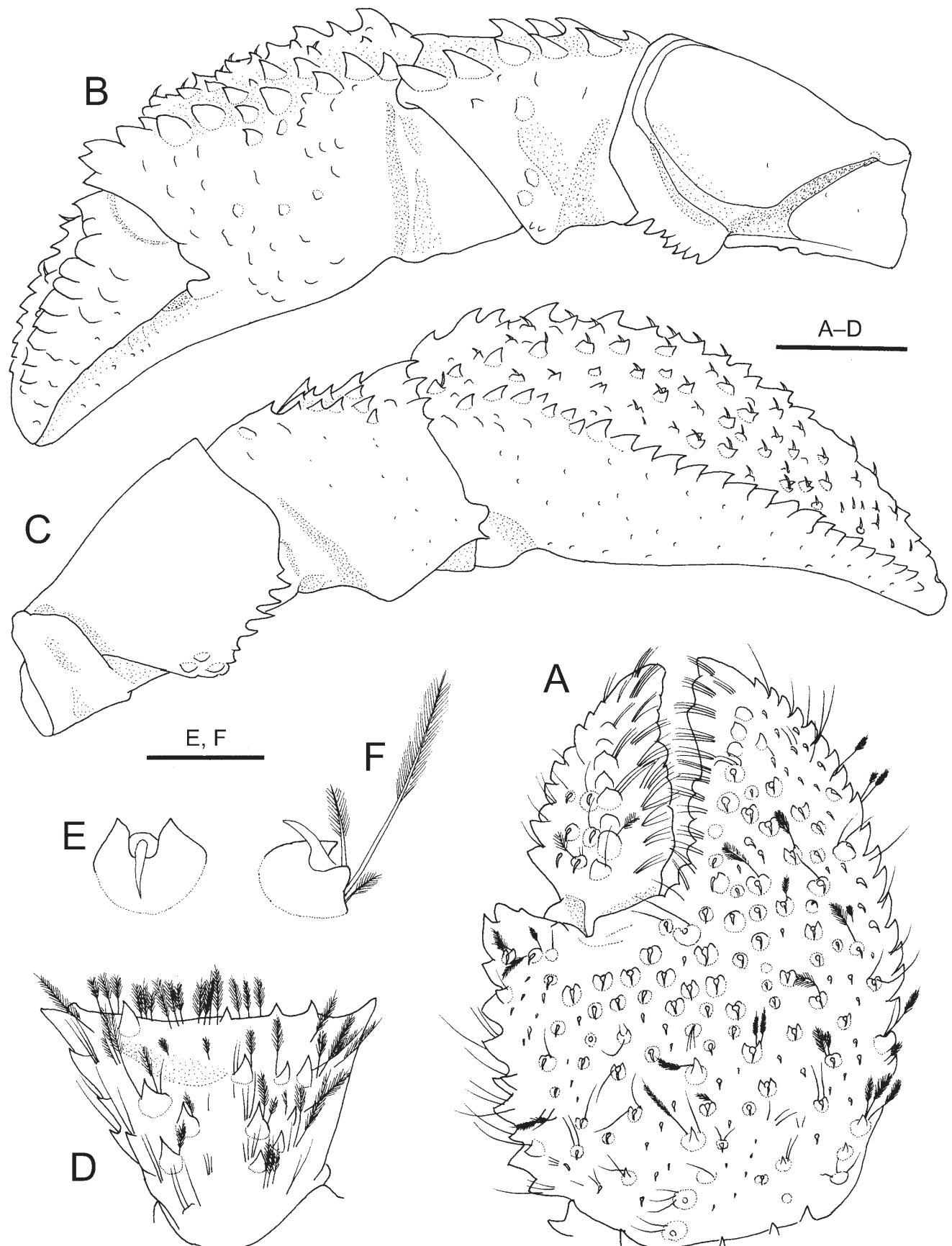


Fig. 3. *Pagurus pergranulatus* (Henderson, 1896), PANGLAO 2004, stn R16, Black Forest, Balicasag Island, ovigerous female (sl 6.0 mm), ZRC 2014.0301. A, right chela, dorsal view; B, right cheliped, mesial view (setae omitted); C, same, lateral view; D, carpus of right cheliped, dorsal view; E, close up of capsule tubercle on right palm, dorsal view (setae omitted); F, same, obliquely lateral view. Scale bars = 2 mm for A–D; 0.5 mm for E, F.

of minute, subacute calcareous denticles in proximal 0.4 and row of minute, closely set corneous teeth in distal 0.6, terminating in small corneous claw. Palm about half length of carpus, subtriangular in cross section; dorsal surface elevated in midline but not forming distinct ridge or crest, with double row consisting of capsulate tubercles or small spines extending onto base of fixed finger; lateral margin with row of small acute spines; dorsolateral surface with capsulate tubercles arranged in irregular longitudinal rows and extending onto proximal half of fixed finger; dorsomesial surface sloping to mesial surface, with few low protuberances accompanied by tufts of long stiff setae; ventral surface with tufts of long setae. Fixed finger with cutting edge bearing row of minute calcareous denticles in proximal 0.7, and bearing corneous plate, fused with terminal claw, in distal 0.3. Carpus subequal in length to merus; dorsolateral margin with row of small sharp spines and low protuberances and with tufts of short feathered setae, no spine located at distal angle; dorsomesial margin with row of moderately small to large spines, 3 clustered spines located at distal angle; lateral surface with some very low protuberances accompanied by tufts of setae, ventrodistal angle produced, bearing 4 small spines; mesial surface also with very low protuberances

accompanied by tufts of long stiff setae, ventrodistal angle with 1 small spine; ventral surface with prominent row of tufts of long feathered setae laterally and scattered tufts of long stiff setae on remaining part. Merus unarmed on dorsodistal margin; dorsal surface with sparse short stiff setae; lateral surface nearly glabrous except for few proximoventral tufts of setae, ventrolateral margin with row of slender, sharp spines and long stiff setae; mesial surface also nearly glabrous except for row of tufts of stiff setae adjacent to dorsal margin and few similar tufts near ventral margin, ventromesial margin with row of long setae and 3 proximal spines; ventral surface with 1 small spine medially and 1 prominent protuberance laterally. Ischium with 4 minute to tiny denticles on ventromesial margin; surfaces unarmed but with tufts of short to moderately long stiff setae.

Ambulatory legs (Fig. 5A, D) moderately long and stout, right second pereopod overreaching tip of extended right cheliped by half length of dactylus. Dactyli 1.0–1.3 times as long as propodi, 6.3–6.5 times longer than broad, in dorsal view nearly straight, in lateral view slightly curving ventrally; dorsal margins each with row of tufts of short to moderately long setae; lateral faces each without median

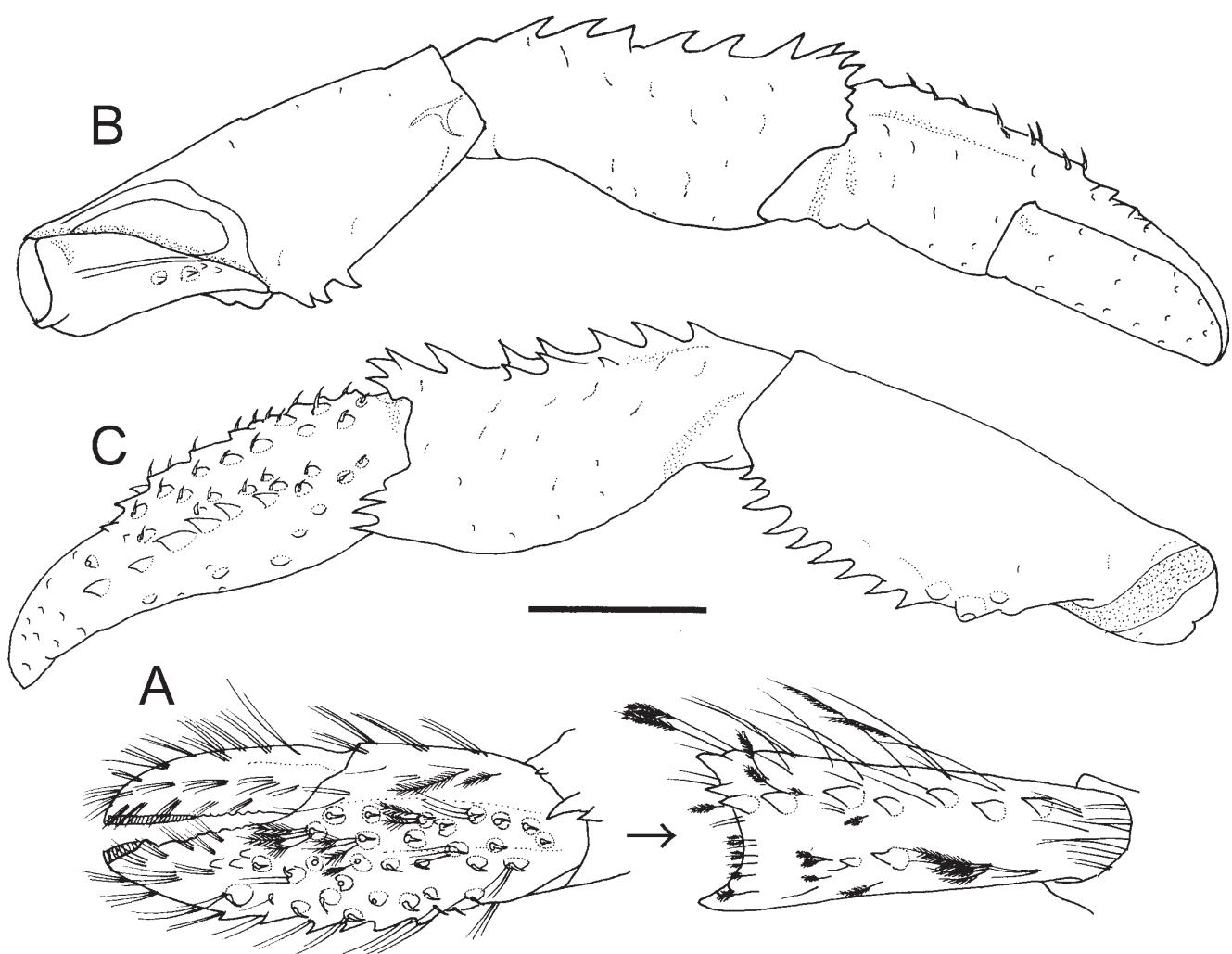


Fig. 4. *Pagurus pergranulatus* (Henderson, 1896), PANGLAO 2004, stn R16, Black Forest, Balicasag Island, ovigerous female (sl 6.0 mm), ZRC 2014.0301. A, chela and carpus of left cheliped, dorsal view; B, left cheliped, mesial view (setae omitted); C, same, lateral view. Scale bar = 2 mm.

sulcus; mesial faces also devoid of median sulcus, armed with 1 row (second; Fig. 5B) or 2 rows (third; Fig. 5E) of corneous spinules adjacent to dorsal margin; ventral margins each with row of 7 small corneous spines increasing in size distally. Propodi not narrowing distally; dorsal surfaces unarmed but with row of long stiff setae; lateral and mesial surfaces with few tufts of long stiff setae; ventral surfaces with few tufts of long stiff setae at least distally and with 1 or 2 corneous spinules on distal half, ventrodistal margins with 4 (second) or 2 (third) spinules mesially. Carpi each with small dorsodistal spine; dorsal margin with 1 additional spine at midlength (second; Fig. 5A, C) or unarmed (third; Fig. 5D) and with row of tufts of long stiff setae; lateral

surface convex, with row of tufts of long stiff setae along midline. Meri each with row of tufts of long stiff setae on dorsal surface; lateral surface almost smooth, with few tufts of long stiff setae distally; ventral surface unarmed but with row of tufts of short to long stiff setae, ventrodistal lateral margin unarmed. Ischia unarmed but with tufts of setae on dorsal and ventral margins.

Fourth pereopods (Fig. 2D) semichelate, similar from right to left, but left slightly shorter than right. Dactylus slightly curved ventrally, terminating in elongate corneous claw (about half-length of corps of dactylus); distal 0.6 of opposable surface with lateral row of long corneous teeth and dense mat

