

**REDESCRIPTION OF *PAGURUS MOLUCCENSIS* HAIG & BALL, 1988, WITH  
DESCRIPTION OF A NEW SPECIES OF *PAGURUS* FROM INDONESIA, AND  
TAXONOMIC NOTES ON THE *PAGURUS ANACHORETUS* GROUP  
(CRUSTACEA: DECAPODA: ANOMURA: PAGURIDAE)**

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**ABSTRACT.** – During a faunal study of the shallow coral reefs in Indonesia, two species of the hermit crab genus *Pagurus*, which show remarkable affinities in morphology and coloration, were recognized. One of them is the little known species, *P. moluccensis* Haig & Ball, 1988, which was known only by the holotype from Maluku region in Indonesia. The second is described herein as new, *P. fungiformis*, new species. *Pagurus moluccensis* is fully redescribed and illustrated in order to supplement the original description and to facilitate comparison with the new species. The strongly bispined interocular lobe immediately separates *P. moluccensis* and the new species from other known species of *Pagurus*. The new species is readily distinguished from *P. moluccensis* by the possession of closely set, flattened, marginally denticulate tubercles on the palms of chelae and brush-like setae on the dactylus and propodus of the left third pereopod. In *P. moluccensis*, the chelae are armed with small, simple or bifid tubercles on the dorsal surface; the left third pereopod lacks brush-like setae. These two species are assigned to the *anachoretus* group of *Pagurus*. Definition of this informal species group is reviewed and emended to accommodate the two species discussed in this study and *P. decimbranchiae*.

**KEY WORDS.** – Crustacea, Decapoda, Anomura, Paguridae, *Pagurus moluccensis*, redescription, *Pagurus fungiformis*, new species, Indonesia, *Pagurus anachoretus* group.

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## INTRODUCTION

Among the collection in the Indonesian Institute of Sciences, Ambon, collected during faunal surveys in the shallow coral reefs, we discovered two species of pagurid hermit crabs from Sulawesi, i.e. the little known species *Pagurus moluccensis* Haig & Ball, 1988 and an undescribed species herein named, *Pagurus fungiformis* new species. *Pagurus moluccensis* was described on the basis of a single male specimen from Maluku region in Indonesia, collected during the 1975 Alpha Helix Expedition. The species was only provisionally assigned to the genus *Pagurus* Fabricius, 1775 by the original authors because of the possession of unusual features for the genus, such as the two-spined interocular lobe and the widely separated lobes on the eighth thoracic sternite. The additional specimens from Sulawesi enabled us to supply a number of morphological details not mentioned by Haig & Ball (1988). The new species, *P. fungiformis* shares some characters including the two-spined interocular lobe and widely separated lobes on the eighth thoracic sternite, as well as

similar coloration in life, with *P. moluccensis*, although there are a number of morphological differences between the two species. In order to facilitate comparison, a full redescription is given for *P. moluccensis*; the new species is fully described and illustrated.

The two species generally fit the definition of the *P. anachoretus* Risso, 1827 group (cf. Forest, 1978; Forest & Ngoc-Ho, 1992; McLaughlin & Forest, 1999), in spite of the characteristic bispined interocular lobe, which distinguishes the two species from all other species of *Pagurus*. Preliminary comparison with several species heretofore assigned to the *P. anachoretus* group and possibly related species (McLaughlin & Forest, 1999) has suggested that *P. moluccensis* and the new species are most closely allied with *P. hedleyi* (Grant & McCulloch, 1906) and *P. kulkarnii* Sankolli, 1961. Thus, *P. moluccensis* and *P. fungiformis* new species are assigned to the *P. anachoretus* group. *Pagurus decimbranchiae* Komai & Osawa, 2001, is also assigned to this species group. Characters shared by species of the

*anachoretus* group are reviewed and the definition of the species group is somewhat modified.

## MATERIAL AND METHODS

The material examined in this study are deposited in the institutions indicated by the following abbreviations: CBM: Natural History Museum and Institute, Chiba, Japan; MNHN: Muséum national d'Histoire naturelle, Paris, France; MZB: Museum Zoologicum Bogoriense, Indonesia; NIOJ: Research Center for Oceanography, Jakarta, Indonesia; ZRC: Raffles Museum of Biodiversity Research, National University of Singapore, Republic of Singapore. The shield length, abbreviated as sl, was measured from the tip of the rostrum to the midpoint of the posterior margin of the shield. Except where otherwise mentioned, the specimens from Indonesia were collected by the junior author. The usage of the terminology in the description follows generally McLaughlin (1997), with exception of the posterior carapace (see Lemaitre, 1995), gill structure (see McLaughlin & de Saint Laurent, 1998), dactylus (dactyli) for dactyls (dactyls) and numbered thoracic sternites. The submedian grooves on the gastric region of the shield are termed as "paragastric grooves" following Komai & Osawa (2001). The drawings were made with the aid of a drawing tube mounted on a Leica MZ8 stereomicroscope. For detailed observation of the surface structure on the integument, the specimens (including removed appendages) were stained with methylene blue solution in water.

## TAXONOMY

### FAMILY PAGURIDAE

#### *Pagurus* Fabricius, 1775

#### *Pagurus moluccensis* Haig & Ball, 1988

(Figs. 1A, 2-5)

*Pagurus moluccensis* Haig & Ball, 1988: 187, figs. 14, 15; Komai & Osawa, 2001: 1291.

**Material examined.** – Holotype - male (sl 2.1 mm) (NIOJ-A 009), north side of Banda Besar, south side of Selat Lontor, 7 Apr.1975.

Other material - 5 males (sl 2.0-2.3 mm), 4 females (sl 1.7-2.0 mm), 1 ovigerous female (sl 1.8 mm) (CBM-ZC 5569), Marsegu Island, intertidal, coll. La Pay, 9 Feb.1994; 1 male (sl 2.1 mm), 1 female (sl 1.8 mm), 1 ovig (sl 1.5 mm) (MZB Cru 1505), same data; 1 male (sl 2.3 mm), 3 ovigerous females (1.9-2.5 mm) (CBM-ZC 5570), Lembah Strait, north of Sulawesi, intertidal, 25 Jun.1996; 1 male (sl. 2.4 mm), 1 ovigerous female (2.0 mm) (ZRC 2002.0517), same data; 1 female (sl 2.0 mm) (CBM-ZC 5571), Tanawanako, north of Sulawesi, intertidal, 21 Dec.1997.

**Redescription.** – Eleven pairs of biserial phyllobranchiae. Calcified parts of integument of body and appendages with low, blister-like tubercles of various shape and size (Figs. 2A, B, F, H, 3G, J).

Cephalothorax somewhat depressed dorsoventrally. Shield (Fig. 2A) about as long as broad; anterior margin between rostrum and lateral projections slightly concave; anterolateral margins sloping; posterior margin truncate; rostrum broadly rounded, slightly exceeding lateral projections; lateral projections obsolete, without terminal spine; dorsal surface flat to slightly convex, with numerous blister-like tubercles; paragastric grooves conspicuous; dorsal surface with tufts of setae laterally. Posterior carapace (Fig. 2B) membranous except for weakly calcified anterior part of posteromedian plate and submedian parts either side of posteromedian plate; submedian parts with numerous small, blister-like tubercles; branchial region with few setae; cardiac sulci converging posteriorly, reaching nearly to posteromedian margin of carapace; sulci cardiobranchialis short, somewhat divergent posteriorly.

Ocular peduncles (Fig. 2A) 0.7-0.8 times as long as shield, moderately stout, weakly inflated basally, corneas not dilated; dorsal surfaces each with row of tufts of short setae mesially. Ocular acicles (Fig. 2C) triangular, terminating in sharp marginal spine; dorsal surfaces nearly flat. Interocular lobe (Fig. 2C) prominent, with paired long processes each terminating acutely or subacutely, not reaching distal margins of ocular acicles.

Antennular peduncles (Figs. 2A, 3A) stout, reaching or slightly overreaching distal margins of corneas; ultimate segment 1.5-1.6 times as long as penultimate segment, somewhat broadened distally in lateral view, with few setae on dorsal surface; basal segment with distolateral margin slightly produced, ventromesial distal margin unarmed, statocyst lobe unarmed on lateral face.

Antennal peduncles (Fig. 2A) overreaching distal margins of corneas by 0.1-0.3 length of fifth segment. Fifth segment moderately stout, with few short setae. Fourth segment with few short setae. Third segment with small tubercle at ventromesial distal angle and few short setae. Second segment with dorsolateral distal angle produced, reaching midlength of fourth segment, terminating in small spine, unarmed on mesial margin; dorsomesial distal angle unarmed, mesial surface with sparse setae. First segment with small spine on laterodistal margin; ventrodistal margin produced, with 1 spinule. Antennal acicle arcuate, not reaching or reaching base of cornea, terminating in slender spine, with row of sparse setae on mesial margin. Antennal flagella long, overreaching extended right cheliped.

Mandible (Fig. 3B) with sharp ridge on molar process. Maxillule (Fig. 3C) with broad proximal endite; endopod moderately broad, internal lobe slightly produced, bearing 1 apical bristle, external lobe small, basally articulated. Maxilla (Fig. 3D) with endopod reaching distal margin of anterior lobe of scaphognathite. First maxilliped (Fig. 3E) with endopod not reaching anterior margin of distal endite; exopod with lateral margin strongly expanded proximally. Second maxilliped (Fig. 3F) with short endopod; exopod broad. Third maxilliped (Fig. 2D) stout; ischium (Fig. 2E) with crista dentata composed of row of sharp corneous teeth and with

2 accessory teeth; merus unarmed on dorsodistal and ventromesial margins; carpus unarmed on dorsodistal margin.

