

A New Genus and New Species of Paguridae (Crustacea: Decapoda: Anomura) from the Bohol Sea, the Philippines

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A new genus and new species of the hermit crab family Paguridae is described and illustrated on the basis of three specimens collected from off Balicasag Island, Bohol Sea, the Philippines. The new genus, *Pliopagurus*, is referred to the “*Pylopagurus-Tomopagurus*” group on account of its having 11 pairs of biserial gills and paired first pleopods in females, and appears closest to *Lophopagurus* McLaughlin, 1981. The possession of short sexual tubes on both coxae of the fifth pereopods in the male and the lack of a median crest or dorsolateral keel of the left chela distinguish *Pliopagurus* from *Lophopagurus*. An emended key to the genera of the “*Pylopagurus-Tomopagurus*” group is presented.

Key Words: *Pliopagurus curvimanus*, *Pylopagurus-Tomopagurus* group, *Lophopagurus*, new genus, Philippines.

Introduction

The marine fauna around Panglao Island in the Bohol Sea, the Philippines, was extensively sampled during expeditions conducted jointly by scientists from the Muséum national d’Histoire naturelle, Paris, National Taiwan Ocean University, the Raffles Museum of Biodiversity Research, National University of Singapore (ZRC), University of San Carlos, Cebu, and the National Museum of the Philippines, Manila (NM), in 2004 and 2005 (PANGLAO 2004 and 2005 Expeditions). Studies of this material have revealed a wealth of hermit crab fauna in local waters (McLaughlin and Rahayu 2005, 2007; McLaughlin 2008; McLaughlin and Lemaitre 2009; Rahayu and Forest 2009; Asakura 2010; Komai and Rahayu 2013a, 2013b; Rahayu and Komai, in press), although a large part of the collection remains unstudied. The present paper serves to describe a new genus and new species of the Paguridae, referred to the “*Pylopagurus-Tomopagurus*” group of genera (cf. McLaughlin 1981a, 1981b, 1982; McLaughlin and Gunn 1994; Lemaitre and McLaughlin 1996, 2003a; McLaughlin and Lemaitre 2001). The new monotypic genus, *Pliopagurus* (type species *P. curvimanus* sp. nov.), appears closest to *Lophopagurus* McLaughlin, 1981, currently represented by 14 species (McLaughlin *et al.* 2010). Differentiating characters between the two genera are discussed.

Material examined in this study is deposited in NM, ZRC, and the Natural History Museum and Institute, Chiba (CBM). General terminology follows McLaughlin *et al.* (2007), except for numbering of thoracomeres. Shield length (sl, in mm), measured from the tip of the rostrum to the midpoint of the posterior margin of the shield, indicates specimen size. Other abbreviations are: coll., collected by; stn, station.

Family Paguridae *Pliopagurus* gen. nov.

Type species. *Pliopagurus curvimanus* sp. nov. by present designation.

Diagnosis. Gills biserial, 11 pairs. Shield with lateral projections moderately separated from rostrum. Ocular acicles triangular, without submarginal spine; separated basally by more than basal width of 1 acicle. Maxillule with external lobe of endopod well-developed, never recurved, internal lobe with 2 bristle-like setae. Maxilla with posterior lobe of scaphognathite moderately broad. First maxilliped with slender endopod. Third maxilliped with well-developed crista dentata and prominent accessory tooth on ischium; merus and merus unarmed on dorsodistal margin. Right cheliped markedly longer larger than left; chela suboperculiform, with dorsomesial margin delimited by row of small spines; angle of articulation of chela and carpus about 30°. Left cheliped with chela not particularly compressed dorsoventrally, fingers not particularly excavated ventrally; angle of articulation of chela and carpus about 45°. Ambulatory legs with dorsodistal spine on each carpus. Fourth pereopods with well-developed dactyli, without preungual process; propodal rasp consisting of single row of corneous scales. Third thoracic sternite with trace of median notch, unarmed; sixth thoracic sternite with subtrapezoidal anterior lobe; no capsulate setae on posterior sternites. Males with coxae of fifth pereopods symmetrical, each having very short, strongly tapering sexual tube; 3 (third to fifth) unpaired, unequally biramous left pleopods. Females with paired gonopores on coxae of third pereopods; pleon with paired first pleopods incompletely 2-segmented and modified as gonopods, and with 4 unpaired (second to fifth) left pleopods, second to fourth with both rami well-developed,

fifth with endopod reduced. Pleon dextrally twisted. Uropods strongly asymmetrical; protopods not strongly produced posteriorly. Telson with faint or shallow lateral indentations; posterior lobes slightly asymmetrical, terminal margins strongly oblique, each with row of minute spinules; posterolateral margins without corneous or calcareous plate.