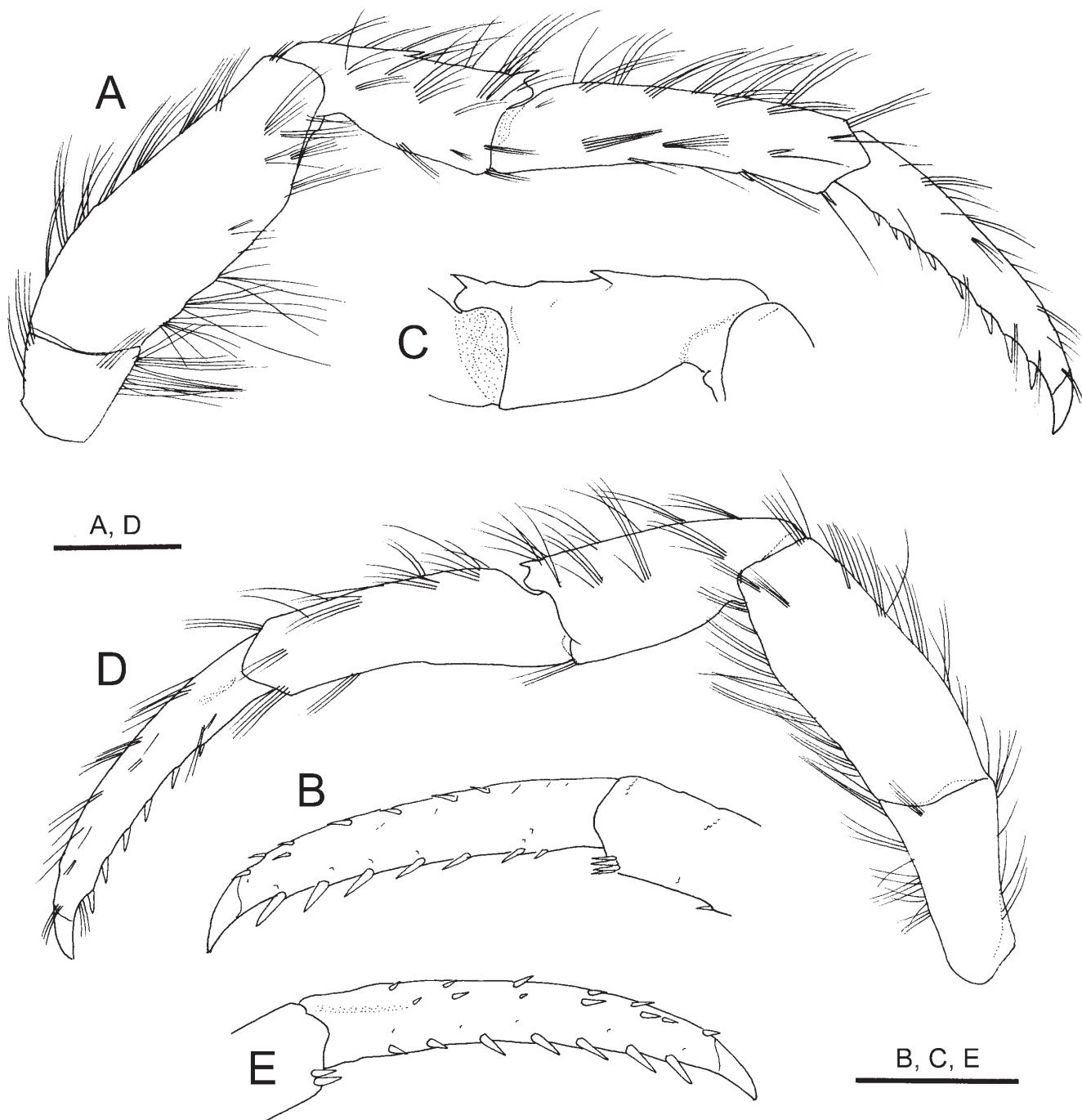


Fig. 5. *Pagurus pergranulatus* (Henderson, 1896), PANGLAO 2004, stn R16, Black Forest, Balicasag Island, ovigerous female (sl 6.0 mm), ZRC 2014.0301. A, right second pereopod, lateral view; B, same, dactylus, mesial view (setae omitted); C, same, carpus, mesial view (setae omitted); D, left third pereopod, lateral view; E, same, dactylus, mesial view (setae omitted). Scale bars = 2 mm.

of setae increasing in length distally, proximal 0.4 glabrous; preungual process rod-like, reaching midlength of terminal claw. Propodal rasp consisting of about 8 rows of corneous scales. All segments with dorsal and/or ventral tufts of long stiff setae.

Thoracic sternite 3 with anterior margin nearly straight, with microscopic denticle on either side of midpoint; ventral surface with prominent tuft of setae medially. Anterior lobe of thoracic sternite 6 (Fig. 2E) subsemicircular, bisected by blunt transverse ridge, sloping anterior surface masked by numerous long setae. Thoracic sternite 8 divided in 2 lobes by shallow median groove, each anterolateral angle slightly produced, with prominent tuft of moderately long setae.

Pleon dextrally twisted (Fig. 1D). Female second to fifth pleopods greatly unequally biramous with much elongate exopods; length fourth>fifth>third>second.

Telson (Fig. 2F) with distinct lateral indentations; posterior lobes strongly produced, rounded, unequal, median cleft very deep; each terminal margin with partially double row of numerous slender spines extending onto lateral margin.

Coloration in life. Fig. 1D. Shield mottled pale purple and white, with complex pattern of thin lines of dark purple. Ocular peduncles basically whitish; narrow tan ring at base of cornea and broad orange band medially; cornea mottled silver. Antennular peduncles orange, ultimate segment with white distal and proximal rings, penultimate segment with white distal ring. Antennal peduncle generally pale purple; second segment with 3 dark purple longitudinal stripes on dorsal surface; flagellum with alternating bands of purple (3 or 4 articles length) and white (1 or 2 articles length). Right cheliped mottled purple and white in general; mesial surfaces of carpus and merus with irregular patterns of purple on white background. Left cheliped with thin purple lines on white background on chela, carpus and merus. Ambulatory legs with thin purple lines on propodi, carpi, meri and ischia; dactyli each with 1 purple median line and 2 broad purple bands (1 subdistal and 1 proximal). Narrow purple lines on chelipeds and ambulatory legs usually not reaching ends of segments, somewhat irregular in form, occasionally broadening and becoming thinner again on each segment.

Distribution. Sri Lanka, Andaman Islands, Peninsular Malaysia, Indonesia (Seram), Australia (Queensland), at depths of 15–100 m. Newly recorded from the Philippines, at depths of 6–22 m.

Remarks. The presence of capsules on the chelae is known in eight species in *Pagurus*, viz., *P. capsularis* McLaughlin, 1997, *P. hirtimanus*, *P. japonicus* (Stimpson, 1858), *P. pergranulatus*, *P. rubrior* Komai, 2003b, *P. similis* (Ortmann, 1892), *P. sinuatus* (Stimpson, 1858), and *P. tabataorum* Osawa, 2012 (McLaughlin, 1997; Komai, 2003b; Osawa, 2012). All the eight species exclusively occur in the Indo-West Pacific region. Osawa (2012) suggested that these species are phylogenetically related based on this possibly synapomorphic character, although no informal species

group has been proposed for them. These species also share a rather uncommon feature in the genus, the possession of a left unpaired second pleopod in males (Komai, 2003b; personal observation).

Although no detailed morphological description in modern standard has been published for *P. pergranulatus*, the present specimen generally agrees with the previous descriptions by Henderson (1896) and Alcock (1905b) except for the ventromesial margin of the merus of the right cheliped, which develops into a distinct, somewhat wing-like, ventrally produced lobe and bears a dense tuft of setae. However, no such development of a distinct ventromesial lobe of the merus of the right cheliped is seen in our female specimen. Komai (2003b) showed that the structure of the ventral part of the merus of the right cheliped could be sexually dimorphic in *P. japonicus*, *P. rubrior* and *P. similis*, and it is reasonable to consider that the discrepancy could be attributable to sexual difference also in *P. pergranulatus*. The coloration in life of our specimen also agrees well with the description given by Haig & Ball (1988).

Pagurus pergranulatus is immediately distinguished from the other seven related species shown above by the characteristic armature of the right palm: the dorsomesial distal angle of the right palm is somewhat produced; vast majority of the capsulate spines on the dorsal surface are distally bifid. In the other seven species, the distomesial margin of the right palm is not produced; capsulate tubercles on the dorsal surface are variable in the shape, but never bifid in the six species other than *P. tabataorum*. *P. tabataorum* has transverse scutes but no spines on chelae. The coloration in life of *P. pergranulatus* is also quite characteristic, particularly in having thin lines or stripes of dark purple on the shield, chelipeds and ambulatory legs. No such lines or stripes are seen in the other seven species (cf. Miyake, 1982 for *P. japonicus*; McLaughlin, 1997 for *P. capsularis*; Komai, 2003b for *P. rubrior* and *P. similis*; Poore, 2004 for *P. sinuatus*; McLaughlin et al., 2010 for *P. hirtimanus*; Osawa, 2012 for *P. tabataorum*).

Pagurus spinulentus (Henderson, 1888) (Figs. 6–9)

Eupagurus spinulentus Henderson, 1888: 68, pl. VII, fig. 3 [type locality: off Tablas Island, Philippines, 100–115 fathoms]; Alcock, 1905b: 176 (list); Forest, 1955: 106.

Eupagurus spinolentus (sic) – Estampador, 1937: 505 (list); 1959: 54 (list).

Pagurus spinulentus – McLaughlin & Forest, 1999: 308–309, fig. 1D, J, L; Gordan, 1956: 335 (bibliography); McLaughlin et al., 2010: 33 (list).

Not *Eupagurus spinulentus* – Stebbing, 1920: 260; Barnard, 1950: 460. = *Pagurus prideaux* Leach, 1815.

Material examined. 1 male (sl 6.3 mm) (ZRC 2014.0302), PANGLAO 2004, stn B9, Napaling, Panglao Island, 09°33.1'N, 123°44.0'E, caves in reef wall, 8–10 m, 8 June 2004; 1 male (sl 9.9 mm) (ZRC 2014.0303), Balicasag Island, coll. Nato, May 2004; 1 male (sl 10.9 mm), 1 ovigerous female (sl 9.4 mm) (NMCR 39116), stn P3, Balicasag Island, 09°31.1'N, 123°41.5'E, ca. 100 m, coll. local fishermen, 31 May 2004, tangle nets; 1 female (sl 5.5 mm) (ZRC 2014.0304), stn P5, Pamilacan Island, 09°30.0'N, 123°54.6'E,

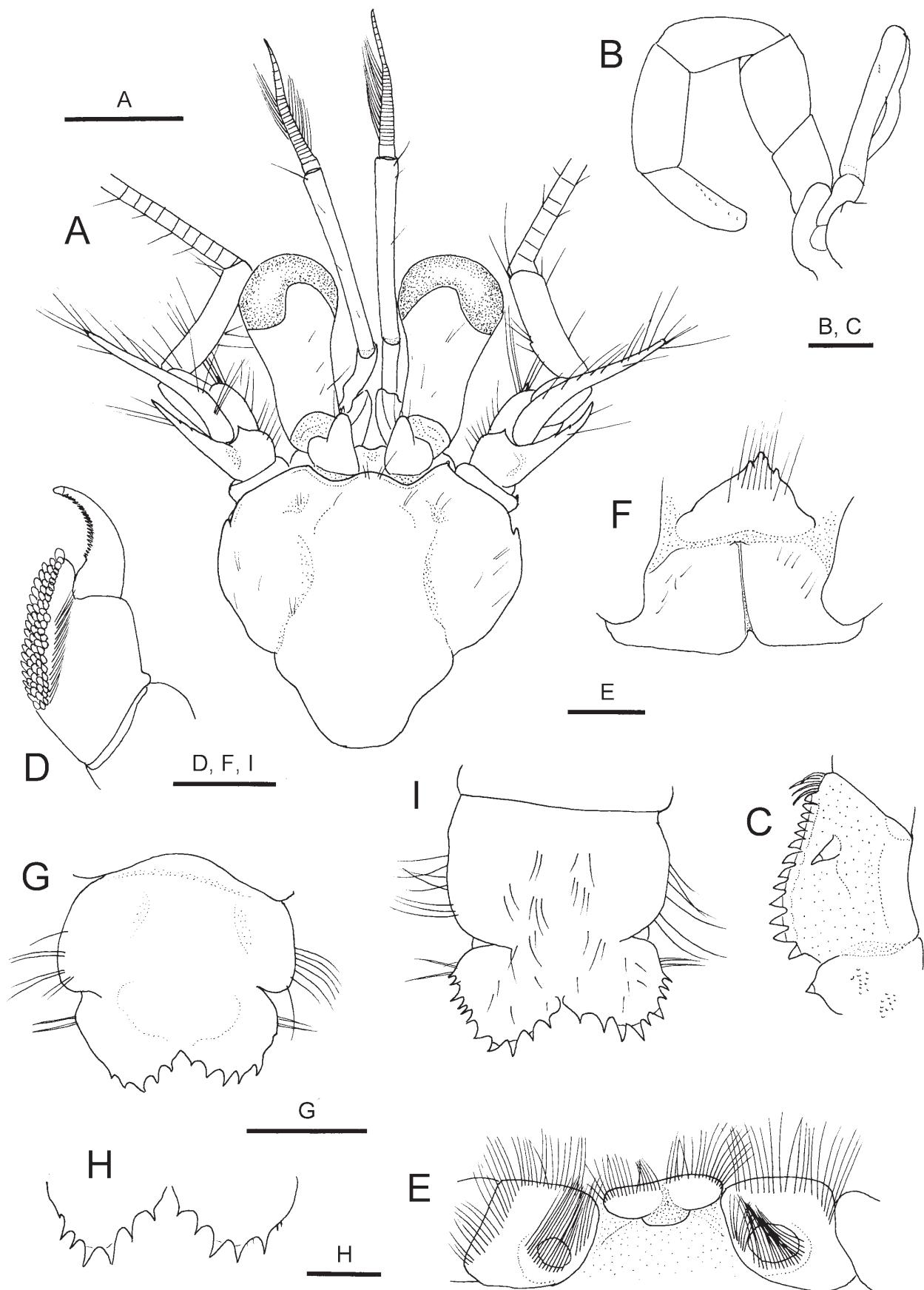


Fig. 6. *Pagurus spinulentus* (Henderson, 1888). A–H, Balicasag Island, male (sl 9.9 mm), ZRC 2014.0303; I, PANGLAO 2004, PN1, male (sl 11.6 mm), ZRC 2014.0305. A, shield and cephalic appendages, dorsal view; B, left third maxilliped, lateral view (setae omitted); C, same, ischium, ventral view; D, dactylus and propodus of left fourth pereopod, lateral view (setae partially omitted); E, coxae of fifth pereopods and thoracic sternite 8, ventral view; F, thoracic sternite 6, ventral view; G, I, telson, dorsal view; H, posterior lobes of telson, perpendicular dorsal view. Scale bars = 5 mm for A; 2 mm for B, D–G, I; 1 mm for C, H.

ca. 100 m, coll. local fishermen, 3 June 2004, tangle nets; 1 male (sl 11.6 mm), 2 ovigerous females (sl 8.6, 8.8 mm) (ZRC 2014.0305), PN1, Balicasag Island, coll. local fisherman, 28–29 May 2004; 1 male (sl 10.5 mm) (CBM-ZC 12488), November; 1 female (sl 10.0 mm) (ZRC 2014.0306), Balicasag Island, coll. local fishermen, November 2003, tangle nets.

Description. Eleven pairs of biserial gills.

Shield (Fig. 6A) slightly wider than long; anterior margin between rostrum and lateral projections gently concave; anterolateral margins sloping; lateral margin with small but distinct, anteriorly directed process; posterior margin roundly truncate; dorsal surface slightly convex transversely, with few tufts of short setae on either side of midline; paragastric grooves shallow but conspicuous. Rostrum broadly rounded, not reaching level of lateral projections, with 1 pair of tufts of short setae. Lateral projections roundly triangular, each with or without small submarginal spine. Posterior carapace (not figured) approximately as long as shield; carapace lateral lobe moderately narrow, well calcified; cardiac sulci nearly parallel in anterior part and then extending posteriorly along posterolateral margin; sulci cardiobranchiales also nearly parallel, not reaching midlength of posterior carapace; posteromedian plate and posterolateral plates well calcified, with few tufts of very short setae; branchiostegite membranous, with scattered short to moderately long setae.