Right cheliped (Figs. 4A-D) larger than left. Right chela subovate in dorsal view, 1.5-1.8 times longer than greatest width at base of dactylus. Dactylus subequal in length to palm; dorsal surface slightly convex, with numerous small spines or tubercles and few tufts of short setae; dorsomesial margin with single or double row of small spines (spines blunt or subacute in males, acute in females); ventral surface with tufts of short setae; in males cutting edge with row of calcareous teeth and subdistal, short row of minute corneous teeth, terminating in small calcareous claw; in females cutting edge with few low calcareous teeth on proximal 0.4 and row of small corneous teeth in distal 0.6, terminating in small corneous claw. Palm subequal in length to carpus; dorsal surface convex, with numerous, small, simple or bifid tubercles and few short setae; dorsolateral margin (including fixed finger) elevated (degree of elevation stronger in females than in males), with single row of small spines (spines blunt or subacute in males, acute in females); dorsomesial margin not elevated (males) or weakly elevated (females), with irregular single or double row of small spines; lateral face almost flat, with small, low protuberances or tubercles adjacent to dorsolateral margin and few short setae; mesial face with small tubercles (simple, bifid or multifid) adjacent to dorsomesial margin and small, low protuberances ventrally; ventral surface weakly convex, with few short setae. In males, cutting edge of fixed finger with row of calcareous teeth, distal teeth occasionally interspersed by short row of minute corneous teeth, terminating in small calcareous claw; in females, cutting edge of fixed finger with few small calcareous teeth in proximal 0.6 and row of small corneous teeth in distal 0.4, terminating in small corneous teeth. Carpus subequal in length to merus, noticeably broadened distally in dorsal view; dorsal surface with small, low tubercles or protuberances and few tufts of very short setae, dorsodistal margin with row of low, blunt teeth; dorsolateral margin not delimited; dorsomesial margin with single or double row of moderately small to large spines (proximal spines blunt); lateral face with few small, low tubercles or protuberances dorsally, ventrolateral margin smooth; mesial face almost flat, with small, low protuberances accompanied by tufts of very short setae, ventrodistal margin with row of small spines; ventral surface with small, low protuberances and few short setae. Merus with smooth dorsal surface, dorsodistal margin with few slender spines; lateral face with few small, low tubercles ventrally, ventrolateral margin slightly protuberant; mesial face smooth, ventrodistal margin with row of small spines (spines relatively larger in females than in males); ventral surface with some blister-like tubercles and tufts of short setae. Ischium unarmed on ventromesial margin; all surfaces with few short setae. Coxa with large blister-like tubercles.

Left cheliped (Figs. 5A-C) reaching midlength of dactylus of right cheliped. Chela 1.9-2.1 times longer than greatest width, elongate subovate in dorsal view. Dactylus 1.5-1.7 times as long as palm; dorsal surface convex, mesially with row of small tubercles; dorsomesial margin delimited by

single or double row of small spines or tubercles; mesial and ventral surface with row of tufts of short setae; cutting edge with row of small corneous teeth in distal 0.7, terminating in small corneous claw. Palm shorter than carpus; dorsal surface slightly convex, with scattered small, low, simple or bifid tubercles, and few tufts of very short setae; dorsolateral margin (including fixed finger) with single row of moderately small spines, becoming blunt and smaller proximally; dorsomesial margin with single or double row of small spines or tubercles; lateral face with small, low, bifid or multifid protuberances, and few short setae; mesial face with bifid or multifid tubercles and short setae; ventral surface weakly convex, with 2 rows of low, small protuberances extending onto fixed finger. Cutting edge of fixed finger with row of small calcareous teeth in proximal 0.7-0.8 and row of small corneous teeth in distal 0.2-0.3 (some distal calcareous teeth interspersed by short row of corneous teeth), terminating in large corneous claw. Carpus subequal in length to merus, somewhat broadened distally in dorsal view; dorsal surface with few low protuberances and short setae, dorsolateral margin not delimited; dorsomesial margin with row of spines; dorsodistal margin irregularly denticulate; lateral face with scattered very short setae, ventrolateral margin smooth; mesial face nearly flat, with few short setae, ventromesial margin smooth; ventral surface weakly convex, with few tufts of moderately long setae. Merus only with few short setae on dorsal surface; dorsodistal margin unarmed; lateral face with tiny, blister-like tubercles and few very short setae, ventrolateral margin with row of small spines or tubercles; mesial face smooth, with few very short setae, ventromesial margin slightly tuberculate; ventral surface with some blister-like tubercles laterally and tufts of long setae. Ischium with few tiny tubercles on ventromesial margin; all surfaces with few short setae. Coxa similar to that of right.

Second and third pereopods (Figs. 5D, F) not overreaching right cheliped, generally similar from right to left. Dactyli 0.8-0.9 times as long as propodi, slightly curved ventrally in lateral view and nearly straight in dorsal view, terminating in large corneous claws; dorsal surfaces each with sparse short setae; lateral and mesial faces each with rows of tufts of setae dorsally and ventrally, lacking longitudinal sulcus, mesial faces (Figs. 5E, G) unarmed; ventral margins each with 5-7 moderately small corneous spines. Propodi distinctly longer than carpi; dorsal surfaces unarmed, with sparse row of tufts of short setae; lateral faces with few very short setae; ventral surfaces each with 3-5 corneous spinules in distal half. Carpi each with small dorsodistal spine; dorsal surfaces each with row of tufts of short setae; lateral faces convex, with row of tufts of short setae on midline; ventral surfaces each with row of short setae (setae longer and more numerous in third than in second). Meri each with row of tufts of moderately short setae on dorsal and ventral surfaces; lateral faces each with tufts of very short setae; ventrolateral distal margins concave, unarmed or occasionally armed with 1 small distal spine in second. Ischia each with sparse setae on dorsal and ventral margins. Coxae each with blister-like tubercles of various sizes. In females moderately large paired gonopores present on third pereopods.

Fourth pereopods (Figs. 3G, J) semichelate, notably unequal with left larger than right. Dactyli (Figs. 3H, K) broad, nearly straight, terminating in small corneous claw; dorsal margins each with row of tufts of setae; ventral margins each with row of small corneous teeth; preungual process arising from ventral margin between distal claw and row of corneous teeth, broad based, rounded, bearing numerous minute setules. Propodi each with long setae on dorsal surface; mesial face divided in two flattened sections by weakly elevated midline bordered by row of long setae in left (Fig. 3I), entirely flattened with only few setae in right (Fig. 3K); ventral margins convex, but in left distal 0.7 almost straight; propodal rasps each composed of single row of small corneous scales. Carpi and meri with numerous long setae on dorsal surfaces; mesial faces of carpi ventrally with row of long setae in left, without long setae in right.

Fifth pereopods chelate; in males, paired gonopores partially obscured by tufts of short setae (Fig. 2G).

Anterior lobe of sixth thoracic sternite (Fig. 2F) broadly semicircular, skewed to left; posterior lobe much broader than anterior lobe. Seventh thoracic sternite with 2 broadly separated, ovate lobes just mesial to coxae of fourth pereopods. Eighth thoracic sternite (Fig. 2G) with 2 subovate

lobes broadly separated and anterolaterally directed, each lobe having flattened ventral surface.

Abdomen twisted, with 3 unpaired pleopods in males, each having well-developed exopod and rudimentary endopod. Females with 4 unpaired pleopods, both rami well developed in second to fourth pleopods; fifth pereopod smaller than others, with rudimentary exopod.

Telson (Fig. 3H) with distinct transverse indentations. Posterior lobes slightly unequal, separated by moderately broad, deep median cleft; lateral margins convex, with few setae; terminal margins weakly convex, each with 5 or 6 prominent spines and interspersing spinules.

**Coloration in life.** – Generally white with black markings (Fig. 1A). Shield with black markings centrally. Ocular peduncles each with dark brown band proximal to midlength. Interocular lobe black or dark brown. Antennular peduncles generally white, each with black distal band on each ultimate and penultimate segments; basal segment with black band proximally. Antennal flagella banded with dark brown and white. Dactyli of chelipeds each with median black spot on dorsal surface; palms each with broad transverse band; carpus and merus with irregular black band submedially. Second

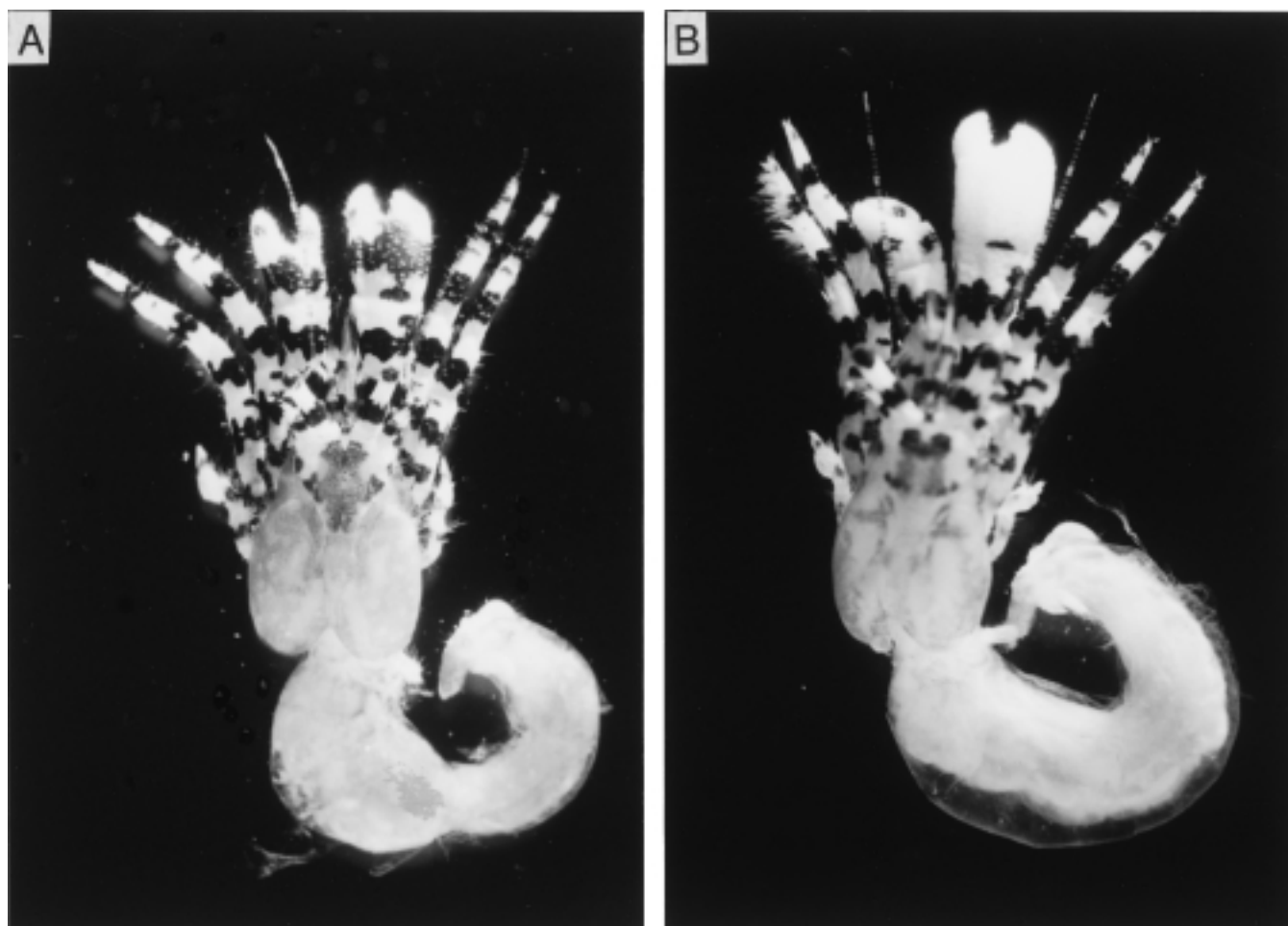


Fig. 1. A, *Pagurus moluccensis* Haig & Ball, 1988, live male from Marsegu Island; B, *Pagurus fungiformis*, new species, live male from Marsegu Island.