Ocular peduncles (including cornea) (Fig. 6A) stout, increasing in width distally, about 0.7 times as long as shield; not inflated basally; cornea dilated, its width about 0.4 of peduncular length; dorsal surface with few tufts of short setae mesially, but no tuft of setae at base of cornea. Ocular acicles roundly subtriangular or subovate, separated basally by width of one acicle, each with small submarginal spine distally; dorsal surface slightly concave. Interocular lobe clearly visible, medially concave.

Antennular peduncles (Fig. 6A), when fully extended, overreaching distal corneal margins by 0.5–0.8 length of ultimate segment. Ultimate segment about twice as long as penultimate segment, slightly widened distally in lateral view; dorsal surface with one moderately long seta near dorsolateral distal angle followed by three or four widely spaced individual setae, becoming shorter proximally. Basal segment with distolateral margin produced as short, setose process; lateral surface with 1 small spine distal to well inflated statocyst lobe; ventromesial distal angle slightly produced, subacutely pointed.

Antennal peduncles (Fig. 6A) overreaching distal corneal margins by 0.2–0.3 length of fifth segment, with supernumerary segmentation. Fifth and fourth segments with some short to moderately long setae on lateral and mesial faces. Third segment with small spine at ventromesial distal angle obscured by prominent tuft of long setae. Second segment with dorsolateral distal angle strongly produced, almost reaching distal margin of fourth segment, terminating in bifid, acute spine, mesial margin of this projection with few minute spinules; dorsomesial distal angle with small spine; mesial margin with short setae. First segment with minute spinule

on lateral face distally, occasionally hardly visible in dorsal view; ventrodistal margin with one prominent tooth lateral to excretory pore. Antennal acicle slightly overreaching distal corneal margin or midlength of fifth peduncular segment, gently sinuous, terminating in small spine partially obscured by tuft of long setae; dorsomesial margin with row of low, small protuberances bearing tufts of moderately long setae. Antennal flagellum exceeding 5 times of shield length; each article with two or three short to moderately long setae (1–5 articles length) every 8–12 articles.

Mouthparts not dissected. Third maxilliped (Fig. 6B) moderately slender; carpus unarmed on dorsodistal margin; merus unarmed on distal and ventral margins; ischium with crista dentata consisting of clearly spaced corneous teeth increasing in size proximally, and with 1 strong accessory tooth (Fig. 6C); basis-ischium fusion incomplete; basis with 1 spinule on mesial margin; exopod overreaching distal margin of carpus.

Chelipeds distinctly unequal and dissimilar. Right cheliped (Figs. 7A, B, 8A–C) moderately stout, not particularly elongate even in males. Chela subtriangular or elongate subovate in dorsal view, about 2.0 times as long as wide; no hiatus between fingers; spines on dorsal surface acuminate, subconical, directed slightly distally, vast majority non-corneous-tipped. Dactylus subequal in length to or slightly longer than palm, nearly straight, overlapped by fixed finger distally; mesial half of dorsal surface unarmed but with longitudinal row of tufts of stiff setae, lateral half with scattered small spines and tufts of short pinnate setae; dorsomesial margin slightly delimited by single row of small spines; mesial surface with numerous small spines becoming two longitudinal rows distally and partially obscured by numerous tufts of long pinnate setae; ventral surface unarmed but with some longitudinal rows of short to moderately long pinnate setae; cutting edge with row of rounded or subtriangular calcareous teeth decreasing in size distally in proximal 0.9, and with minute corneous teeth in distal 0.1, terminating in small corneous claw. Palm about 0.8 times as long as carpus; dorsal surface gently convex, armed with numerous tiny to small spines almost scattered, and with shallow, unarmed longitudinal sulcus adjacent to dorsomesial margin; short tufts of pinnate setae (about equal in length to spines) arising anterior to bases of spines; dorsomesial margin delimited by single or double row of small spines, dorsolateral margin delimited by row of small spines decreasing in size distally; lateral surface with numerous small, simple or bifid spines becoming flattened and blunt ventrally, and with numerous tufts of long pinnate setae partially obscuring armature; mesial surface nearly flat, with numerous small spines or multispinose protuberances and tufts of moderately long stiff setae; ventral surface gently convex, with numerous small, low protuberances or tubercles, occasionally distally multidenticulate, each bearing tuft of short stiff setae. Fixed finger nearly straight, somewhat depressed dorsoventrally; dorsal surface and dorsolateral margin with small spines continued from palm; ventral surface unarmed, but with tufts of long stiff setae arranged in some longitudinal rows; cutting edge with large, rounded calcareous teeth and four

or five small distal denticles, terminating in small calcareous claw. Carpus moderately widened distally, subequal in length to merus; dorsal surface with numerous scattered; small to moderately large spines extending onto sloping lateral surface and dense short to moderately short pinnate setae partially obscuring spines; shallow transverse groove present adjacent to dorsodistal margin; dorsodistal margin with row

of minute to small spines; dorsomesial margin delimited by single row of moderately large spines; lateral surface with numerous small spines or spiniform tubercles partially obscured by dense pinnate setae, ventrolateral distal angle with 1 small spine; mesial surface shallowly concave in general, with scattered, numerous small spines or tubercles, partially obscured by numerous tufts of short to long pinnate

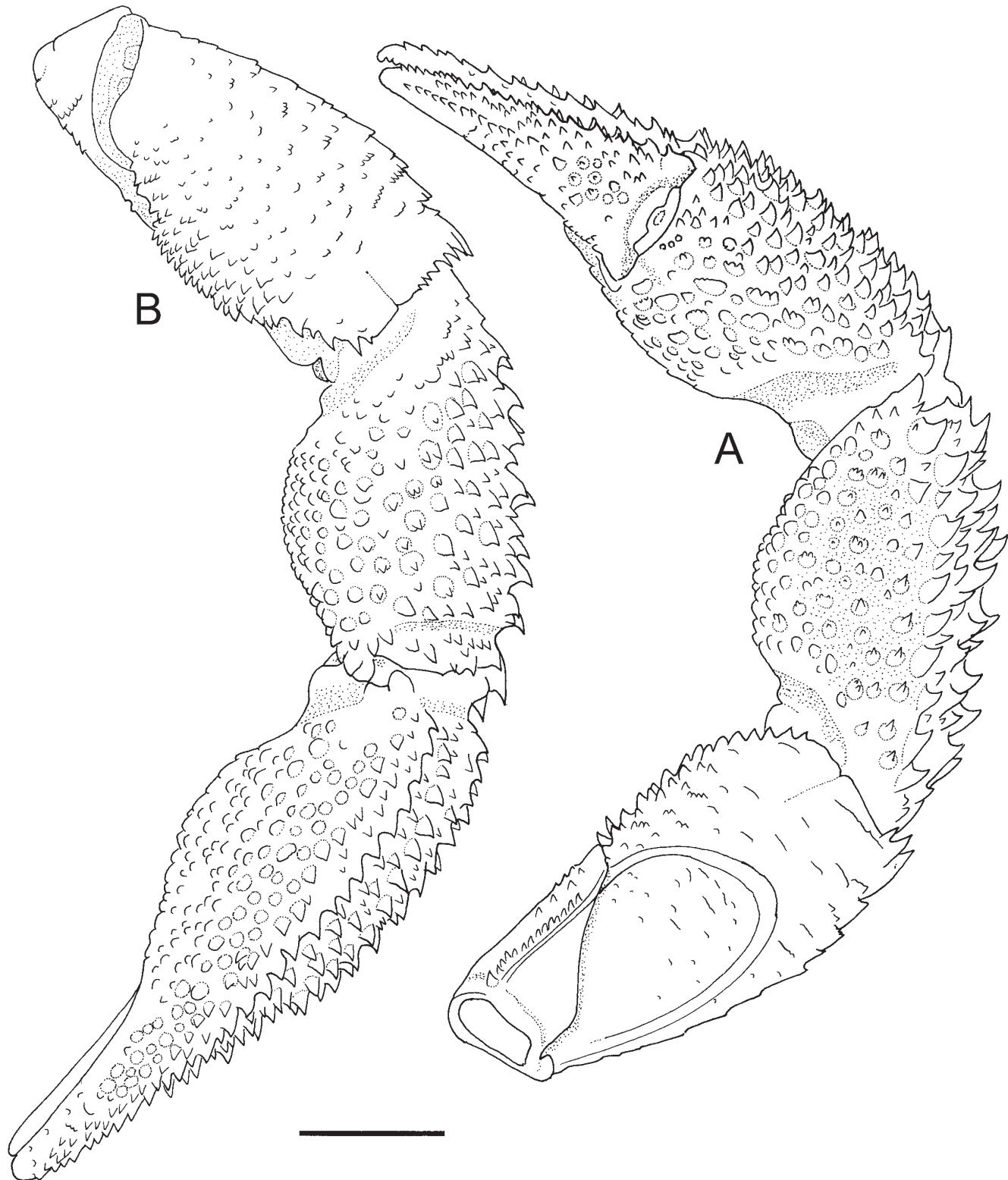


Fig. 7. *Pagurus spinulentus* (Henderson, 1888). A, B, Balicasag Island, male (sl 9.9 mm), ZRC 2014.0303. A, right cheliped, mesial view (setae omitted); B, same lateral view. Scale bar = 5 mm.

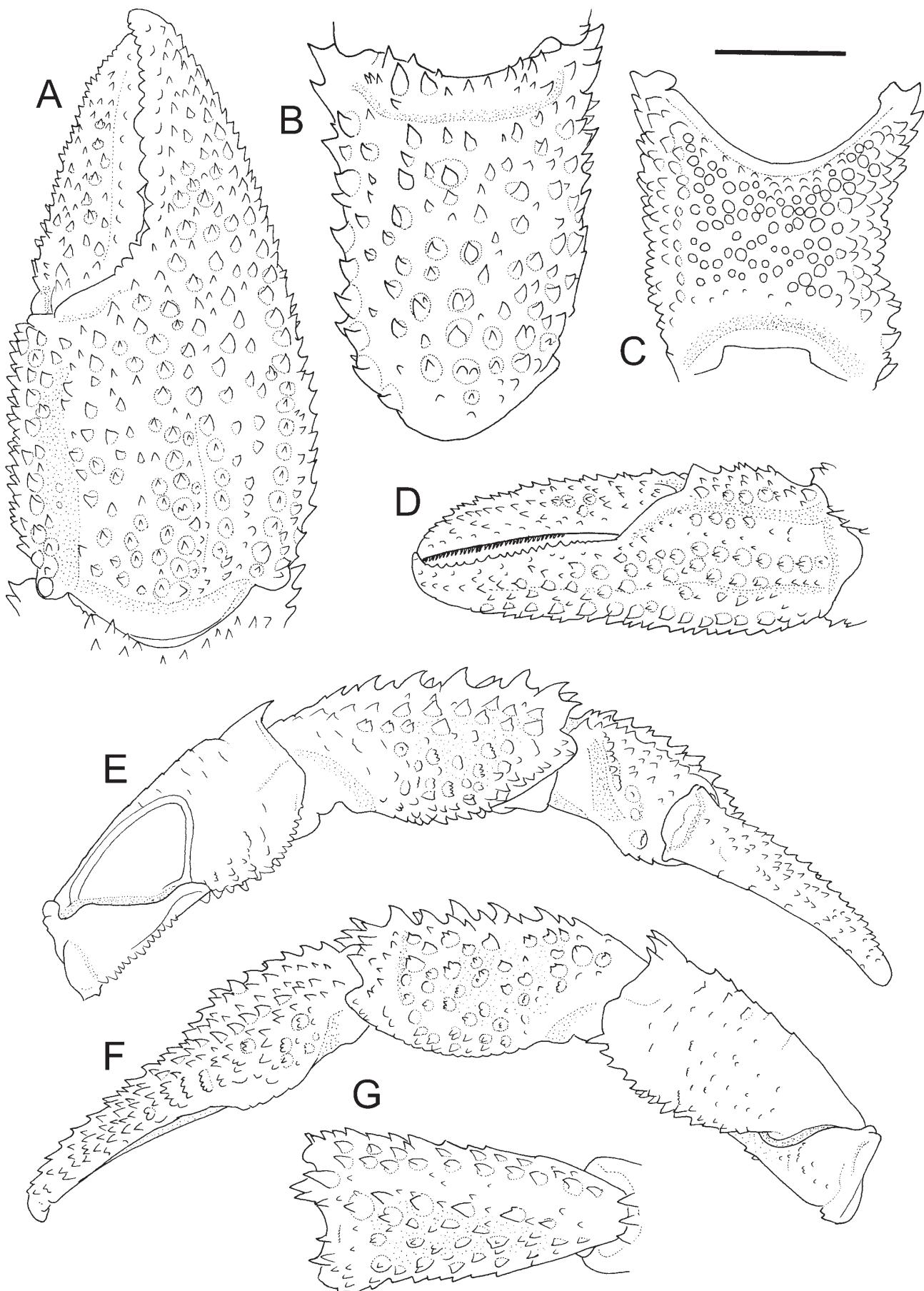


Fig. 8. *Pagurus spinulentus* (Henderson, 1888). A–G, Balicasag Island, male (sl 9.9 mm), ZRC 2014.0303. A, chela of right cheliped, dorsal view (setae omitted); B, carpus of right cheliped, dorsal view (setae omitted); C, same, ventral view; D, chela of left cheliped, dorsal view (setae omitted); E, left cheliped, mesial view; F, same, lateral view; G, carpus of left cheliped, dorsal view. Scale bar = 5 mm.

setae; ventral surface convex, with numerous small tubercles obscured by dense pinnate setae, no pinhole-like foramen present (rarely shallow depression present). Merus with dorsal surface bearing irregular rows of short transverse ridges (sometimes marginally multidenticulate) becoming weak proximally, each ridge bearing tuft of short to long simple setae; dorsodistal margin with row of prominent spines decreasing in size laterally; lateral surface with sparse, minute spiniform tubercles and short, multidenticulate ridges dorsally, ventrolateral margin with row of small spines; mesial surface with scattered, minute tubercles and short vertical ridges dorsally and ventrally, and with tufts of short to moderately long setae arising from armature, ventromesial margin with row of small spines; ventral surface armed with numerous small spines and tubercles, and these armature completely or partially concealed by dense, short to moderately long pinnate setae. Ischium with row of small spiniform tubercles on ventromesial margin; ventrolateral and ventral surfaces with several spinules or minute spiniform tubercles. Coxa unarmed.