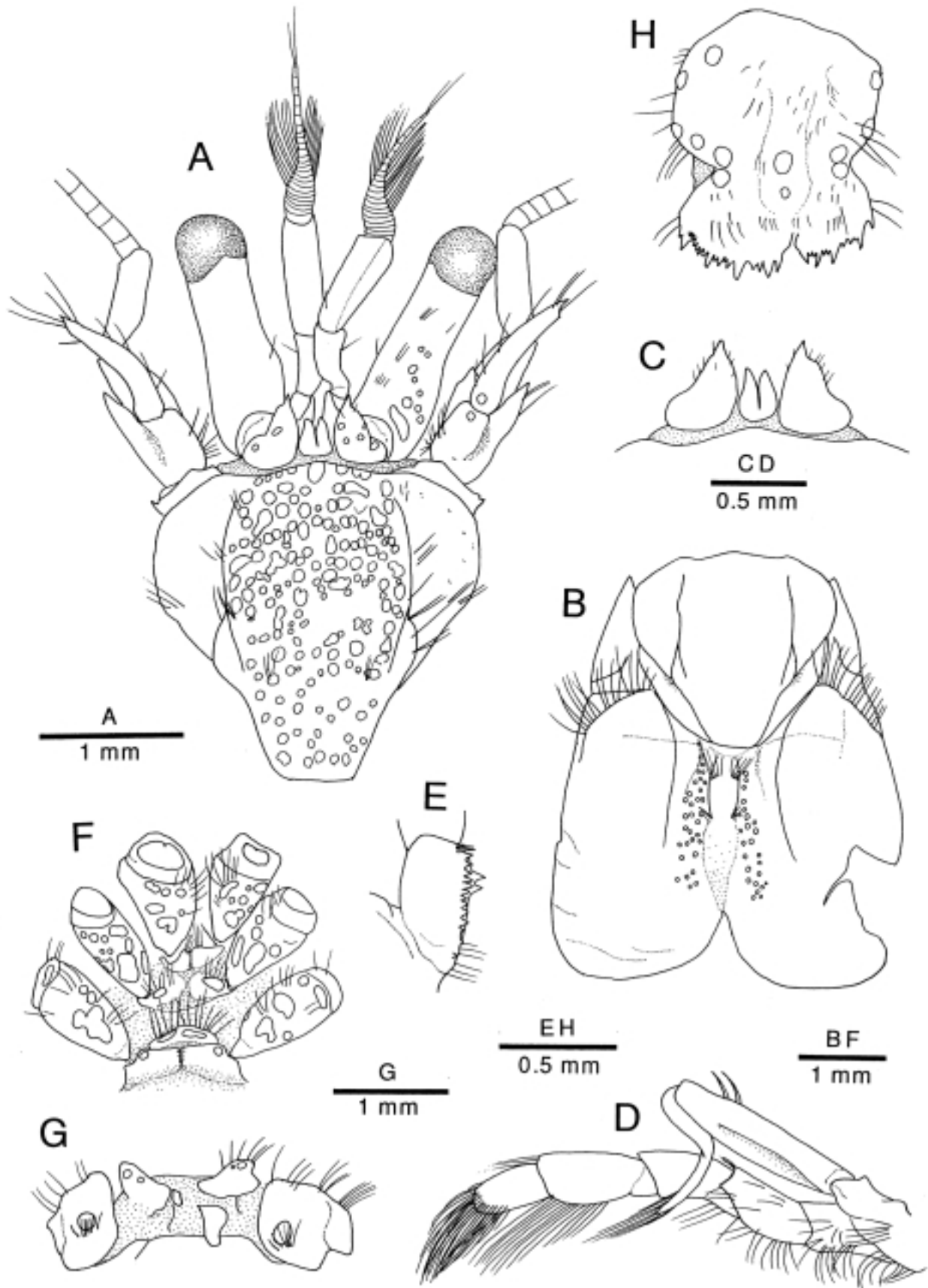


Fig. 2. *Pagurus moluccensis* Haig & Ball, 1988. A-G, holotype male from Banda Besar (sl 2.1 mm; NIOJ-A 009); H, male from Marsegu Island (sl 2.3 mm; CBM-ZC 5569). A, shield and cephalic appendages, dorsal; B, carapace, dorsal (right branchial region broken); C, ocular acicles and interocular lobe, dorsal; D, left third maxilliped, lateral; E, ischium of left third maxilliped, dorsal; F, coxae of first to third pereopods and fifth and sixth thoracic sternites, ventral; G, coxae of fifth pereopods and eighth thoracic sternite, ventral (sternite broken); H, telson, dorsal.

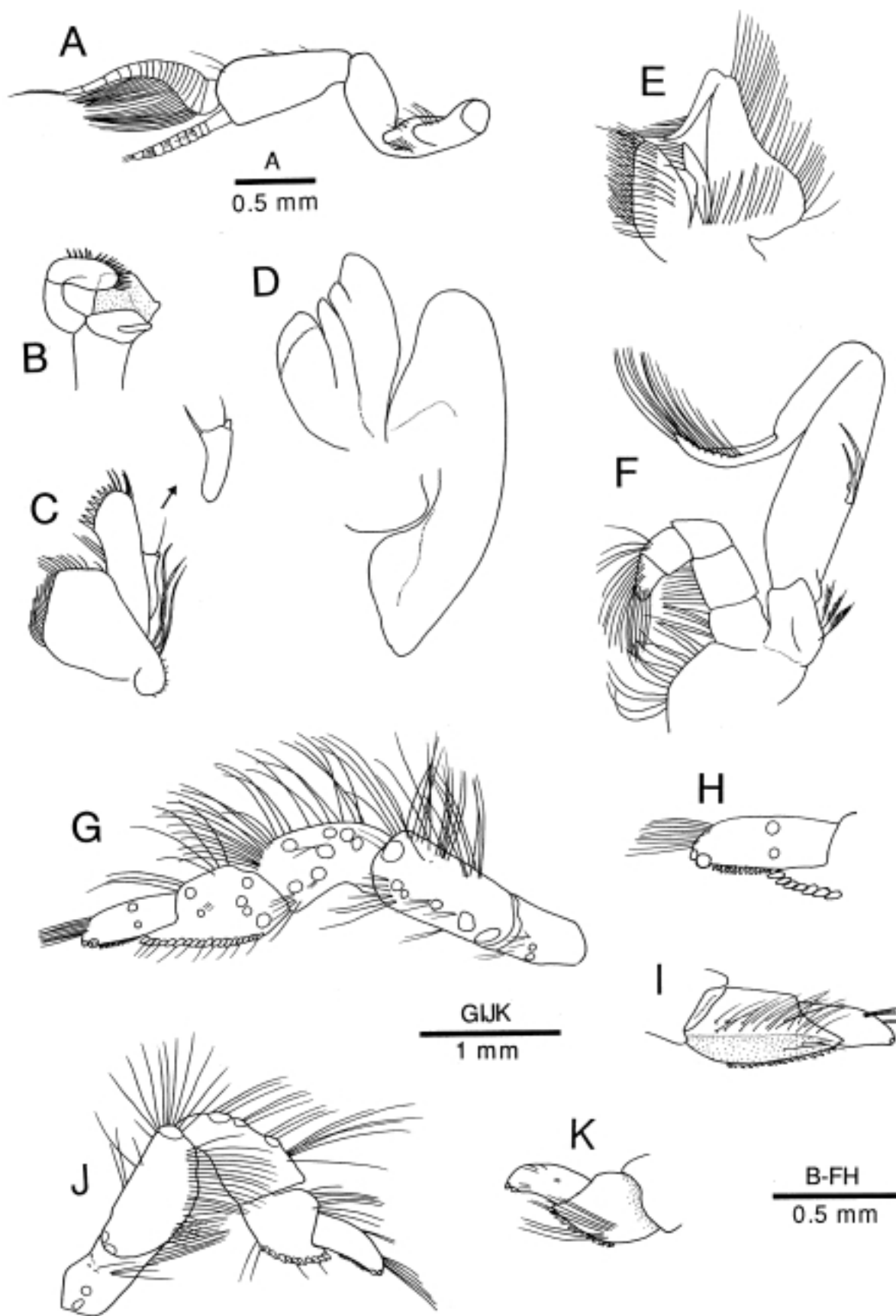


Fig. 3. *Pagurus moluccensis* Haig & Ball, 1988. A-F, male from Marsegu Island (sl 2.3 mm; CBM ZC 5569); G-K, female (sl 1.9 mm; same lot). A, left antennule, lateral; B, left mandible, dorsal; C, left maxillule, ventral; D, left maxilla, ventral (setae omitted); E, left first maxilliped, ventral; F, left second maxilliped, ventral; G, left fourth pereopod, lateral; H, dactylus of left fourth pereopod, lateral; I, dactylus and propodus of left fourth pereopod, mesial (only setae on mesial face depicted); J, right fourth pereopod, lateral; K, dactylus and propodus of right fourth pereopod, mesial (only setae on mesial face depicted).