Left cheliped (Fig. 8D–G) moderately slender. Chela about 2.4–2.6 times as long as wide (greatest width at base of dactylus); no hiatus between fingers. Dactylus about 1.8 times as long as palm; surfaces with tufts of short to long pinnate setae partially obscuring armature; dorsal surface with partially double row of small spines on midline; mesial surface with numerous smaller spines, becoming two rows distally; ventral surface unarmed; cutting edge with row of small, slender corneous teeth on at least distal 0.7, terminating in moderately large corneous claw. Palm about half length of carpus; dorsal surface gently convex transversely with slightly elevated midline, armed with numerous small spines arranged in several irregular longitudinal rows, median row particularly conspicuous, and tufts of short pinnate setae arising distal to bases of spines; dorsomesial margin delimited by single row of small spines; dorsolateral margin delimited by row of small spines extending onto fixed finger; lateral surface with numerous small spines and multidenticulate protuberances and tufts of long simple setae; mesial surface with 2 rows of small spines dorsally and several multispinose protuberances ventrally, partially obscured by tufts of simple or pinnate setae; ventral surface gently convex, with low protuberances and tufts of long setae. Fixed finger with numerous small spines on dorsal surface, extending from palm; ventral surface with tufts of long simple setae arranged in 3 longitudinal rows; cutting edge of fixed finger with row of small, subacute calcareous teeth over entire length, terminating in small corneous claw. Carpus subequal in length to merus; surfaces with numerous tufts of short to long pinnate setae partially obscuring armature (setae on dorsolateral margin particularly long); dorsal surface very narrow, sloping mesially, with some minute spines; dorsolateral margin somewhat elevated, with partially double row of moderately large spines extending onto distal margin; dorsomesial margin with row of small spines; lateral surface with numerous small, simple or bifid spines, ventrolateral distal angle with tiny spine; mesial surface with numerous small simple or multifid spines; ventral surface nearly flat transversely, with scattered small tubercles, devoid of trace of depression or foramen. Merus

with short, occasionally multidenticulate, transverse ridges and tufts of long simple setae on dorsal surface, dorsodistal margin with two or three prominent spines; lateral surface with small, multidenticulate ridges or minute tubercles, particularly conspicuous on ventral side, and with tufts of short to moderately long simple setae arising from armature, ventrolateral distal margin with row of moderately small spines; mesial surface with scattered, short vertical ridges (particularly conspicuous and multidenticulate on ventral side), and with tufts of simple setae, ventromesial distal margin with row of small spines or spiniform tubercles; ventral surface slightly convex, with numerous small spines or tubercles and tufts of moderately long simple setae. Ischium with row of tiny spines or denticles on ventromesial margin; lateral surface with vertical row of minute denticles adjacent to distal margin; ventral surface smooth, unarmed. Coxa unarmed.

Ambulatory legs (Fig. 9A, F) moderately long and slender in general, right second pereopod overreaching tip of extended right cheliped by half length of dactylus. Dactyli elongate, 1.6–1.8 times as long as propodi, 10.0–15.0 times longer than broad, in dorsal view slightly twisted, in lateral view gently curving ventrally; dorsal margins each with row of spinules or denticles in proximal 0.5–0.7 (those on left third smaller than on other legs) and with short to moderately short bristle-like stiff setae becoming shorter proximally (proximal setae interspersing spinules or denticles); lateral faces each with shallow median sulcus in proximal 0.3 and single row of short to moderately short bristle-like setae ventral to midline (these setae closely set in distal part, becoming more widely spaced and shorter toward proximal); mesial faces (Fig. 9B, G) each with widely spaced tufts of very short stiff setae dorsally and partially double row of moderately short, closely spaced bristle-like stiff setae ventrally (Fig. 9C; in third pereopods, proximal setae becoming widely spaced and shorter, showing like corneous spinules); ventral margins each with row of about 30–40 minute, slender, corneous spinules, these spinules closely spaced, partially overlap in distal part (Fig. 9C), becoming more widely spaced towards proximal end. Propodi somewhat narrowing distally; dorsal surfaces each with single or double row of small spines and sparse, short pinnate setae, dorsodistal margin with 1 spine (second) or unarmed (third); lateral surfaces with minute sharp granules dorsally and minute pits, these occasionally with tufts or single minute setae; mesial surfaces (Fig. 9D, H) almost glabrous, with several spinulose tubercles dorsally; ventral surfaces with scattered, minute spinulose tubercles or minute protuberances bearing minute setae (second) or almost smooth (third). Carpi each with row of small to moderately large spines decreasing in size proximally; lateral faces with scattered tufts of very short setae arising from very low, minute protuberances or minute pits. Dorsal surfaces of meri each with spinulose transverse ridges (second) or low, non-spinulose transverse ridges (third), and tufts of moderately long pinnate setae arising from these ornateations; lateral and mesial faces almost glabrous; ventrolateral margins each with row of minute to small spines on distal 0.6 (second) or only with small distal spine (third), ventral surfaces with scattered small spines or tubercles extending to mesial faces

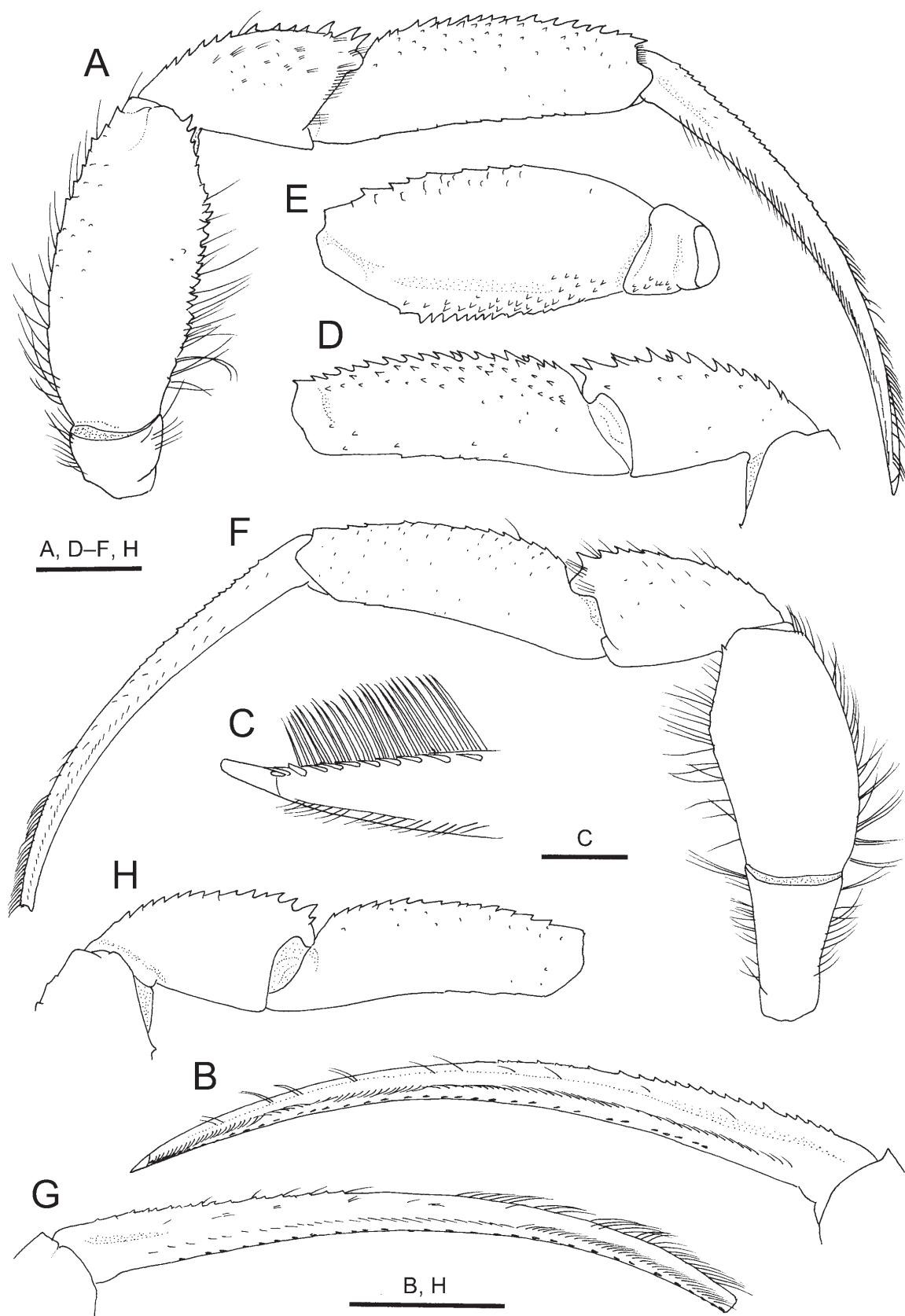


Fig. 9. *Pagurus spinulentus* (Henderson, 1888). A–H, Balicasag Island, male (sl 9.9 mm), ZRC 2014.0303. A, right second pereopod, lateral view; B, same, dactylus, mesial view (only mesial setae shown); C, same, distal part, ventral view; D, same, propodus and carpus, mesial view (setae omitted); E, same, merus, mesial view (setae omitted); F, left third pereopod, lateral view (claw of dactylus broken off); G, same, dactylus, mesial view; H, same, propodus and carpus, mesial view (setae omitted). Scale bars = 5 mm for A, B, D–H; 1 mm for C.

(in second pereopods, armature more numerous in right than in left; Fig. 9E), or some minute tubercles (third), all with tufts of moderately long pinnate setae. Ischia each with tiny tubercles ventromesially (second) or nearly smooth (third); short simple or pinnate setae on dorsal and ventral margins. Female with paired gonopores on coxae of third pereopods.

Fourth pereopods (Fig. 6D) semichelate, stiff long setae on dorsal margins of dactyli to meri and ventral margin of meri. Dactyli strongly arcuate, terminating in small corneous claw, each with row of minute, closely spaced corneous teeth on ventral margin; no preungual process. Propodal rasp consisting of three to five rows of corneous scales.

Fifth pereopods chelate. Coxae (Fig. 6E) of males each with gonopore partially masked by tuft of setae.

Thoracic sternite 3 with anterior margin nearly straight, with pair of minute denticles on either side of midpoint; ventral surface with prominent tuft of setae medially. Anterior lobe of thoracic sternite 6 (Fig. 6F) broadly triangular, distinctly wider than long, skewed to left, armed anteriorly with one to three small spines or denticles and subdistal tuft of moderately long setae. Thoracic sternite 8 (Fig. 6E) vertically compressed, weakly divided in two slightly asymmetrical lobes; anterior margin with row of moderately short setae, each anterolateral angle slightly produced.

Pleon dextrally twisted. Male with 3 (third to fifth) unpaired, very unequally biramous left pleopods (endopods greatly reduced, bud-like). Female with 4 (second to fifth) unpaired, unequally biramous left pleopods (in fifth, endopod greatly reduced, bud-like). Uropods markedly asymmetrical; protopods unarmed.

Telson (Fig. 6G–I) with distinct lateral indentations; posterior lobes rounded, slightly unequal, median cleft V-shaped, each terminal margin with row of small to strong, corneous-tipped spines sometimes extending onto lateral margin (3–10 main spines on left, 3–9 on right, and some additional spinules on both lateral margins).

Coloration. In preservative. Entirely light grayish brown.

Distribution. Known only from the Philippines, at depths of 100–207 m. The collection data from stn B9 (depths 8–10 m) for one male specimen (ZRC 2014.0302) is questionable.

Remarks. *Pagurus spinulentus* was originally described on the basis of a single ovigerous female from off Tablas Island, the Philippines, at depths of 100–115 fathoms (= 180–207 m) (Henderson, 1888; as *Eupagurus*). Since the original description, Stebbing (1920) and Barnard (1950) recorded the species from South Africa, but Forest (1955) concluded that the South African specimens actually represent *P. prideaux* Leach, 1815 after comparing with the holotype of *P. spinulentus*. McLaughlin & Forest (1999) clarified differentiating characters between *P. cavicarpus* and *P. spinulentus*, and published figures of some selected parts of the holotype of *P. spinulentus*. Komai et al. (2013)

discussed differentiating characters between their new species *P. spinossior* and *P. spinulentus*, but their comparison was only based on the published accounts on the holotype of *P. spinulentus*. Other references of *P. spinulentus* (Alcock, 1905b; Estampador, 1937, 1959; Gordan, 1956; McLaughlin et al., 2010) are faunal or bibliographic listings. Consequently, the present material represents the rediscovery of the species since the original description.

The present 10 specimens agree well with the account of *P. spinulentus* by McLaughlin & Forest (1999). McLaughlin & Forest (1999) noted that the median ventral foramen on the carpus of the right cheliped in the holotype of *P. spinulentus* was not depressed, nor is an actual opening present. In seven of the eight right chelipeds available for examination, there is no trace of such a depression; only one specimen (male, sl 6.3 mm, stn B9) has a very shallow, uncalcified depression on the ventral surface of the carpus of the right cheliped. It is reasonable to consider that this species normally lacks the ventral foramen.

As discussed by Komai et al. (2013), *Pagurus spinulentus* appears closest to *P. spinossior*. Komai et al. (2013) cited five characters to differentiate the two species, but the present study demonstrates that the presence or absence of a ventral depression on the right cheliped carpus is not valid as distinguishing character. Other characters (the setation of ventrodistal margins of cheliped meri, the dorsal armature of dactyli of second pereopods, the general setation of chelipeds and ambulatory legs, and the shape of the anterior lobe of thoracic sternite 6) are still valid. Furthermore, the armature of chelae is generally weaker in *P. spinulentus* than in *P. spinossior*.

McLaughlin & Forest (1999) cited five characters to differentiate *P. spinulentus* from *P. cavicarpus*, viz., the strength of the dorsolateral distal angle of the second segment of the antennal peduncle, the armature of the mesial surface of the dactylus and palm of the right cheliped, the armature of the dorsal surface of the carpus of the left cheliped, the setation of the ventrodistal margins of cheliped meri, and the general setation of the chelipeds and ambulatory legs. Our examination of the present newly collected specimens confirms the validity of these characters. In addition to them, the shape of the anterior lobe of sixth thoracic sternite 6 is useful to distinguish the two species: in *P. spinulentus*, the anterior lobe is strongly widened proximally with the basal width being greater than the length, whereas in *P. cavicarpus*, it is distinctly longer than wide (McLaughlin & Forest, 1999). As noted by McLaughlin & Forest (1999), the right cheliped carpus usually has a pinhole-like foramen on the ventral surface in *P. cavicarpus*, which is always absent in *P. spinulentus*.

***Pagurus truncatispinosus*, new species**
(Figs. 10–13)

Material examined. Holotype: male (sl 7.2 mm) (NMCR 39117), PANGLAO 2004, PN1, Balicasag Island, coll. local fisherman, 29 April 2004, tangle nets.

Paratypes: 1 ovigerous female (sl 3.8 mm) (ZRC 2014.0307), PANGLAO 2004, stn T2, 3 Bolod, Panglao Island, 09°32.4'N, 123°47.8'E, 152 m, coarse sand, 31 May 2004; 1 male (sl 4.1 mm) (ZRC 2014.0308), stn T27, between Panglao and Pamilacan islands, 09°33.4'N 123°51.0'E, 106–137 m, fine sand and mud with echinoderms, 25 June 2004; 3 males (sl 3.0–4.6 mm), 3 juveniles (sl 1.8–2.3 mm) (ZRC 2014.0309), stn T36, Cervera Shoal, West Pamilacan Island, 09°29.3'N, 123°51.5'E, 95–128 m, sand, echinoderm beds, 4 July 2004; 1 ovigerous female (sl 3.5 mm) (CBM-ZC 12487), stn T37, same locality, 09°28.2'N, 123°50.7'E, 134–190 m, 4 July 2004; 2 males (sl 3.5, 5.2 mm) (NMCR 39118), stn T39, same locality, 09°30.1'N, 123°50.4'E, 100–138 m, muddy sand, 6 July 2004; 1 male (sl 2.8 mm) (ZRC 2014.0310), stn T41, same locality, 09°29.7'N, 123°50.2'E, 110–112 m, 6 July 2004; 1 male (sl 7.0 mm) (ZRC 2014.0311), Balicasag Island, May 2004, coll. Nato; 1 male (sl 4.5 mm) (ZRC 2014.0312), Maribohoc Bay, Panglao Island, 100–300 m, coll. local fishermen, November 2003 to April 2004, tangle nets.

Description. Eleven pairs of biserial gills.

Shield (Fig. 10A) slightly wider than long or as long as wide; anterior margin between rostrum and lateral projections gently concave; anterolateral margins sloping, each with shallow excavation posteriorly; posterior margin roundly truncate; dorsal surface very slightly convex transversely, with few tufts of short setae on either side of midline, median part uncalcified; paragastric grooves faint. Rostrum broadly rounded or broadly triangular, slightly falling short of or reaching level of lateral projections. Lateral projections roundly triangular, each with minute submarginal spine. Posterior carapace (not figured) approximately as long as shield; carapace lateral lobe moderately narrow, well calcified; cardiac sulci slightly diverging posteriorly, reaching nearly to posterodorsal margin; sulci cardiobranchiales nearly parallel, not reaching midlength of posterior carapace; posteromedian plate and posterolateral plates moderately well calcified, almost glabrous; branchiostegite membranous, with sparse short to moderately long, plumose setae.

Ocular peduncles (including cornea) (Fig. 10A) stout, slightly constricted at proximal 0.3 and increasing in width distally, 0.7–0.8 times as long as shield; not particularly inflated basally; cornea dilated, its width about 0.6 of peduncular length; dorsal surface with two to four tufts of short setae on midline and one additional tuft mesially. Ocular acicles roundly subtriangular, separated basally by width of one acicle, each with minute submarginal spine distally; dorsal surface shallowly concave. Interocular lobe clearly visible, medially concave.

Antennular peduncles (Fig. 10A), when fully extended, overreaching distal corneal margins by 0.7–0.8 length of ultimate segment. Ultimate segment about 2.0 times as long as penultimate segment, slightly widened distally in lateral view, with widely spaced, moderately long setae on dorsal surface (tuft of two or three setae at dorsolateral distal angle). Basal segment with distolateral margin not distinctly produced; statocyst lobe weakly inflated, lateral margin fringed with

short stiff setae and with minute spine distally; ventromesial distal angle not produced, bluntly pointed.

Antennal peduncles (Fig. 10A) overreaching distal corneal margins by 0.2–0.3 length of fifth segment, with supernumerary segmentation. Fifth and fourth segments with some tufts of long setae mesially and laterally. Third segment with small spine at ventromesial distal angle partially obscured by tuft of long setae. Second segment with dorsolateral distal angle moderately produced, reaching midlength of fourth segment, terminating in simple or bifid, acute spine partially obscured by tuft of moderately long setae; dorsomesial distal angle with minute spine; mesial face with sparse short setae. First segment with spinule distally on lateral face; ventrodistal margin with one prominent process lateral to excretory pore. Antennal acicle slightly overreaching distal corneal margin, slightly sinuous, terminating in small spine obscured by distal long setae; dorsomesial margin with several tufts of long setae. Antennal flagellum exceeding five times as long as shield; each article with some very short setae on distal margin.

Mouthparts not dissected. Third maxilliped (Fig. 10B) moderately slender; dactylus subequal in length to propodus; carpus unarmed on dorsodistal margin; merus unarmed on dorsodistal and ventral margins; ischium with crista dentata consisting of clearly spaced, relatively large, blunt corneous teeth (middle teeth largest), and with one strong accessory tooth (Fig. 10C); basis-ischium fusion incomplete; basis with one or two denticles on mesial margin (not illustrated); exopod nearly reaching midlength of carpus.

Chelipeds distinctly unequal and dissimilar (Figs. 11, 12). Right cheliped (Fig. 11A–E) moderately stout, not particularly elongate. Chela elongate subovate in dorsal view, 2.5–2.8 times as long as wide; spines on dorsal surface large, erect, subcylindrical, each with slightly forwardly curved, roundly truncate apex; no hiatus between fingers. Dactylus subequal in length to palm, nearly straight, overlapped by fixed finger distally; dorsal surface with three or four prominent spines in proximal half, unarmed in distal half; dorsomesial margin with row of prominent spines decreasing in size distally and becoming double row proximally; mesial surface with irregular row of small tubercles extending nearly to tip; ventral surface unarmed; all surfaces with scattered tufts of short to long stiff setae, setae on dorsomesial margin particularly long; cutting edge with row of low, rounded calcareous teeth of various sizes, terminating in tiny corneous claw. Palm about 0.8 times as long as carpus; dorsal surface gently convex, armed with prominent spines arranged in 5–7 irregular longitudinal rows and sparse tufts of short setae; distalmost spine of median row, located at proximal to base of dactylus, particularly prominent, bearing scattered short setae, but other spines mostly glabrous or with few short setae at base; proximal transverse groove very deep; dorsomesial margin delimited by row of prominent spines; dorsolateral margin delimited by single or double row of small acute spines on palm and by prominent, subtruncate spines on fixed finger, and with tufts of long setae directed laterally; lateral surface with numerous scattered, small blunt tubercles

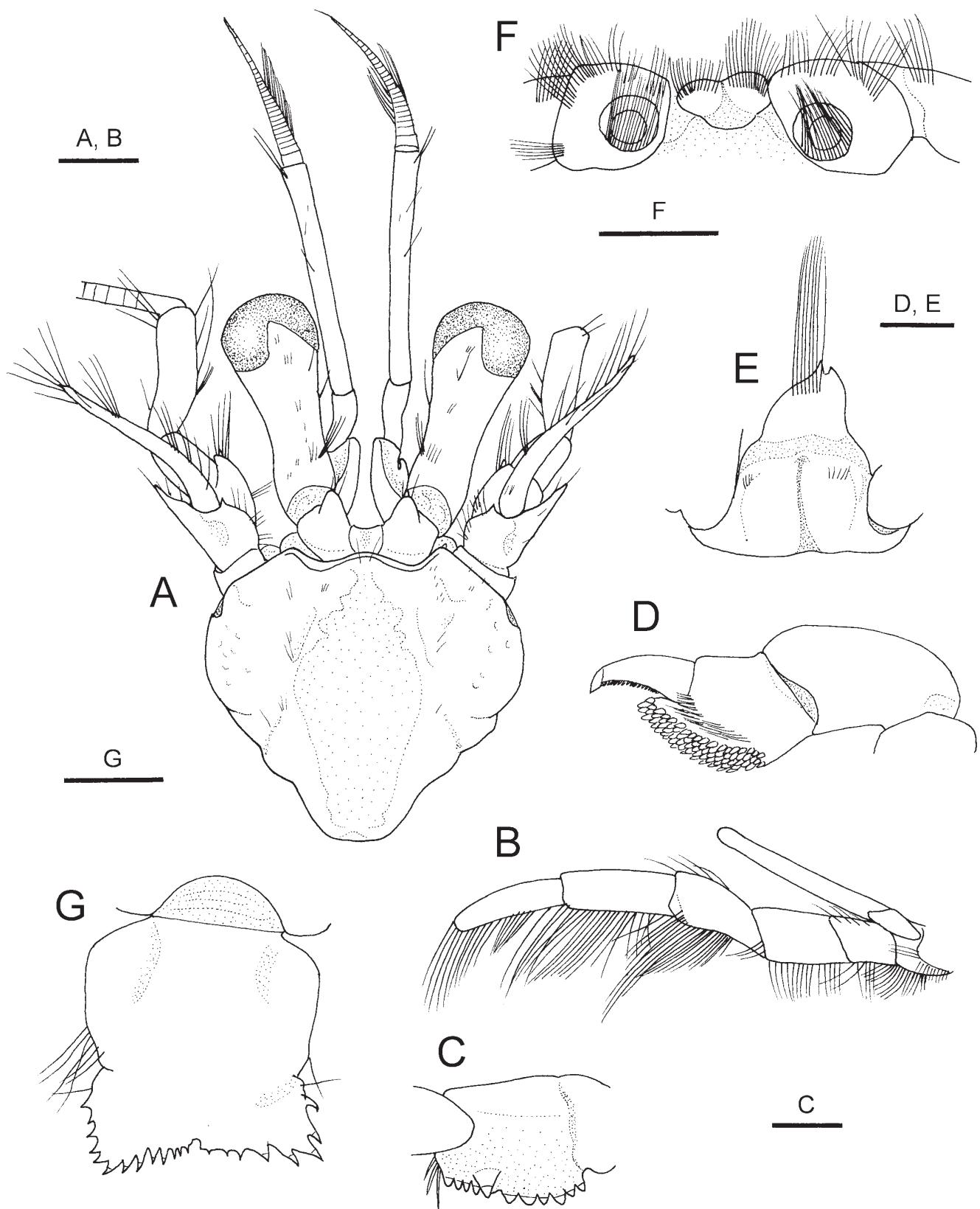


Fig. 10. *Pagurus truncatispinosus*, new species, PANGLAO 2004, PN1, holotype, male (sl 7.2 mm), NMCR 39117. A, shield and cephalic appendages, dorsal view; B, left third maxilliped, lateral view; C, same, ischium, ventral view (setae omitted); D, distal three segments of left fourth pereopod, lateral view (setae omitted); E, thoracic sternite 6, ventral view; F, coxae of fifth pereopods and thoracic sternite 8, ventral view; G, telson, dorsal view. Scale bars = 2 mm for A, B, F; 1 mm for C-E, G.

each bearing tuft of moderately long setae; mesial face with row of subtruncate spines dorsally and several scattered tubercles each bearing tuft of moderately long setae; ventral surface gently convex, with scattered tiny, low tubercles or protuberances each bearing tufts of short setae. Fixed finger nearly straight, somewhat depressed dorsoventrally; dorsal surface and dorsolateral margin with prominent subtruncate spines continued from palm; ventral surface unarmed, with tufts of long stiff setae arranged in some longitudinal rows; cutting edge with row of low calcareous teeth in proximal 0.7, crenulate in distal 0.3, terminating in small calcareous claw. Carpus moderately widened distally, subequal in length to merus; dorsal surface with 2 irregular longitudinal rows of small to moderately large spines in mesial half and with scattered, moderately small blunt tubercles each bearing tuft of long setae, extending onto lateral surface; dorsomesial margin delimited by double row of moderately small to large spines; dorsodistal margin with row of tiny spines; dorsolateral margin not delimited; lateral surface with numerous scattered, setae-bearing tubercles, becoming smaller and more closely spaced ventrally; mesial surface faintly concave, with scattered, numerous small tubercles and tufts of long setae obscuring armature; ventral surface flat, covered with tiny tubercles, provided with large, deep, pinhole-like foramen medially (Fig. 11E). Merus dorsally with irregular rows of short transverse ridges or low protuberances (margins of these structures multidenticulate) becoming weak proximally, each ridge bearing tuft or row of moderately short setae; dorsodistal margin minutely denticulate, with four prominent spines; lateral surface with short vertical ridges and small ventral spines or tubercles, ventrolateral distal margin with row of prominent spines; mesial surface with sparse, short vertical ridges or minute granules and several small ventral spines or tubercles (these armature bearing tufts of short setae), ventromesial distal margin with row of small tubercles; ventral surface armed with numerous small spines or tubercles and with numerous tufts of moderately long plumose setae partially obscuring armature. Ischium with row of tiny, low tubercles on ventromesial margin; lateral surface nearly smooth, ventrolateral distal angle with one or two spinules or spiniform tubercles. Coxa unarmed.