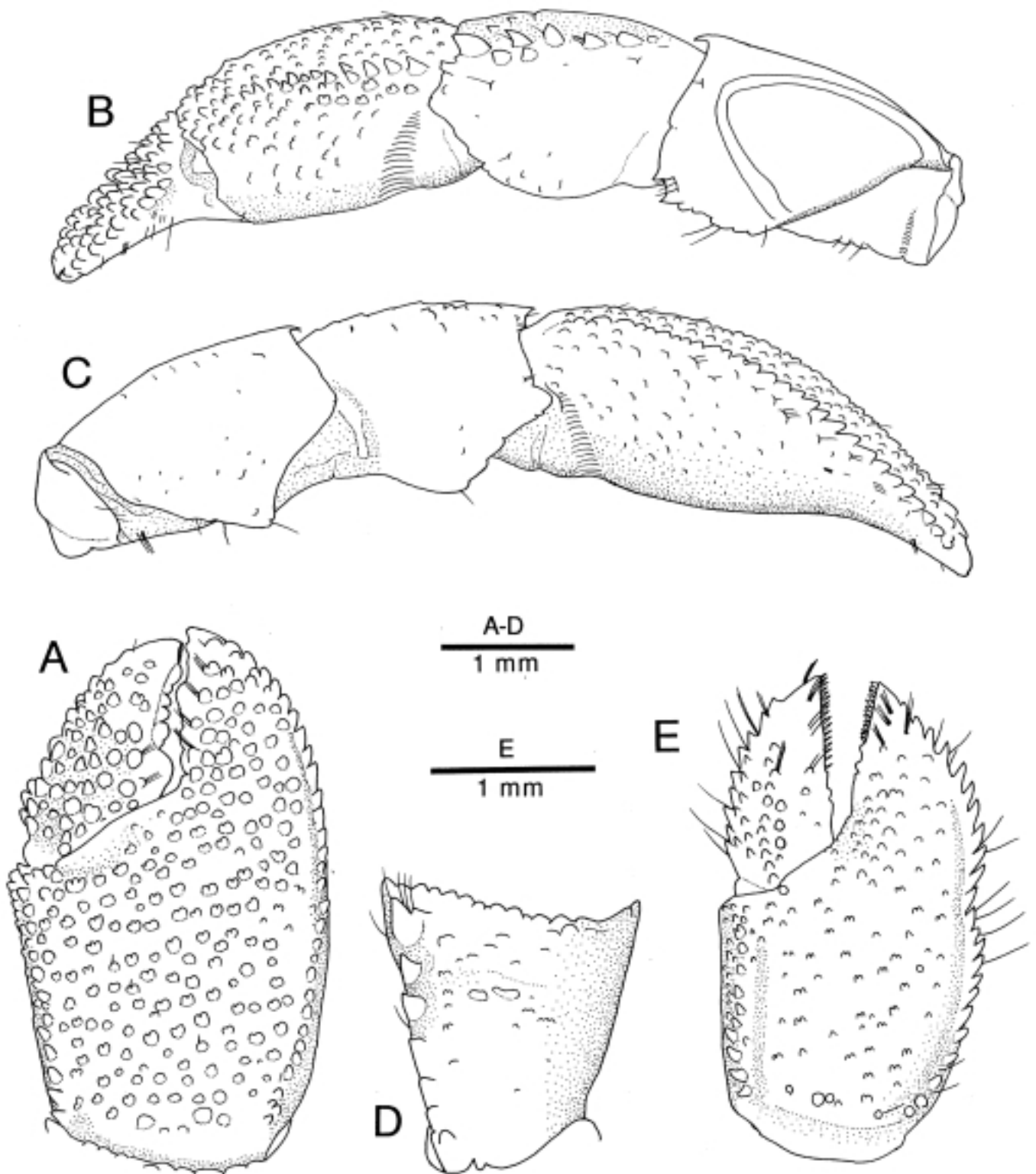


Fig. 4. *Pagurus moluccensis* Haig & Ball, 1988. A-D, holotype male from Banda Besar (sl 2.1 mm; NIOJ-A 009); E, female from Marsegu Island (sl 1.9 mm; CBM-ZC 5569). Right cheliped. A, E, chela, dorsal (setae partially omitted); B, entire right cheliped, mesial; C, same, lateral; D, carpus, dorsal.

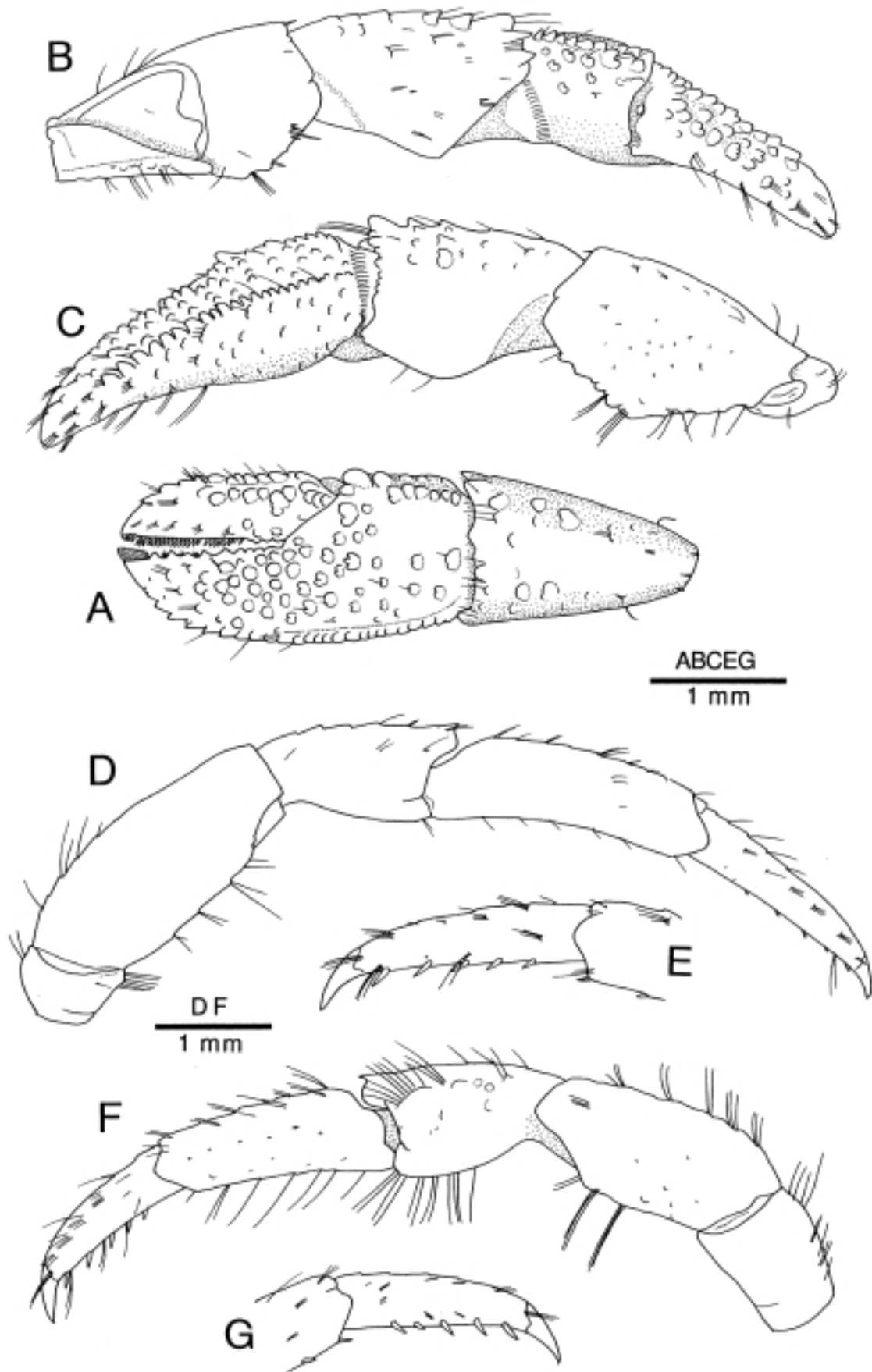


Fig. 5. *Pagurus moluccensis* Haig & Ball, 1988. Holotype from Banda Besar (sl 2.1 mm; NIOJ-A 009). A, chela and carpus of left cheliped, dorsal; B, entire left cheliped, mesial; C, same, lateral; D, right second pereopod, lateral; E, dactylus of right second pereopod, mesial; F, left third pereopod, lateral; G, dactylus of left third pereopod, mesial.



and third pereopods each with irregular subproximal band and small spot on dactylus, propodus, carpus and merus.

**Distribution.** – Known only from Banda Islands and north of Sulawesi, Indonesia; shallow water of coral reefs.

**Variation.** – As is apparent from the redescription, the shape of the spines on the dorsomesial margin of the dactylus and dorsolateral margin of the palm of the right cheliped and armature of the cutting edges of the fingers of the right cheliped seem to be different between males and females. Those spines are larger and sharper in females than in males. The dorsolateral margin and dorsomesial margin of the palm of the right cheliped are more strongly elevated in females than in males. The calcareous teeth on the cutting edges are better developed in males than in females, although the rows of corneous teeth are better developed in females than in males.

**Remarks.** – Although Haig & Ball's (1988) original description is detailed enough for species recognition, the following important characters, which may be useful to assess interspecific relationships, are supplemented here: the presence of blister-like tubercles or protuberances on the calcified integument of the body and appendages; the basally articulated external lobe on the endopod of the maxillule; and the noticeably dissimilar fourth pereopods. Further, the dorsal surface of the palm of the right cheliped was described as granular in the original description, although only mesial "granules" are depicted in the given illustrations (Haig & Ball, 1988, fig. 14E, F). The dorsal surface of the right palm is actually armed with numerous, small, simple or bifid tubercles.

As Haig & Ball (1988) indicated, *P. moluccensis* is readily distinguished from all other known species of *Pagurus* by the possession of a prominent, bi-spined interocular lobe. Only *P. fungiformis*, new species, described in this study, has a similarly bi-spined interocular lobe. Differences between the two species are discussed under "Remarks" of the latter species.

***Pagurus fungiformis*, new species**  
(Figs. 1B, 6-9)

**Material examined.** – Holotype - male (sl 3.6 mm) (MZB Cru 1506), Bitung, Sulawesi, intertidal, 26 Jul.1996.

Paratypes - 1 female (sl 2.1 mm) (MZB), same data as for holotype; 1 male (sl 2.7 mm), 1 female (sl 1.9 mm) (CBM-ZC 5572), Tanawanako, north of Sulawesi, intertidal, 23 Dec.1997; 1 male (sl 2.5 mm) (ZRC 2002.0518), same data; 3 males (sl 1.4-1.9 mm), 3 ovigerous females (sl 2.1-2.1 mm) (MZB Cru 1507), Tial, Ambon Island, intertidal, 28 Feb.1998; 1 male (sl 2.0 mm), 2 ovigerous females (sl 2.1, 2.1 mm) (MNHN-Pg 6343), same data.