Left cheliped (Fig. 12A–D) moderately slender. Chela 2.5–2.8 times as long as wide (greatest width at base of dactylus), with numerous tufts of short to long setae on lateral, mesial and ventral surfaces; no hiatus between fingers. Dactylus approximately twice longer than palm; dorsal surface with partially double row of moderately small, subcylindrical spines with blunt apices; mesial surface with irregular longitudinal rows of low protuberances or small spines obscured by tufts of long setae; ventral surface unarmed; cutting edge with row of minute corneous teeth, terminating in small corneous claw. Palm about half length of carpus; dorsal surface slightly convex transversely, armed with very large spines arranged in four irregular longitudinal rows, extending onto fixed finger into single row, and decreasing in size distally; each spine slightly curved forward, with slightly inflated, rounded or subtruncate distal part; dorsomesial margin with single row of smaller, but similarly shaped spines; dorsolateral margin weakly delimited with row of

small to moderately large spines extending nearly to tip of fixed finger and decreasing in size distally; lateral and mesial surfaces with few small spines dorsally and scattered small, low, setae-bearing protuberances ventrally; ventral surface with scattered, very low, tiny protuberances and tufts of moderately short setae; cutting edge of fixed finger with row of tiny, obsolescent calcareous teeth interspersed by two or three fused, minute corneous teeth, terminating in moderately small corneous claw. Carpus subequal in length to merus, with tufts of short to long setae each arising from armature on every surface; dorsal midline bluntly carinate, with partially double row of small acute or subacute spines increasing in size distally; lateral and mesial surfaces with numerous scattered, small, low protuberances; ventral surface nearly flat, with numerous tiny tubercles, devoid of even trace of median foramen. Merus with short transverse ridges on dorsal surface, dorsodistal margin with 1 prominent spine; lateral surface with scattered, very short vertical ridges, becoming protuberance-like ventrally, and tufts of short setae, ventrolateral margin with row of moderately large spines decreasing in size proximally; mesial surface with sparse, very short vertical ridges and some small ventral tubercles, and tufts of short setae, ventromesial distal margin with row of tiny spines or tubercles; ventral surface faintly concave medially, with scattered tiny tubercles and tufts of moderately short setae. Ischium with row of minute tubercles on ventromesial margin; ventrolateral margin with row of short, multidenticulate ridges.

Ambulatory legs (Fig. 13A, E) moderately long and stout in general, right second pereopod overreaching tip of extended right cheliped by half length of dactylus. Dactyli 1.3–1.5 times as long as propodi, 10–12 times longer than broad, in dorsal view slightly twisted, in lateral view gently curving ventrally; dorsal margins each with row of numerous, short to moderately long (decreasing in length proximally), bristle-like setae, but without conspicuous spines or spinules (proximal parts apparently minutely denticulate because of pockets of bristle-like setae); lateral faces each with faint median sulcus and single row of moderately short to long stiff setae along midline; mesial faces (Fig. 13B, F) each with faint to shallow median sulcus flanked dorsally by row of widely spaced, individual or sets of two or three short, bristle-like setae, and ventrally by row of numerous bristle-like setae increasing in length distally; ventral margins each with row of about 30–50 minute, slender corneous spinules becoming widely spaced proximally, distal 10–15 spinules closely spaced, overlapping each other (Fig. 13C). Propodi (Fig. 13D, G) somewhat narrowing distally; dorsal surfaces each with single or partially double row of tiny spines (spines weaker in third than in second) and short setae, dorsodistal margin with minute granule or spinule (second) or unarmed (third); lateral and mesial surfaces each with sparse minute pits often bearing individual or tufts of short setae, mesial faces of second pereopods bearing minute spinules dorsally; ventral surfaces each with sparse, very short setae (second) or almost glabrous (third), without any armature. Carpi (Fig. 13D, G) each with row of small spines on dorsal margin, decreasing in size proximally, and row of sparse short setae (spines much weaker in third than in second); lateral faces

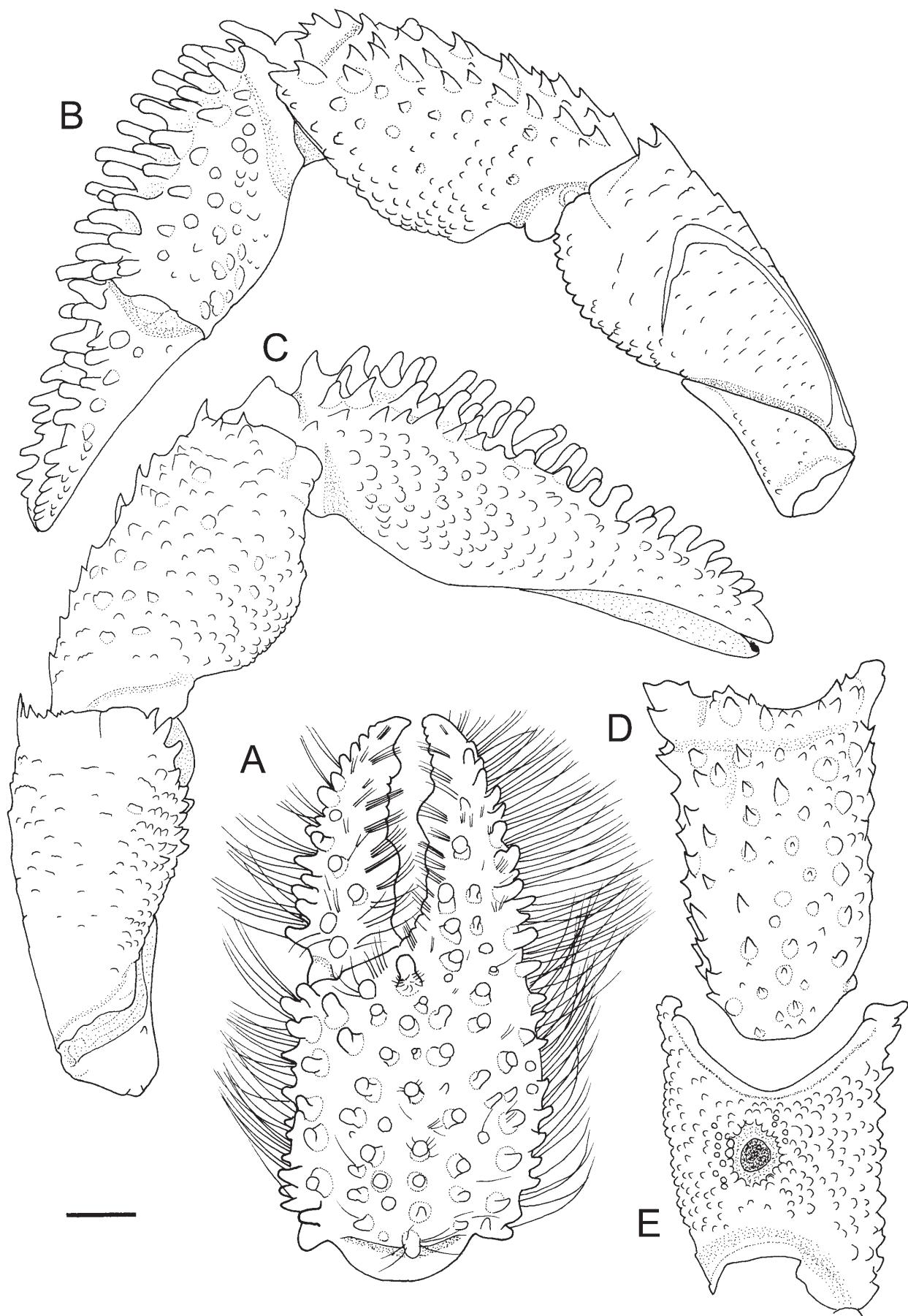


Fig. 11. *Pagurus truncatispinosus*, new species, PANGLAO 2004, PN1, holotype, male (sl 7.2 mm), NMCR 39117. A, right chela; B, right cheliped, mesial view (setae omitted); C, same, lateral view; D, carpus of right cheliped, ventral view (setae omitted); E, same, ventral view. Scale bar = 2 mm.

convex, with some scattered short setae. Dorsal surfaces of meri with tiny, low protuberances and tufts of short to moderately long setae (second) or only with tufts of similar setae (third); lateral and mesial faces almost glabrous except for few tufts of short setae; ventrolateral distal margins each with 1 tiny spine (second) or unarmed (third), ventral surfaces each with two or three irregular rows of tiny spines or tubercles (on second, armature more numerous in right than in left), or unarmed (third), and with tufts of short to long setae. Ischia unarmed, with moderately short to long setae on dorsal and ventral margins. Female with paired gonopores on coxae of third pereopods.

Fourth pereopods (Fig. 10D) semichelate, with stiff long setae on dorsal margins of dactyli to meri and ventral margin of meri. Dactyli gently curved, terminating in prominent

corneous claw, each with row of minute, closely spaced corneous teeth on ventral margin; no preungual process. Propodal rasp consisting of four rows of corneous scales.

Fifth pereopods chelate. Coxae of male (Fig. 10F) each with gonopore partially masked by tuft of setae.

Thoracic sternite 3 with anterior margin nearly straight, with paired denticles medially; ventral surface with prominent tuft of setae medially. Anterior lobe of thoracic sternite 6 (Fig. 10E) subtriangular, approximately as long as wide, distinctly skewed to left, terminally with two small spines; ventral surface with subterminal tuft of long setae. Thoracic sternite 8 (Fig. 10F) divided in two similar lobes by shallow median groove; each anterolateral angle slightly produced, with prominent tuft of short setae.

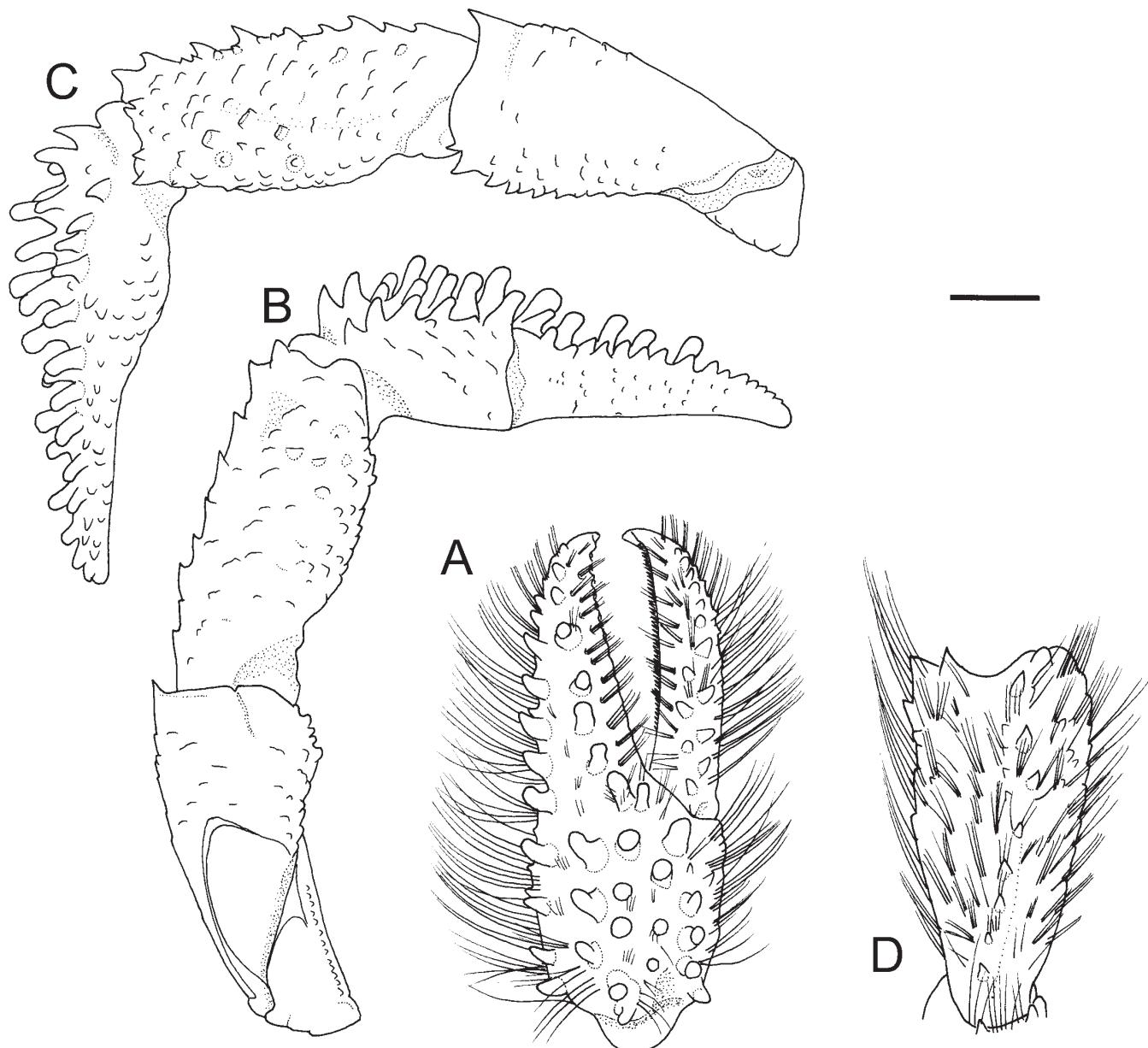


Fig. 12. *Pagurus truncatispinosus*, new species, PANGLAO 2004, PN1, holotype, male (sl 7.2 mm), NMCR 39117. A, left chela, dorsal view; B, left cheliped, mesial view (setae omitted); C, same, lateral view; D, carpus of left cheliped, dorsal view. Scale bar = 2 mm.