**Description.** – Eleven pairs of biserial phyllobranchiae; 2 well-developed arthrobranchs on third maxilliped. Calcified integument of carapace and thoracic appendages with small blister-like tubercles (Figs. 6A, B, H, K, 9A, C, E, G).

Shield (Fig. 6A) 1.0-1.1 times as long as broad; anterior margin between rostrum and lateral projections weakly concave; anterolateral margins sloping; posterior margin roundly truncate; rostrum broadly rounded, slightly overreaching lateral projections; lateral projections obsolete, without marginal or submarginal spine; dorsal surface with some tufts of short setae laterally; paragastric grooves conspicuous. Posterior carapace similar to that of *P. moluccensis*.

Ocular peduncles (Fig. 6A) 0.7-0.8 times as long as shield, moderately stout (about 3.5 times longer than width of cornea), slightly inflated basally; corneas not dilated; dorsal surface with row of tufts of short setae mesially. Ocular acicles (Fig. 6B) subovate, each with small marginal spine. Interocular lobe (Fig. 6B) with elongate 2 processes, each terminating acutely and reaching nearly distal margins of ocular acicles.

Antennular peduncles (Fig. 6A), when fully extended, reaching distal margins of corneas. Ultimate segment moderately stout, about 1.9 times longer than penultimate segment, increasing in depth distally, with few tufts of short setae on dorsal surfaces. Basal segment devoid of distolateral lobe; statocyst-bearing lobe unarmed.

Antennal peduncles (Fig. 6A) overreaching distal margins of corneas by 0.1-0.2 length of fifth segment. Fifth and fourth segments with few very short setae. Third segment unarmed on ventromesial distal angle, mesial face with short setae. Second segment with dorsolateral distal angle produced, not reaching midlength of fourth segment, terminating in small spine; dorsomesial distal angle unarmed; mesial margin with setae. Basal segment with small spine on lateral face; ventrodorsal margin with 3 spinules just laterad of antennal gland opening. Antennal acicle slightly overreaching distal margin of fourth segment, somewhat arcuate, terminating in small spine, with sparse moderately short setae on mesial margin. Antennal flagella moderately long, each article with very short setae on distal margin.

Mouthparts generally similar to those of *P. moluccensis* (Figs. 6C-E). Maxillule (Fig. 6C) with 1 apical bristle on distinctly produced internal lobe of endopod; external lobe of endopod rounded, basally articulated. Third maxilliped (Fig. 6F) with crista dentata on ischium (Fig. 6G) composed of row of small corneous spines increasing in size distally; 2 unequal accessory teeth on ischium; merus unarmed on dorsodistal or ventromesial margin; carpus unarmed on dorsodistal margin; exopod reaching midlength of carpus.

Right cheliped (Figs. 7A-E) appreciably larger than left. Right chela 1.6-1.7 times longer than greatest width at base of dactylus. Dactylus 0.8-0.9 times as long as palm, somewhat curved ventrally; dorsal and mesial surfaces covered with closely set, flattened, rounded tubercles (often marginally denticulate); dorsomesial margin not delimited in males (Fig. 7A), distinctly delimited by row of small spines in females (Fig. 7E); ventromesial margin delimited by row of flattened tubercles, proximal tubercles distally denticulate, distal

tubercles simple or bifid; ventral surface unarmed, with 3 rows of tufts of short setae; cutting edge with row of small calcareous teeth (blunt in males, blunt to acute in females) in proximal 0.7-0.8 and row of small corneous teeth in distal 0.2-0.3, terminating in small corneous claw. Palm slightly shorter than carpus; dorsal surface convex (degree of convexity weaker in females than in males), covered with closely set, flattened, marginally denticulate tubercles and few short setae (tubercles occasionally poorly developed in females; see Fig. 7E); in females, shallow longitudinal sulcus present adjacent to dorsomesial border (Fig. 7E); dorsolateral margin of palm proper not delimited, that of fixed finger only slightly delimited by row of small tubercles in males (Figs. 7A, C), distinctly delimited by row of small spines in females (Fig. 7E); dorsomesial margin not delimited; lateral face with scattered low, simple or denticulate tubercles; mesial face with numerous small tubercles (tubercles spaced, distally bifid or multifid); ventral surface weakly convex, with scattered low, distally denticulate tubercles and short setae. In males, cutting edge of fixed finger in males with row of blunt calcareous teeth, terminating in minute corneous claw; in females, cutting edge of fixed finger with row of blunt to acute calcareous teeth (distal teeth interspersed by short rows of small corneous teeth), terminating in small corneous claw. Carpus slightly shorter to slightly longer than merus, noticeably broadened distally in dorsal view; dorsal surface with small, bifid or denticulate tubercles laterally and mesially and few short setae, median part unarmed, dorsodistal margin with small tubercles or spines; dorsomesial margin delimited by single or double row of bifid or denticulate tubercles, dorsolateral margin not delimited; lateral face with scattered low, bifid tubercles or denticulate short ridges and few short setae, ventrolateral margin with short row of small spines distally; mesial surface flat, with small bifid or trifid tubercles and short setae adjacent to dorsomesial margin and scattered tiny tubercles, ventromesial margin with row of small, closely set spines; ventral surface weakly convex, with small to moderately large, low protuberances and short setae. Merus with low, occasionally denticulate protuberances on dorsal surface distally, dorsodistal margin unarmed, but with short setae; lateral face with scattered low, blister-like tubercles and few very short setae, ventrolateral margin with row of protuberances; mesial face only with few, short setae, ventromesial margin slightly crested, with row of small spines or denticulate tubercles; ventral surface somewhat concave, with row of low protuberances medially and scattered short setae. Ischium with tiny denticles on ventromesial margin; ventral surface with small blister-like tubercles and tufts of short setae. Coxa with blister-like tubercles or low protuberances.

Left cheliped (Figs. 8A-C) somewhat compressed laterally, reaching base to midlength of dactylus of right cheliped; propodal-carpal articulation about 15-20° from horizontal plane. Chela 2.2-2.3 times longer than wide. Dactylus about twice length of palm, slightly curved ventrally; dorsal surface with irregular double row of moderately small, distally denticulate tubercles and short setae on midline and single row of tiny tubercles mesiad of midline; dorsolateral margin not delimited; mesial face with 2 irregular rows of small, low

tubercles or protuberances and tufts of short setae; ventral surface with 2 rows of tufts of short setae; cutting edge with row of small, acute calcareous teeth in proximal half and row of small corneous teeth in distal half, terminating in large corneous claw. Palm about half length of carpus; dorsal surface (including fixed finger) strongly oblique, with numerous denticulate tubercles; dorsolateral margin not delimited; dorsomesial part somewhat elevated, with small denticulate or simple tubercles and few short setae; ventrolateral margin of fixed finger delimited by row of denticulate tubercles; ventral surface (including fixed finger) with few low, distally denticulate protuberances and tufts of short to long setae. Cutting edge of fixed finger with row of small, acute or subacute calcareous teeth in proximal 0.6 and row of small corneous teeth in distal 0.4, terminating in large corneous claw. Carpus shorter than merus, widened distally in dorsal view; dorsal surface strongly oblique, with several low, denticulate protuberances laterally, dorsodistal margin with row of spines increasing in size laterally; dorsomesial margin with row of small spines or distally denticulate tubercles decreasing in size proximally and short setae; mesial face with few low protuberances or short denticulate ridges dorsally, nearly smooth ventrally; lateral face with scattered, short denticulate ridges, ventromesial margin with row of small spines distally; ventral surface convex, with few low protuberances and tufts of setae. Merus with dorsal surface almost smooth, bearing few short setae; dorsodistal margin unarmed; lateral face with scattered blister-like tubercles, ventrolateral margin with row of small spines on distal half; mesial face with few tiny tubercles dorsally and with long setae ventrally, ventromesial margin with row of moderately small spines; ventral surface weakly concave, with few small spines and numerous tufts of long setae. Ischium with few spinules on ventromesial margin; all surfaces with sparse short setae. Coxa similar to that of right.

Second and third pereopods (Figs. 9A, C) not overreaching right cheliped, generally similar from right to left in second, greatly dissimilar in setation in third. Dactyli approximately as long as propodi, slightly curved ventrally in lateral view and nearly straight in dorsal view, terminating in large corneous claws; dorsal surfaces each with sparse row of tufts of setae (second and right third) or with row of long setae (left third); lateral faces each with few tufts of short setae (second and right third) or with numerous long setae (left third); mesial faces (Figs. 9B, D) unarmed, with rows of tufts of short setae dorsally and ventrally; no median sulcus on lateral or mesial faces; ventral margins each with 5-7 moderately small corneous spines. Propodi longer than carpi, slightly curved ventrally (second and right third) or straight (left third), dorsal surfaces unarmed, but row of tufts of short setae (second and right third) or with row of short transverse rows of long setae occasionally extending onto lateral face (left third); lateral faces with few tufts of short setae (second and right third) or with tufts of long setae dorsally and ventrodistally (left third) and occasionally with small blister-like tubercles; ventral surfaces each with 3-6 corneous spinules and few short setae (second and right third) or with row of tufts of long setae, giving brush-like structure (in left third). Carpi each with small dorsodistal spine; dorsal surfaces

each with row of tufts of setae (setae longer in left third than in other pereopods); lateral faces convex, with small blister-like tubercles and row of sparse tufts of short to moderately short setae dorsally and (setae more numerous in left third than in other pereopods); ventral surfaces each with few short setae (second and right third) or row of tufts of long setae (left third). Meri each with row of moderately long setae on dorsal and ventral margins; lateral faces with small blister-like tubercles and few tufts of short setae; ventral margins each with tufts of short to long setae, ventrolateral distal margins slightly concave, unarmed. Ischia with short setae on dorsal and ventral surfaces. Coxae with large blister-like protuberances. In females moderately large, paired gonopores present on third pereopods.

Fourth pereopods (Figs. 9E, G) semichelate, markedly unequal with left larger than right. Dactyli broad, slightly curved or nearly straight, terminating in small, curved corneous claws; dorsal margins convex, each with row of tufts of short setae; ventral margins each with row of tiny, blunt corneous teeth; rounded, naked preungual process arising from ventral margin between claw and row of corneous teeth. Propodi each with long setae on dorsal surfaces; mesial face of left divided in two sections by slightly elevated median line bordered by row of long setae in left (Fig. 9F); mesial face of right flat, with few tufts of long setae ventrally (Fig. 9H); ventral margins convex, each with rasp composed of single row of small corneous scales. Carpi and meri each with moderately long to long setae on dorsal surface (setae more numerous in left than in right); mesial faces of carpi ventrally with row of long setae in left, without long setae in right.

Fifth pereopods in males with paired gonopores partially masked by tufts of short setae (Fig. 6J).

Anterior lobe of sixth thoracic sternite (Figs. 6H, I) broadly semicircular, skewed to left; posterior lobe broader than anterior lobe. Seventh and eighth thoracic sternite similar to those of *P. moluccensis*.

Telson (Fig. 6K) with distinct transverse indentations; posterior lobes slightly unequal, separated by moderately broad, deep median cleft; terminal margins weakly convex or nearly straight, each with 5-8 spines interspersed by spinules.

**Coloration in life.** – Color in general white with black or dark brown markings (Fig. 1B). Shield with black markings centrally; posterior carapace tinged with light brown. Ocular peduncles each with dark brown band proximal to midlength and brown spot just proximal to base of cornea on ventral surface. Interocular lobe black or dark brown. Antennular peduncles generally white, ultimate and penultimate segments each with band distally; basal segment with proximal band. Palms of chelipeds entirely white or with black blotches on dorsal surfaces; carpi and meri each with irregular transverse band. Dactyli of second and third pereopods with subdistal and subproximal black bands; propodi each with distal blotch and broad subproximal black band; carpi with broad black

band and dorsodistal blotch; meri each with irregular markings on lateral face.

**Distribution.** – Known only from Sulawesi; shallow water of coral reefs.

**Habitat.** – Occupying a variety of gastropod shells.

**Etymology.** – The species is named for the Latin *fungiformis* (= mushroom-like shaped), in reference to the mushroom-like tubercles on the palms of the chelipeds.

**Variations.** – As is apparent from the description, this new species exhibits a considerable variation in the armature of the right cheliped.

**Remarks.** – As mentioned before, *P. moluccensis* and *P. fungiformis*, new species are distinctive in the genus *Pagurus* in having two-spined interocular lobe in the genus *Pagurus*. In other species of *Pagurus*, the interocular lobe is never two-spined as such, although the anterior surface of the interocular lobe is slightly convex or slightly concave (except for *P. decimbranchiae*, see above). Similarly a two-spined interocular lobe has been reported only in two species of *Anapagurus* (see Garcia-Gomez, 1994). The basally articulated external lobe on the endopod of the maxillule found in *P. moluccensis* and *P. fungiformis*, new species may be also unusual for the genus, as the external lobe is not basally articulated usually in species of *Pagurus* (personal observation). In addition, the new species and *P. moluccensis* are strikingly similar in coloration in life. Recent studies have demonstrated that the coloration in life is often very useful for discrimination of closely related or sibling species of decapod crustaceans (Knowlton & Mills, 1992). The two species demonstrate that preliminary identifications based only on color may lead to errors. In spite of the suggested close relationship, there are a number of morphological differences between *P. fungiformis*, new species, and *P. moluccensis*. In the new species, the dactyli and palms of the chelipeds are provided with closely set, flattened, often marginally denticulate tubercles, instead of widely spaced, simple or bifid tubercles in *P. moluccensis*. The dorsolateral and dorsomesial margins of the palms of the chelipeds are not delineated in the new species, while those margins are clearly delimited with a row of small spines in *P. moluccensis*. The dorsomesial margin of the carpus of the right cheliped bears a row of multifid spines or denticulate protuberances in *P. fungiformis*, new species, in contrast to having a row of large spines in *P. moluccensis*. The left cheliped has a rotation of propodal-carpal articulation greater than 15° from the horizontal plane in the new species, while the propodal-carpal articulation of the right cheliped is not rotated in *P. moluccensis*. The interocular lobe is more elongate in *P. fungiformis*, new species, than in *P. moluccensis*; further, each distal prolongation terminates acutely in *P. fungiformis*, new species, rather than bluntly in *P. moluccensis*. The left third pereopod is provided with brush-like, thick long setae mainly on the ventral surface of the dactylus and propodus in *P. fungiformis*, new species, which are absent in *P. moluccensis*.

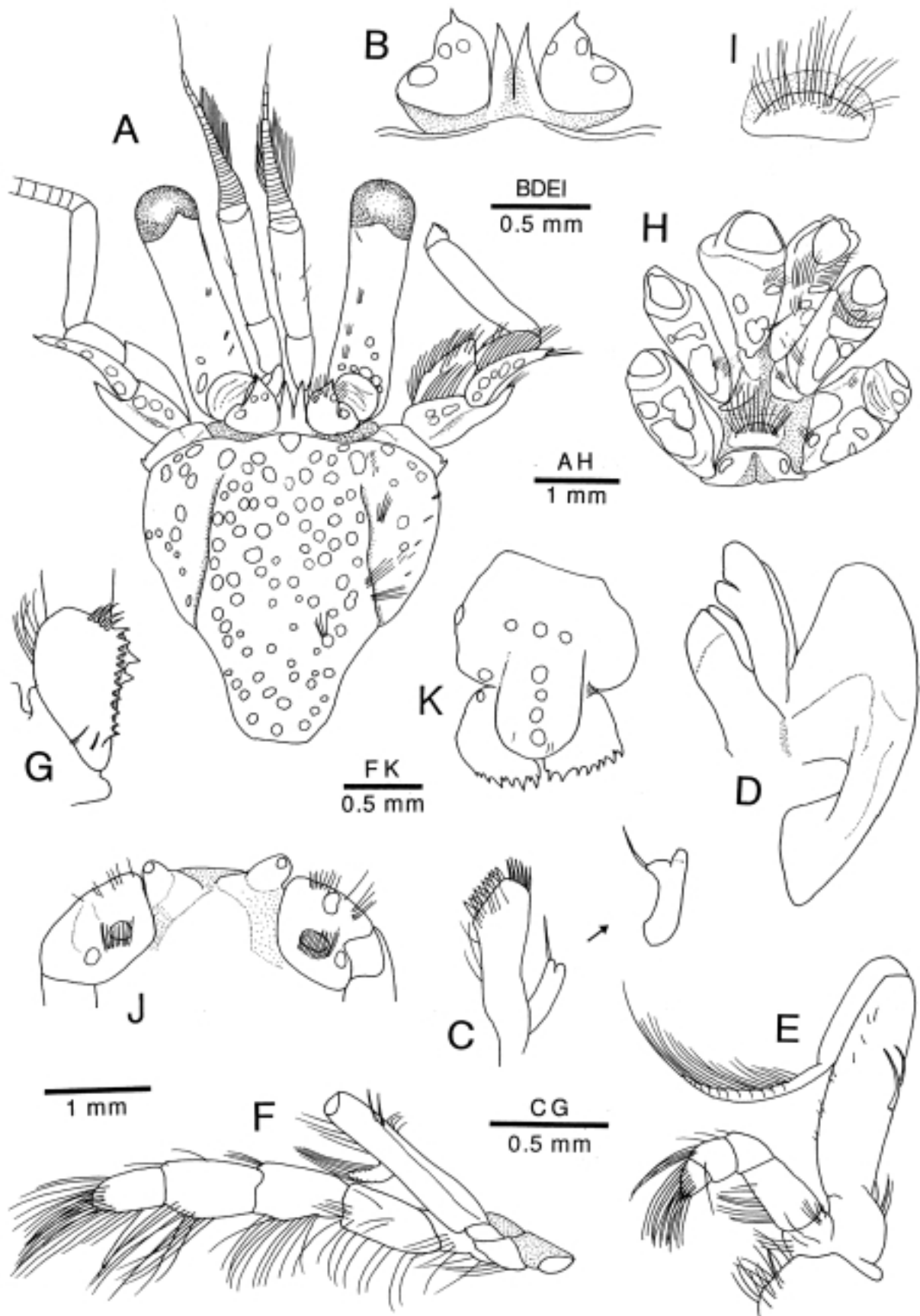


Fig. 6. *Pagurus fungiformis*, new species. Holotype male from Bitung, Sulawesi (sl 3.6 mm; MZB Cru 1506). A, shield and cephalic appendages, dorsal (setae omitted on left); B, ocular acicles and interocular lobe, dorsal; C, maxillule, ventral (coxal endite broken off); inset, endopod, lateral; D, left maxilla, ventral (setae omitted); E, left second maxilliped, ventral; F, left third maxilliped, lateral; G, ischium of left third maxilliped, dorsal; H, coxae of first to third pereopod and fifth and sixth thoracic sternites, ventral; I, anterior lobe of sixth thoracic sternite, ventral; J, coxae of fifth pereopods and eighth thoracic sternite, ventral; K, telson, dorsal.