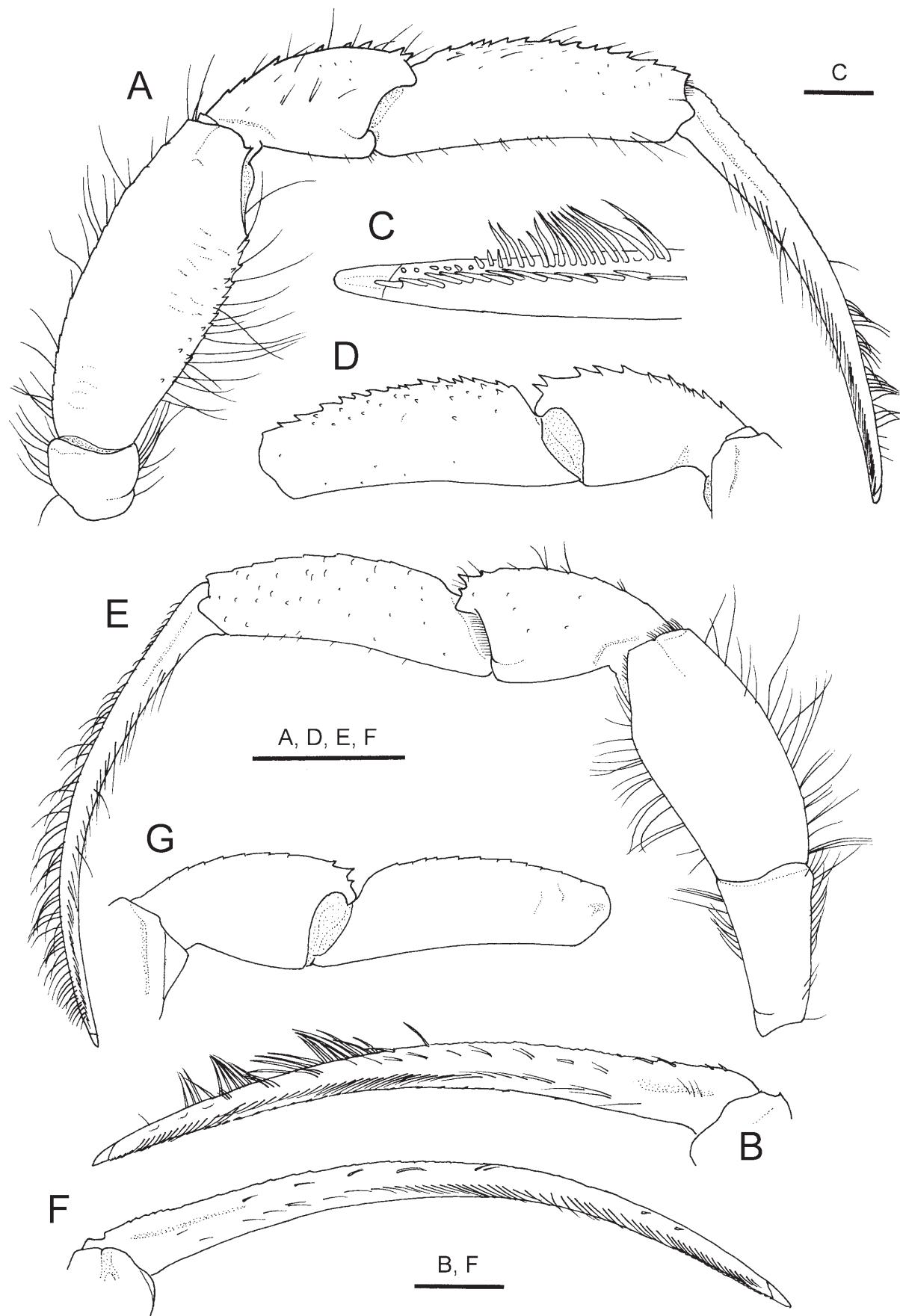


Fig. 13. *Pagurus truncatispinosus*, new species, PANGLAO 2004, PN1, holotype, male (sl 7.2 mm), NMCR 39117. A, right second pereopod, lateral view (bristle-like setae on proximal half of dorsal margin of dactylus broken off); B, same, dactylus, mesial view; C, same, detail of distal part of dactylus, mesial view; D, same, propodus and carpus, mesial view (setae omitted); E, left third pereopod, lateral view; F, same, dactylus, mesial view (dorsal setae omitted); G, same, propodus and carpus, mesial view (setae omitted). Scale bars = 5 mm (A, D, E, G); 2 mm (B, F); 0.5 mm (C).

Pleon dextrally twisted. Male with three (third to fifth) unpaired, very unequally biramous left pleopods. Female with subequally or slightly unequally biramous, second to fourth pleopods; fifth pleopod greatly unequally biramous with strongly reduced endopod.

Telson (Fig. 10G) with distinct lateral indentations; posterior lobes subrectangular, unequal, with median cleft very shallow, U-shaped; each terminal margin with row of corneous-tipped spines extending onto lateral margin (9–13 on left, 5–9 in right), these spines strongest around lateral angles.

Coloration. In preservative. Entirely light grayish brown.

Distribution. Known only from the Bohol Sea, the Philippines, at depths of 95–300 m.

Etymology. From the combination of the Latin, *truncatis* (= truncate) and *spinosis* (spinose), in reference to the terminally truncate or rounded spines on the palms of the chelipeds.

Remarks. *Pagurus truncatispinosus*, new species, shares the possession of a pinhole-like ventral foramen on the right cheliped carpus, representing an uncommon feature in Paguridae, with *P. cavicarpus*, *P. conformis*, and *P. carpoformatus*, though McLaughlin & Forest (1999) and the present study report that the carpal foramen is not always present in *P. cavicarpus* and *P. conformis*, respectively. Other diagnostic characters shared with the four species include: rostrum broadly rounded; ocular peduncle stout with dilated cornea; and propodi and carpi of second pereopods with row of spines on dorsal margins; male with four unpaired left pleopods (Alcock, 1905b; McLaughlin & Forest, 1999; Komai, 2004; this study). A shallow excavation or notch on the lateral margin of the shield and the triangular anterior lobe of the thoracic sternite 6 are also seen in the new species, *P. cavicarpus* and *P. conformis*; these characters are not known for *P. carpoformatus* because of the lack of a modern description. The characteristic shape of dorsal spines on the palms of both chelipeds immediately distinguishes the present new species from the other three relatives. In *P. truncatispinosus*, new species, the dorsal spines on the palms of chelipeds have slightly inflated and distally subtruncate or rounded apices, though those spines are acute or subacute and much smaller in the other species. In particular, in *P. conformis*, the dorsal spines are so small that they are partially obscured by surrounding setae. Furthermore, the proximal transverse groove of the right cheliped palm is unusually deep in *P. truncatispinosus*, new species; the carpal foramen on the right pereopod is better developed in the new species than in the other three species, though examination of more specimens might reveal that the development of the foramen is variable also in the new species.

Pagurus spinulentus and *P. spinossior* also resemble *P. truncatispinosus*, new species, in most of the characters mentioned above, though distinct pinhole-like foramen is absent in the former two species. We suppose that those six species (*P. carpoformatus*, *P. cavicarpus*, *P. conformis*, *P. spinossior*, *P. spinulentus*, and *P. truncatispinosus*, new

species) might constitute a monophyletic group. *Pagurus spinulentus* and *P. spinossior* are immediately distinguished from the new species in having the strongly produced dorsolateral distal angle of the second segment of the antennal peduncle (reaching the midlength of the fourth peduncular segment versus reaching nearly to the distal margin of the fourth peduncular segment), much more numerous, acuminate spines on both chelae and a shallow, transverse proximal groove on the right cheliped palm. The unarmed dorsal margins of dactyli of the second pereopods (versus armed with row of tiny spines), and the proportionally narrower anterior lobe of the thoracic sternite 6 also distinguish *P. truncatispinosus*, new species, from *P. spinulentus*.

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LITERATURE CITED

Alcock A (1905a) Marine crustaceans. XIV. Paguridae. In: Gardiner JS (ed.) The Fauna and Geography of the Maldivian and Laccadive Archipelagoes. Being an Account of the Work Carried on and the Collections Made by an Expedition during the years 1899 and 1900, 2: 827–835. University Press, Cambridge.

Alcock A (1905b) Anomura, Fascicules 1, Pagurides. Catalogue of the Indian decapod Crustacea in the collections of the Indian Museum, 2: i–xi, 1–197, 16 pls.

Alcock A & Anderson AR (1897) Crustacea, Part V. In: Illustrations of the Zoology of the Royal Indian Marine Surveying Steamer Investigator under the Command of Commander C. F. Oldham, R. N. Trustees of the Indian Museum, Calcutta. Pls. 28–32.

Asakura A (2010) A new species of hermit crabs of the *teevana* group of *Pylopaguropsis* (Decapoda: Anomura: Paguridae) from the western Pacific collected during the PANGLAO Expedition. Nauplius, 18(1): 35–43.

Baba K, Hayashi K & Toriyama M (1986) Decapod Crustaceans from Continental Shelf and Slope around Japan. The Intensive Research on Unexploited Fishery Resources on Continental Slopes. Japan Fisheries Resource Conservation Association, Tokyo. 336 pp.

Barnard KH (1950) Descriptive catalogue of the South African decapod Crustacea (crabs and shrimps). Annals of the South African Museum, 38: 1–837.

Bouchet P, Ng PKL, Largo D & Tan SH (2009) PANGLAO 2009 – Investigation of the marine species richness in the Philippines. Raffles Bulletin of Zoology, Supplement 20: 1–19.

Davie PJF (2002) Crustacea: Malacostraca: Eucarida (Part 2): Decapoda — Anomura, Brachyura. In: Wells A & Houston WWK (eds.) Zoological Catalogue of Australia, Volume 19.3B. CSIRO Publishing, Australia. xiv + 641 pp.

De Haan W (1849) Crustacea. In: von Siebold PF (ed.) *Fauna Japonica sive Descriptio Animalium, quae in Itinere per Japoniam, Jussu et Auspiciis Superiorum, qui Summum in India Batava Imperium Tenent, Suscepto, Annis 1823–1830 Collegit, Notis, Observationibus et Adumbrationibus Illustravit*. *Lugduni-Batavorum*, Leiden. xvi + 243 pp.

De Man JG (1888) Bericht über die im indischen Archipel vom Dr. J. Brock gesammelten Decapoden und Stomatopoden. *Archiv für Naturgeschichte*, 53: 215–600.

De Saint Laurent M & McLaughlin PA (2000) Superfamily Paguroidea, Family Paguridae. In: Forest J, De Saint Laurent M, McLaughlin PA & Lemaitre R (eds.) *The Marine Fauna of New Zealand: Paguridea* (Decapoda: Anomura) Exclusive of the Lithodidae. NIWA Biodiversity Memoir, 114: 104–209.

Estampador EP (1937) A check list of Philippine crustacean decapods. *Philippine Journal of Science*, 62: 465–559.

Estampador EP (1959) Revised list of Philippine crustacean decapods. *Natural and Applied Science Bulletin*, 17: 1–127.

Fabricius JC (1775) *Systema Entomologiae, Sistens Insectorum Classes, Ordines, Genera, Species, Adiectis Synonymis, Locis, Descriptionibus, Observationibus. Officina Luboraria Kortii*, 832 pp.

Forest J (1955) Crustacés Décapodes, Pagurides. *Expédition Océanographique Belge dans les Eaux Côtières Africaines de l'Atlantique Sud (1948–1949). Résultats Scientifiques*, 3: 23–147.

Forest J & De Saint Laurent M (1968) Résultats scientifiques des campagnes de la “Calypso”, Part VII. Campagne de la Calypso au large des côtes Atlantiques de l’Amérique du Sud (1961–1962). 6. Crustacés Décapodes: Pagurides. *Annales de l’Institut Océanographique de Monaco*, n.s., 45(2): 45–172.

Grant FE & McCulloch AR (1906) On a collection of Crustacea from the Port Curtis district, Queensland. *Proceedings of the Linnean Society of New South Wales*, 1906: 1–53.

Gordan J (1956) A bibliography of pagurid crabs, exclusive of Alcock, 1905. *Bulletin of the American Museum of Natural History*, 108: 253–352.

Haig J & Ball E (1988) Hermit crabs from North Australian and eastern Indonesian waters (Crustacea Decapoda: Anomura: Paguroidea) collected during the 1975 Alpha Helix Expedition. *Records of the Australian Museum*, 40: 151–196.

Haig J & McLaughlin PA (1991) The identity of *Pagurus lepidus* (Bouvier) (Decapoda, Anomura, Paguridae) and description of a new eastern Pacific insular species. *Contributions in Science*, 425: 1–12.

Harvey A & McLaughlin PA (1991) Two new hermit crabs of the genus *Pagurus* (*provenzanoi* group) (Crustacea, Anomura, Paguridae) from the eastern Pacific, with notes on their ecology. *Contributions in Science*, 425: 13–21.

Henderson JR (1888) Report on the Anomura collected by H.M.S. Challenger during the years 1873–76. Reports on the Scientific Results of the Exploratory Voyage of HMS Challenger, (Zoology) 27: i–xi, 1–221. Her Majesty’s Stationery Office, Edinburgh, UK.

Henderson JR (1896) Natural history notes from H. M. ‘Investigator’ Commander C. F. Oldham, R. N., commanding — Series II, No. 24. Report on the Paguridae collected during the season 1893–94. *Journal of the Asiatic Society of Bengal*, 65: 516–536.

Humann P & Deloach N (2010) *Reef Creature Identification. Tropical Pacific*. New World Publications, Florida, 497 pp. + index.

Ingle R (1993) *Hermit Crabs of the Northeastern Atlantic Ocean and the Mediterranean Sea*. Natural History Museum Publications. Chapman & Hall, London, vi + 495 pp.

Komai T (1998) The taxonomic position of *Pagurus gracilipes* (Stimpson) and *Pagurus nipponensis* (Yokoya), and description of a new species of *Pagurus* from Japan (Decapoda: Anomura: Paguridae). *Zoosystema*, 20: 265–288.

Komai T (1999) Re-examination of the type material of *Pagurus sagamiensis* Miyake (Decapoda: Anomura: Paguridae). *Natural History Research*, 5: 79–92.

Komai T (2000a) Redescription of *Pagurus pectinatus* (Crustacea: Decapoda: Anomura: Paguridae). In: Komai T (ed.) *Results of Recent Research on Northeast Asian Biota*. Natural History Research, Special Issue, 7: 333–348.

Komai T (2000b) The identity of *Pagurus brachiomastus* and descriptions of two new species of *Pagurus* (Decapoda: Anomura: Paguridae) from the northwestern Pacific. *Species Diversity*, 5: 229–265.

Komai T (2003a) Reassessment of *Pagurus pilosipes* (Stimpson), supplemental description of *P. insulae* Asakura, and descriptions of three new species of *Pagurus* from East Asian waters (Crustacea: Decapoda: Anomura: Paguridae). *Natural History Research*, 7: 115–166.

Komai T (2003b) Identities of *Pagurus japonicus* (Stimpson, 1858) and *P. similis* (Ortmann, 1892), with description of a new species of *Pagurus*. *Zoosystema*, 25: 377–411.

Komai T (2004) Redescription of *Pagurus conformis* De Haan, the senior synonym of *Pagurus megalops* (Stimpson). *Species Diversity*, 9: 343–358.

Komai T (2013) A new genus and new species of Paguridae (Crustacea: Decapoda: Anomura) from the Bohol Sea, the Philippines. *Species Diversity*, 18: 1–10.

Komai T & Imafuku M (1996) Redescription of *Pagurus lanuginosus* with the establishment of a neotype, and description of a new closely related species (Decapoda: Anomura: Paguridae). *Journal of Crustacean Biology*, 16: 782–796.

Komai T & Mishima S (2003) A redescription of *Pagurus minutus* Hess, 1865, a senior synonym of *Pagurus dubius* (Ortmann, 1892) (Crustacea: Decapoda: Anomura: Paguridae). *Benthos Research*, 58: 15–30.

Komai T & Rahayu DL (2004) Redescription of *Pagurus moluccensis* Haig & Ball, 1988, and description of a new species of *Pagurus* from Indonesia (Crustacea: Decapoda: Anomura: Paguridae). *Raffles Bulletin of Zoology*, 52: 183–200.

Komai T & Rahayu (2013a) Records of the hermit crab genus *Pagurixus* Melin, 1939 (Decapoda: Anomura: Paguridae) from shallow coral reefs in the Panglao Islands, the Philippines, with description of a new species. *Raffles Bulletin of Zoology*, 61: 133–141.

Komai T & Rahayu DL (2013b) Species of the pagurid hermit crab genus *Catapaguroides* A. Milne-Edwards & Bouvier, 1892 (Crustacea: Decapoda: Anomura) from the Bohol Sea, the Philippines, with descriptions of eight new species. *Raffles Bulletin of Zoology*, 61: 143–188.

Komai T & Rahayu DL (2013c) Six new species of the hermit crab genus *Decaphyllus* De Saint Laurent, 1968 (Crustacea: Decapoda: Anomura: Paguridae) from the Bohol Sea, the Philippines, and the Ryukyu Islands, Japan. *Raffles Bulletin of Zoology*, 61: 589–620.

Komai T, Reshmi R & Biju Kumar AN (2013) Rediscovery and range extension of *Ciliopagurus liui* Forest, 1995 and description of a new species of *Pagurus* Fabricius, 1775 (Crustacea: Decapoda: Anomura: Paguroidea) from the Kerala State, southwestern India. *Zootaxa*, 3710: 467–484.

Komai T & Ueshima R (in press) Decapod crustaceans (exclusive of Brachyura) preserved in the Department of Zoology, the University Museum, the University of Tokyo. The University of Tokyo Materials Reports, The University Museum, University of Tokyo.

Komai T, Yang CH, Okuno J & Chan TY (2011) Revisiting *Pagurus pilosipes* (Stimpson, 1858) (Crustacea: Decapoda: Anomura: Paguridae). *Zootaxa*, 3096: 41–52.

Komai T & Yu HP (1999) Identity of *Pagurus obtusifrons* (Ortmann), with description of a new species of *Pagurus* (Decapoda: Anomura: Paguridae). *Journal of Crustacean Biology*, 19: 188–205.

Leach WE (1815) *Malacostraca Podophthalmata Britanniae; or Descriptions of Such British Species of the Linnean Genus Cancer as Have Their Eyes Elevated on Footstalks*. No. 4 (unpaginated). London.

Lewinsohn C (1969) *Die Anomuren des Roten Meeres* (Crustacea: Decapoda: Paguridea, Galatheidea, Hippidea). *Zoologische Verhandelingen*, 104: 3–213, pls. 1, 2.

McLaughlin PA (1974) The hermit crabs (Crustacea, Decapoda, Paguridea) of northwestern North America. *Zoologische Verhandelingen*, 130: 1–396.

McLaughlin PA (1975) On the identity of *Pagurus brevidactylus* (Stimpson) (Decapoda: Paguridae), with the description of a new species of *Pagurus* from the western Atlantic. *Bulletin of Marine Science*, 25: 359–376.

McLaughlin PA (1997) Crustacea Decapoda: Hermit crabs of the family Paguridae from the KARUBAR cruise in Indonesia. In: Crosnier A & Bouchet P (eds.) *Résultats des Campagnes MUSORSTOM*, Vol. 16. *Mémoires du Muséum National d'Histoire Naturelle*, Paris, 172: 433–572.

McLaughlin PA (2002) A review of the hermit-crab (Decapoda: Anomura: Paguridea) fauna of southern Thailand, with particular emphasis on the Andaman Sea, and descriptions of three new species. *Phuket Marine Biological Center Special Publication*, 23: 385–460.

McLaughlin PA (2003) A new genus and species of hermit crab (Decapoda: Anomura: Paguridae) from seamounts off south-eastern Tasmania, Australia. *Memoirs of Museum Victoria*, 60, 229–236.

McLaughlin PA (2008) A new species of the hermit crab genus *Cancellus* (Decapoda: Paguroidea: Diogenidae) from the Panglao Expedition to the Philippine Islands. *Raffles Bulletin of Zoology*, Supplement 19: 83–90.

McLaughlin PA & Forest J (1999) Hermit crabs of the genus *Pagurus* Fabricius (Crustacea, Decapoda, Paguridae) from south-eastern South Africa. *Annals of the South African Museum*, 105: 297–344.

McLaughlin PA & Haig J (1993) Two new species of the Pacific component of the *provenzanoi* group of *Pagurus* (Decapoda: Anomura; Paguridae) and a key to the regional species. *Bulletin of Marine Science*, 52: 642–668.

McLaughlin PA & Lemaitre R (2009) A new classification for the Pylochelidae (Decapoda: Anomura: Paguroidea) and description of a new taxa. *Raffles Bulletin of Zoology*, Supplement 20: 159–231.

McLaughlin PA & Rahayu DL (2007) *Pseudopagurodes* McLaughlin, 1997 (Crustacea: Anomura: Paguroidea; Paguridae) revisited. *Raffles Bulletin of Zoology*, Supplement 16: 21–27.

McLaughlin PA, Komai T, Lemaitre R & Rahayu DL (2010) Annotated checklist of anomuran decapod crustaceans of the world (exclusive of the Kiwaoidea and families Chirostyliidae and Galatheidae of the Galatheoidea) Part I. Lithodoidea, Lomisoidea and Paguroidea. *Raffles Bulletin of Zoology*, Supplement 23: 5–107.

McLaughlin PA, Rahayu DL, Komai T & Chan TY (2007) A Catalog of the Hermit Crabs (Paguroidea) of Taiwan. National Taiwan Ocean University, Keelung. viii + 365 pp.

Miers EJ (1880) On a collection of Crustacea from the Malaysian region — Part III. Crustacea Anomura and Macrura (except Penaeidea). *Annals and Magazine of Natural History*, Series 5, 5: 370–384.

Minemizu R (2000) *Marine Decapod and Stomatopod Crustaceans Mainly from Japan*. First Edition. Bun'ichi Sogo Shuppan Co. Ltd., Tokyo, 344 pp. [In Japanese]

Miyake S (1978) *The Crustacean Anomura of Sagami Bay*. Biological Laboratory, Imperial Household, Tokyo, 200 pp. [In English], 161 pp. [In Japanese].

Miyake S (1982) *Japanese Crustacean Decapods and Stomatopods in Color*, Volume I. First printing. Hoikusha Publishing Co., Ltd., Osaka, vii + 261 pp., 56 pls. [In Japanese]

Moradmand M & Sari A (2007a) Littoral hermit crabs (Decapoda: Anomura: Paguroidea) from the Gulf of Oman, Iran. *Iranian Journal of Biosystematics*, 3: 25–36.

Moradmand M & Sari A (2007b) New record of the hermit crab *Pagurus kulkarnii* Sankolli, 1961 (Anomura: Paguridae) from the Gulf of Oman, Iran. *Zoology in the Middle East*, 42: 112–114.

Morgan GJ (1987) Hermit crabs (Decapoda, Anomura: Coenobitidae, Diogenidae, Paguridae) of Darwin and Port Essington, northern Australia. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences*, 4: 165–186.

Morgan GJ (1990) A collection of Thalassinidea, Anomura and Brachyura (Crustacea: Decapoda) from the Kimberley region of northwestern Australia. *Zoologische Verhandelingen*, 265: 1–90.

Naderloo R, Moradmand M, Sari A & Türkay M (2012) An annotated check list of hermit crabs (Crustacea, Decapoda, Anomura) of the Persian Gulf and the Gulf of Oman with five new records and an identification key to the North Indian Ocean genera. *Zoosystematics and Evolution*, 88: 63–70.

Naderloo R & Türkay (2012) Decapod crustaceans of the littoral and shallow sublittoral Iranian coast of the Persian Gulf: Faunistics, biodiversity and zoogeography. *Zootaxa*, 3374: 1–67.

Olgún N & Mantelatto FL (2013) Molecular analysis validates of some informal morphological groups of *Pagurus* (Fabricius, 1775) (Anomura: Paguridae) from South America. *Zootaxa*, 3666: 436–448.

Ortmann AE (1892) *Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen*, IV. Die Abtheilungen Galatheidea und Paguridea. *Zoologischen Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere*, 6: 241–326, pls. 11, 12.

Osawa M (2012) A new species of the genus *Pagurus* Fabricius, 1775 (Crustacea: Decapoda: Anomura: Paguridae) from the Ryukyu Islands, southwestern Japan. In: Naruse T, Chan TY, Tan HH, Ahyong ST & Reimer JD (eds.) *Scientific Results of the Marine Biodiversity Expedition — KUMEJIMA 2009*. *Zootaxa*, 3367: 155–164.

Paul'son O (1875) *Izsledovaniya rakoobraznykh krasnago morya s zametkami otnositel'no rakoobraznykh drugikh morei*. Chast' 1. *Podophthalmata i Edriophthalmata* (Cumacea). S.V. Kul'zhenko, Kiev, 144 pp. [Studies on Crustacea of the Red Sea with Notes Regarding Other Seas. Podophthalmata and Edriophthalma (Cumacea).] Translation, Israel Program for Scientific Translations, 1961, National Science Foundation and Smithsonian Institution.

Poore GCB (2004) *Marine Decapod Crustacea of Southern Australia. A Guide to Identification*. CSIRO Publishing, Australia, ix + 574 pp.

Poupin J, Bouchard J-M, Dinhut V, Cleva R & Dumas J (2013) Anomura (Crustacea Decapoda:) from the Mayotte region, western Indian Ocean. *Atoll Research Bulletin*, 593: i–iv, 1–73.

Poupin J & Juncker M (2010) *Guide des Crustacés Décapodes du Pacifique Sud / A Guide to South Pacific's Decapod Crustaceans. Guide de terrain – Field Guide*. CRISP, CPS, Nouméa (French/English), 317 pp.

Rahayu DL (1996) Notes on littoral hermit crabs (excluding Coenobitidae) (Crustacea: Decapoda: Anomura) mainly from Singapore and Peninsular Malaysia. *Raffles Bulletin of Zoology*, 44: 335–355.

Rahayu DL (2000) Hermit crabs from the South China Sea (Crustacea: Anomura: Diogenidae, Paguridae, Parapaguridae). Raffles Bulletin of Zoology, Supplement 8: 377–404.

Rahayu DL & J Forest (2009) Le genre *Paguristes* Dana aux Philippines avec la description de deux nouvelles espèces (Decapoda, Anomura, Diogenidae). Crustaceana, 82: 1307–1338.

Rahayu DL & T Komai (2013) Two new species of *Pseudopagurodes* McLaughlin, 1997 (Crustacea, Decapoda, Anomura, Paguridae) from the Philippines. In: Ahyong ST, Chan TY, Corbari L & Ng PKL (eds.) Tropical Deep-Sea Benthos, Volume 27. Mémoires du Muséum National d'Histoire Naturelle, Paris, 204: 423–435.

Sandberg L & McLaughlin PA (1993) Re-examination of *Pagurus minutus* Hess, 1865, and *Pagurus filholi* (De Man, 1887) (Crustacea: Anomura: Paguridae). Zoologische Mededelingen, 67: 197–206.

Sankolli KN (1962) On a new species of hermit crab *Pagurus kulkarnii* sp. nov. (Anomura: Paguridae). Journal of the Zoological Society of India, 13: 136–142.

Siddiqui FA & Kazmi QB (2003) A checklist of marine anomurans (Crustacea: Decapoda) of Pakistan, northern Arabian Sea. Memoirs of Museum Victoria, 60: 87–89.

Stebbing TRR (1920) South African Crustacea. Annals of the South African Museum, 17: 231–272.

Stimpson W (1858) Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Pars IV. Crustacea Cancroidea et Corystoidea. Proceedings of the Academy of Natural Sciences of Philadelphia, 10: 31–40.

Stimpson W (1907) Reports on the Crustacea (Brachyura and Anomura) collected by the North Pacific Exploring Expedition, 1853–1856. Smithsonian Miscellaneous Collections, 49: 1–240.

Terao A (1913) A catalogue of hermit-crabs found in Japan (Paguridea excluding Lithodidae), with descriptions of four new species. Annotationes Zoologicae Japonenses, 8: 355–391.

Tirmizi NM & Siddiqui FA (1982) The Marine Fauna of Pakistan: 1. Hermit Crabs (Crustacea, Anomura). University Grants Commission, University of Karachi, Islamabad, 103 pp.

White A (1847) List of the Specimens of Crustacea in the Collection of the British Museum. British Museum, London, viii + 143 pp.

Yap-Chiongco V (1938) The littoral Paguridea in the collection of the University of the Philippines. Philippine Journal of Science, 66: 183–219.

Yokoya Y (1933) On the distribution of decapod Crustacea inhabiting the continental shelf around Japan, chiefly based upon materials collected by S.S. "Soyo Maru" during the years 1923–1930. Journal of the College of Agriculture, Tokyo Imperial University, 12: 1–236.