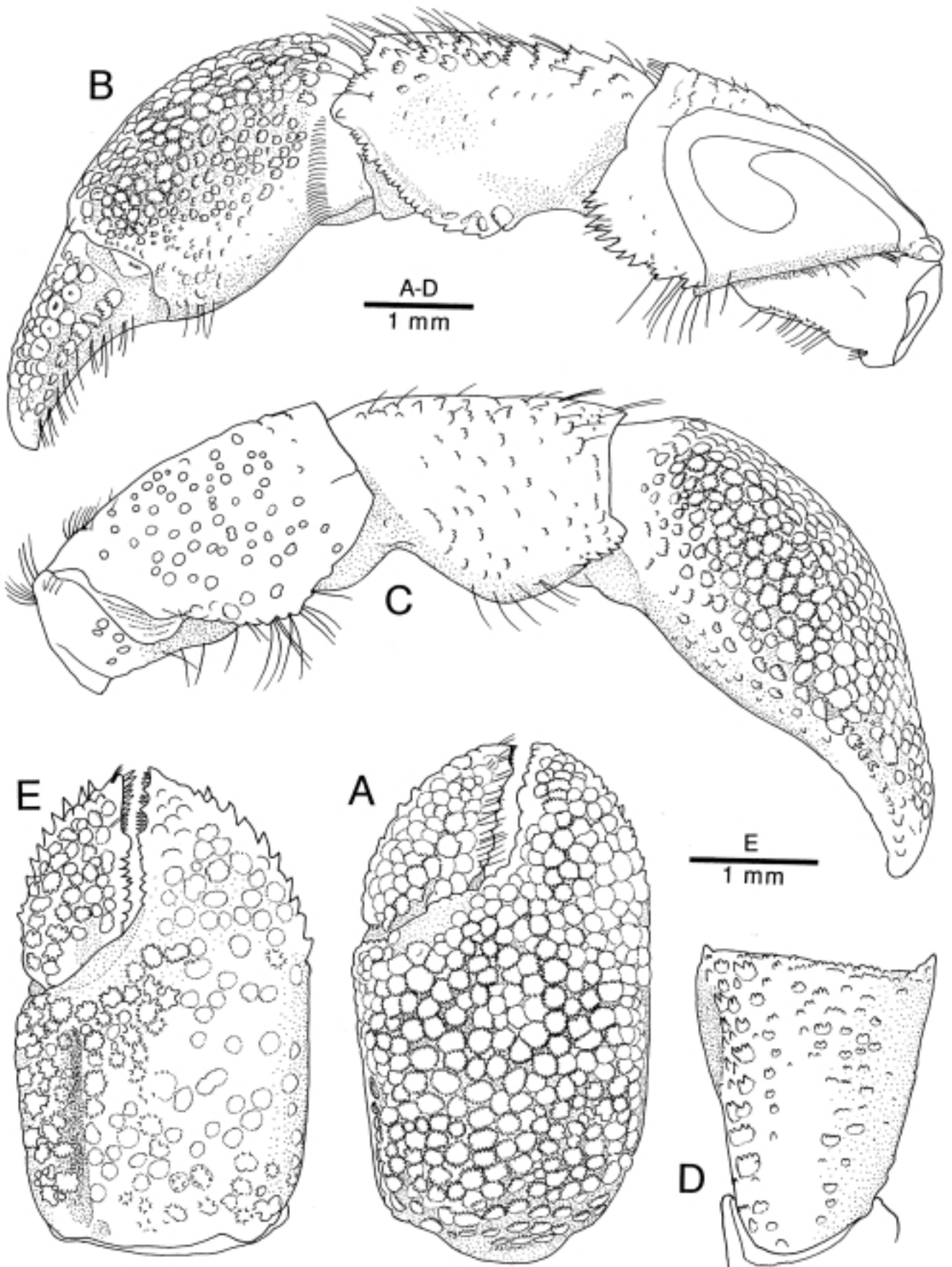


Fig. 7. *Pagurus fungiformis*, new species. A-D, holotype male from Bitung, Sulawesi (sl 3.6 mm; MZB Cru 1506); E, paratype female from same locality (sl 2.1 mm; MZB Cru 1507). Right cheliped. A, E, chela, dorsal (setae omitted); B, entire cheliped, mesial; C, same, lateral; D, carpus, dorsal.

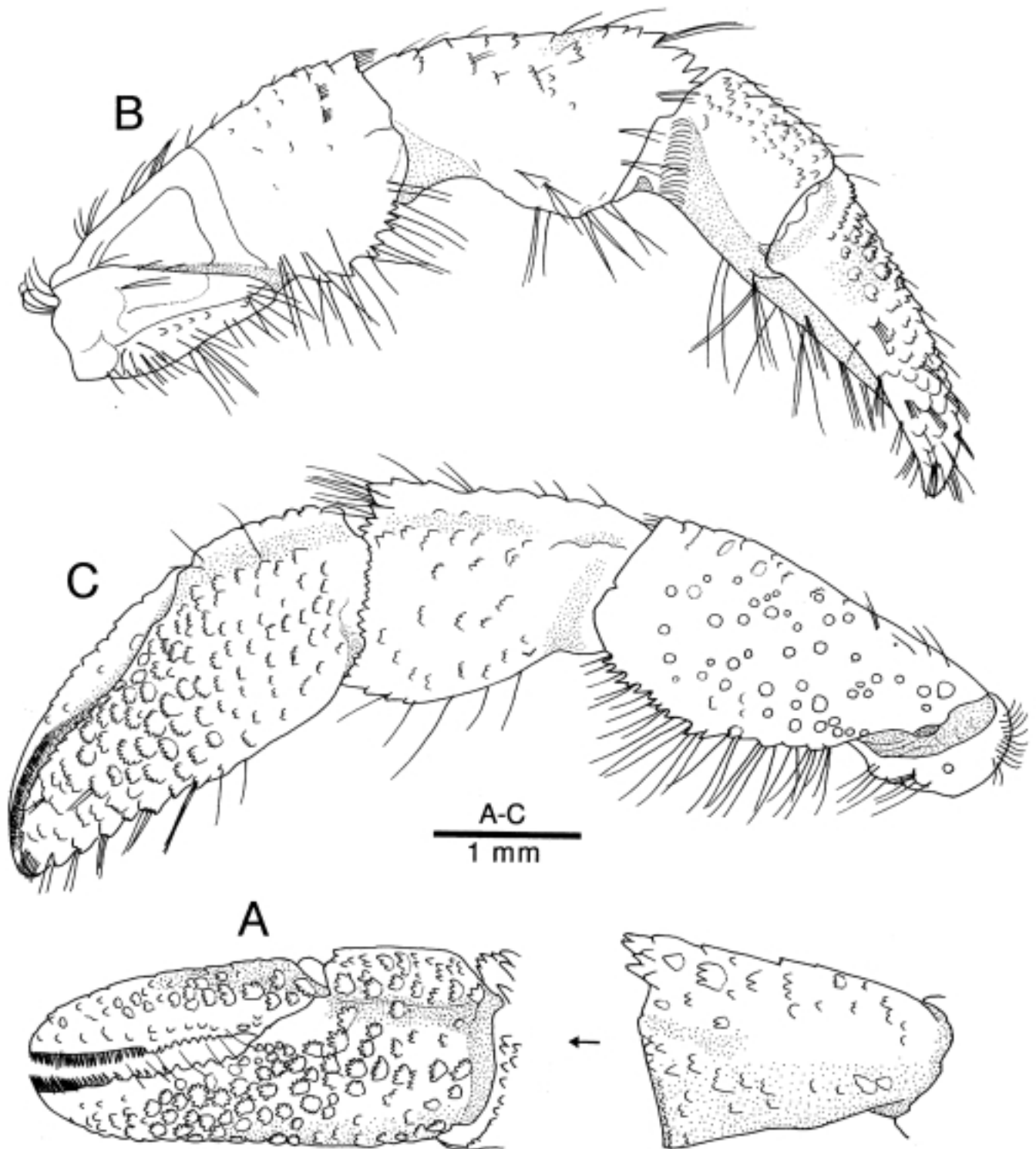


Fig. 8. *Pagurus fungiformis*, new species. Holotype male from Bitung, Sulawesi (sl 3.6 mm; MZB Cru 1506). Left cheliped. A, chela and carpus, dorsal (setae omitted); B, entire left cheliped, mesial; C, same, lateral.

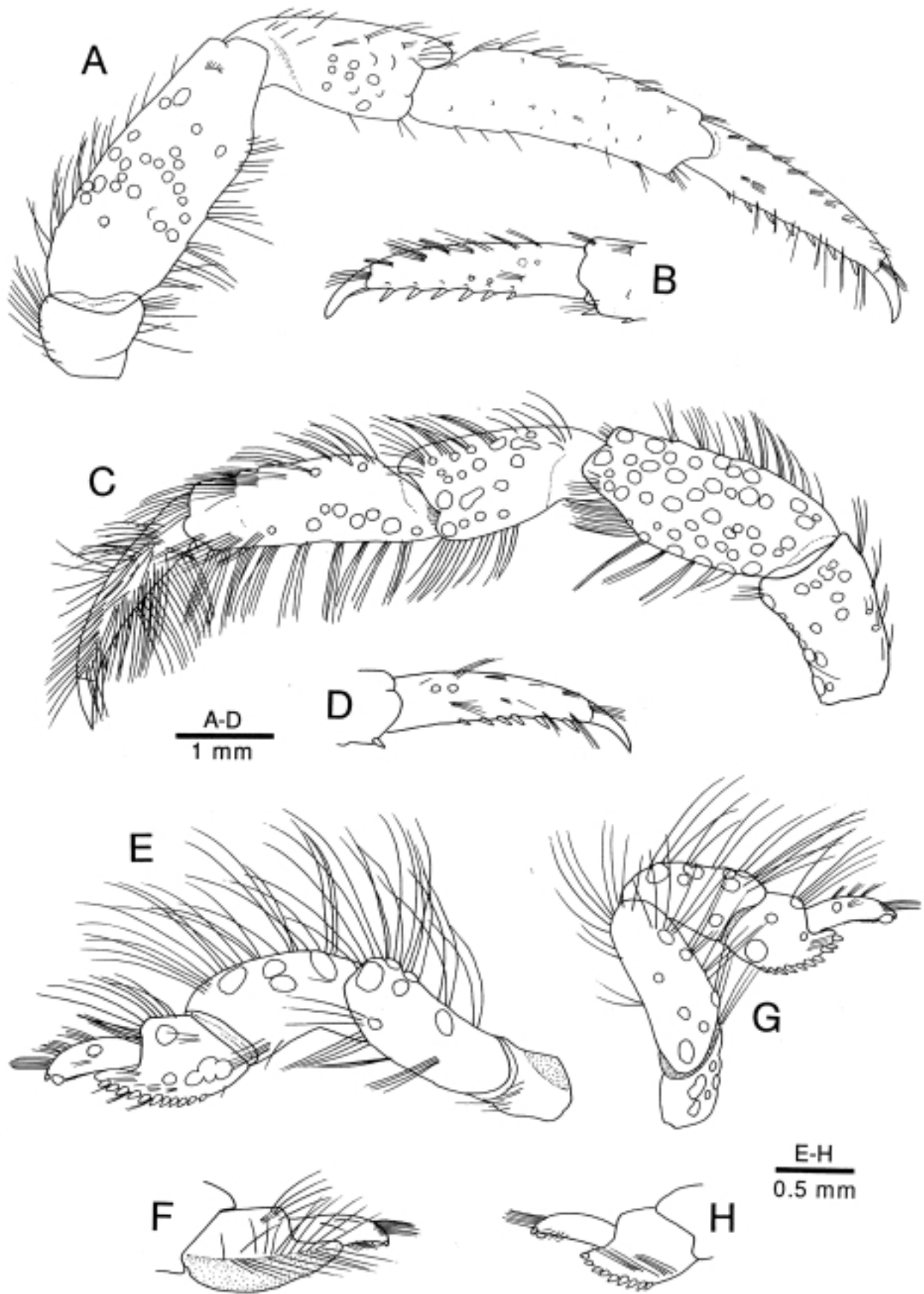


Fig. 9. *Pagurus fungiformis*, new species. A-D, holotype male sl 3.6 mm from Bitung, Sulawesi (sl 3.6 mm; MZB Cru 1506); E-H, female paratype from same locality (sl 2.1 mm; MZB Cru 1507). A, right second pereopod, lateral; B, dactylus of right second pereopod, mesial; C, left third pereopod, lateral; D, dactylus of left third pereopod, mesial; E, left fourth pereopod, lateral; F, dactylus and propodus of left fourth pereopod, medial; G, right fourth pereopod, lateral; H, dactylus and propodus of right fourth pereopod, mesial.

*Pagurus fungiformis*, new species and *P. moluccensis* are assignable to the *Pagurus anachoretus* group (cf. Forest, 1978), as they generally fit the definition of the species group (Forest & Ngoc-Ho, 1992; McLaughlin & Forest, 1999). This species group, named for its first member, *Pagurus anachoretus* (Risso, 1827) from the Mediterranean, includes *P. anachoretoides* Forest, 1966, *P. gordonae* (Forest, 1956), *P. laurentae* Forest, 1978 and *P. souriei* (Forest, 1952) from the tropical eastern Atlantic, *P. liochele* (Barnard, 1947) and *P. emmersoni* McLaughlin & Forest, 1999 from South Africa, and the Indo-West Pacific *P. kulkarnii* Sankolli, 1961, and *P. hedleyi* (Grant & McCulloch, 1906) (see Forest, 1978; Forest & Ngoc-Ho, 1992; McLaughlin & Forest, 1999). Four other species from the tropical eastern Atlantic, *P. alcocki* (Balss, 1911), *P. dartevelei* (Forest, 1952), *P. fimbriatus* Forest, 1956, and *P. triangularis* (Chevreaux & Bouvier, 1892), also fitted the definition of the *P. anachoretus* group with the exception of the cheliped form (Forest & Ngoc-Ho, 1992; McLaughlin & Forest, 1999). Komai & Osawa (2001) suggested the possible affinities among *P. decimbranchiae* Komai & Osawa, 2001, *P. boriaustraliensis* Morgan, 1990, *P. moluccensis*, *P. pitagsaleei* McLaughlin, 2002 (as *Pagurus* sp. cf. *boriaustraliensis*). McLaughlin (2002) compared *P. pitagsaleei* with *P. boriaustraliensis*, *P. hedleyi* and *P. kulkarnii*, although she did not make formal assignment of *P. pitagsaleei* and *P. boriaustraliensis* to the *P. anachoretus* group. During this study, we attempted to make a preliminary assessment of the affinities among the two species treated in this study and species of the *P. anachoretus* group. Seven species heretofore assigned to the *P. anachoretus* group and three of the four related species from the tropical eastern Atlantic have been examined during this study (see Appendix).

Although the group was well defined by the previous authors (Forest & Ngoc-Ho, 1992; McLaughlin & Forest, 1999), two supplemental characters may be added, i.e. the presence of low, blister-like tubercles on the calcified integuments of the body and pereopods and the widely separated anterolateral lobes on the eighth thoracic sternite, as the species of the *P. anachoretus* group examined here all have these characters. It is remarkable that the characters are shared also by *P. dartevelei*, *P. fimbriatus* and *P. triangularis*. The blister-like tubercles or protuberances on the calcified integuments are very low, and not easy to recognize without staining, and therefore, have been overlooked by previous authors. Specimens used by the senior author during the taxonomic studies of *Pagurus* in the northwestern Pacific (Komai, 1993, 1994a, b, 1996, 1997, 1998, 1999, 2000a, b, 2003a, b; Komai & Imafuku, 1996; Komai & Mishima, 2003; Komai & Yu, 1999) have been routinely stained with methylene blue for observation. So far, the presence of the blister-like tubercles or protuberances is known only in species formally assigned to the *P. anachoretus* group and allied species.

Observations have been made also for other characters not fully mentioned by previous authors, such as the development of the paragastric grooves on the shield and the structure of the fourth pereopods. These characters were used by Komai & Osawa (2001) in suggesting the affinities among *P.*

*moluccensis*, *P. decimbranchiae*, *P. boriaustraliensis* and *P. pitagsaleei*. It has been found that the two characters vary interspecifically among the species examined. It is interesting to note that the paragastric grooves on the shield are inconspicuous in the eight Eastern Atlantic species, but conspicuous in the two Indo-West Pacific species, *P. hedleyi* and *P. kulkarnii*. The degree of asymmetry of the fourth pereopods has been found to be variable among the 10 species of the *P. anachoretus* group personally examined during this study. In *P. anachoretus*, *P. dartevelei* and *P. triangularis*, the fourth pereopods are entirely similar between right and left, although either only male or only female specimen(s) have been available for these three species. In *P. anachoretoides*, *P. fimbriatus* and *P. souriei*, the asymmetry of the fourth pereopods appears variable between male and female; in males, the fourth pereopods are similar, but in females, the left pereopod is slightly to somewhat longer than the right and the mesial face of the left propodus bears a median row of long setae. In *P. gordonae*, *P. hedleyi*, *P. kulkarnii* and *P. laurentae*, the asymmetry of the fourth pereopods is most obvious, occurring in both sexes, as in *P. moluccensis* and *P. fungiformis*, new species. These two characters seem to be useful in assessing the relationships among species in the *P. anachoretus* group.

Our comparison supports the assumption that *P. moluccensis*, *P. fungiformis*, new species, the species heretofore assigned to *P. anachoretus* group, *P. dartevelei*, *P. fimbriatus* and *P. triangularis* form a homogenous assemblage within heterogeneous *Pagurus*. Furthermore, it is suggested that *P. moluccensis* and the new species are closely related to *P. hedleyi* and *P. kulkarnii*. These four species share the following set of characters: the conspicuous paragastric grooves on the shield; the markedly unequal fourth pereopods in both male and female; the more or less rounded dorsal surface of the palm of the right chela with more or less convex, symmetrical mesial and lateral margins.

It is interesting to note that *P. decimbranchiae* also fits generally with the definition of *P. anachoretus* group and even has the set of the characters shared by *P. moluccensis*, *P. fungiformis*, new species, *P. hedleyi* and *P. kulkarnii*. The distinctly bilobed interocular lobe of *P. decimbranchiae* is also indicative the close relationship of the species to *P. moluccensis* and *P. fungiformis*. The characteristic of *P. decimbranchiae* is the greatly reduced arthrobranch above the third maxilliped represented only by a single rudimentary bud. However, it can be assumed that this character is presumably autapomorphic for the species, although the number of the gills has been used as a generic character in the paguroid systematics (e.g. McLaughlin, 1997). Therefore, we formally assign *P. decimbranchiae* to the *P. anachoretus* group.

McLaughlin & Forest (1999) suggested that the strong wing-like projection of the ventromesial margin of the carpus and merus of the right cheliped, especially well-developed in the large males, is one of the characteristics of the *anachoretus* group. However, they clearly mentioned in the original description of *P. emmersoni* that the ventromesial margins



of the carpus and merus of the right cheliped are not produced into wing-like projections in that species. Furthermore, no development of the wing-like projection on the right cheliped is seen in *P. anachoretoides*, *P. anachoretus*, *P. gordonae*, *P. laurentae* and *P. souriei*, as well as *P. moluccensis*, *P. fungiformis*, new species, and *P. decimbranchiae*. Therefore, this character is not useful for defining the *P. anachoretus* group.

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## APPENDIX

### LIST OF COMPARATIVE MATERIAL

- Pagurus anachoretoides* Forest, 1966** - 1 male (holotype, sl 4.1 mm) (MNHN-Pg 64), San Tome, Gulf of Guinea, 0-6 m, RV *Calypso*, stn 68, 18 Jun.1956; 1 female (paratype, 4.1 mm) (MNHN-Pg 65), San Tome, 3-8 m, RV *Calypso*, stn 75, 21 Jun.1956.
- Pagurus anachoretus* (Risso, 1827)** - 2 males (sl 3.5, 5.8 mm), 2 ovig (sl 4.4, 5.5 mm) (MNHN-Pg 71), Ibiza, Barbaric Islands, Mediterranean, 5-7 m, station SA 26, 11 Aug.1953.
- Pagurus dartevellei* (Forest, 1952)** - 2 females (sl 4.8, 5.9 mm) (MNHN-Pg 4697), Point Noire, Congo, coll. A. Crosnier, 29 Jan.1967.
- Pagurus fimbriatus* Forest, 1966** - 1 male (holotype, sl 4.7 mm) (MNHN-Pg 3974), San Tome, Gulf of Guinea, stn T27, 16 Jun.1956.
- Pagurus gordonae* (Forest, 1956)** - 1 male (sl 4.1 mm), 2 ovig. (sl 2.9, 3.7 mm) (MNHN-Na), locality not indicated, 1 Mar.1953.
- Pagurus hedleyi* (Grant & McCulloch, 1906)** - 2 males (sl 4.7, 4.8 mm) (MNHN-Pg 2297), Hong Kong, 1983.
- Pagurus kulkarnii* Sankolli, 1961** - 3 males (sl 2.9-3.5 mm), 1 female (sl 2.9 mm) (MNHN-Pg 5101), Bai dua, Viet Nam, intertidal, coll. D. Ngoc-Dung & T. Phi Hung, 8 May.1993.
- Pagurus laurentae* Forest, 1978** - 3 males (sl 2.4-3.4 mm), 2 females (sl 2.5, 2.8 mm) (paratypes, MNHN-Pg 5524), Bight of Benin, Nigeria, 04°07'N, 05°40'E, RV *Pillsbury*, stn 248, 13 May.1965.
- Pagurus souriei* (Forest, 1952)** - 1 female (sl 3.1 mm) (MNHN-Na 4823), Goree Bay, Gulf of Guinea, 15-20 m, coll. J. M. Manchad, Jan.1955; 4 males (sl 2.2-4.3 mm) (MNHN-Pg 4851), Dakar, Senegal, Gulf of Guinea, 23 m, 13 Jan.1955.
- Pagurus triangularis* (Chevreaux & Bouvier, 1892)** - 1 male (sl 4.3 mm) (MNHN-Pg 5118), data not indicated; 1 male (sl 4.4 mm) (MNHN-Pg 5119), locality not indicated, 15 Nov.1992.