Remarks. In her initial revision of the “*Pylopagurus-Tomopagurus*” group, McLaughlin (1981a) subdivided *Pylopagurus* A. Milne-Edwards and Bouvier, 1891 into 11 genera [*Agaricochirus* McLaughlin, 1981, *Anisopagurus* McLaughlin, 1981, *Australeremus* McLaughlin, 1981, *Enallopaguropsis* McLaughlin, 1981, *Enallopagurus* McLaughlin, 1981, *Haigia* McLaughlin, 1981 (renamed *Haigiopagurus* McLaughlin, 2005 because of homonymy; see McLaughlin 2005), *Lophopagurus* McLaughlin, 1981, *Manucomplanus* McLaughlin, 1981, *Phimochirus* McLaughlin, 1981, *Pylopagurus sensu stricto*, and *Rhodochirus* McLaughlin, 1981] and rediagnosed *Tomopagurus* to include species in which female first pleopods might not develop. Lemaitre and McLaughlin (1996) subsequently described a new genus, *Protomopagurus* Lemaitre and McLaughlin, 1996, and added it to the “*Pylopagurus-Tomopagurus*” group. De Saint Laurent and McLaughlin (2000) reduced *Australeremus* to a subgenus of *Lophopagurus*, because they considered that *Eupagurus kirkii* Filhol, 1883 links morphological extremes in the two generic taxa. McLaughlin and Lemaitre (2001) rediagnosed *Pylopagurus* and further described and added one new genus, *Pylopaguridium* McLaughlin and Lemaitre, 2001, to the “*Pylopagurus-Tomopagurus*” group. Prior to McLaughlin and Lemaitre (2001), the development of any form of male secondary sexual characters (e.g., the development of sexual tubes) had not been recognized in this group of genera, but McLaughlin and Lemaitre (2001) found that two species of *Pylopagurus* [*P. discoidalis* (A. Milne-Edwards, 1880) and *P. macgeorgei* McLaughlin and Lemaitre, 2001] could have short sexual tube(s) on one or both gonopores of the coxae of the fifth pereopods in males. Lemaitre and McLaughlin (2003a) further noticed that species of *Agaricochirus*, *Enallopaguropsis*, and *Enallopagurus* could occasionally have vasa deferentia produced to form short, tubular papillae.

The present new species is linked to the 13 genera of the “*Pylopagurus-Tomopagurus*” group by the possession of 11 pairs of biserial gills and the presence of paired first female pleopods modified as gonopods. In the general morphology of the shield and chelipeds, *Pliopagurus* gen. nov. appears closest to *Lophopagurus*, but the structure of the left chela of the new genus is characteristic in the lack of a median elevation on the dorsal surface and in having a rounded dorsolateral or lateral surface. In all known species currently assigned to *Lophopagurus*, the left chela has a dorsomedian crest and/or a keeled and spinose lateral margin (McLaughlin and Gunn 1994; de Saint Laurent and McLaughlin 2000). Furthermore, the smooth dorsal surface of the right chela and the presence of “very short” [following the protocol proposed by McLaughlin (2003)] but prominent, abruptly tapering sexual tubes on the coxae of the fifth pereopods in males distinguish the new genus from *Lophopagurus*. There are no species of *Lophopagurus* with sexual tubes or protrusions

of the vasa deferentia. The dorsal surface of the right chela is usually armed with numerous spines or tubercles in species assigned to *Lophopagurus*.

Following the key of genera of the “*Pylopagurus-Tomopagurus*” group by Lemaitre and McLaughlin (2003a), the present new genus is placed close to *Tomopagurus* and *Haigiopagurus* (as *Haigia*). Nevertheless, species of *Tomopagurus* all have a non-suboperculiform, strongly spinose or tuberculate right chela and a spinose or tuberculate left chela, with fingers ventrally forming a spoon-like excavation when closed (McLaughlin 1981a; Lemaitre and McLaughlin 2003a). In contrast, in *Pliopagurus* gen. nov., the right chela is suboperculiform, the dorsal surfaces of both chelae are almost unarmed except for spines or tubercles on the dorsolateral and/or dorsomesial margins, and the fingers of the left chela are not distinctly excavated ventrally, thus not forming a spoon-like structure. As for *Haigiopagurus*, the lateral margin of the left chela is noticeably expanded into a keel that bears a row of strong spines (McLaughlin and Lemaitre 2001). Finally, in *Haigiopagurus*, development of sexual tubes in males is not seen and both chelae have numerous tufts of short stiff setae (McLaughlin and Lemaitre 2001).

Without examination of the female, the present new species might be easily misidentified as a species of *Anapagrades* de Saint Laurent-Dechancé, 1966. In particular, superficial similarity between *Pliopagurus curvimanus* sp. nov. and *A. aequalis* Komai, 1999 is substantial in the general shape and armature of the right cheliped and the possession of very short sexual tubes on both coxae of the fifth pereopods in males, although the new species is readily distinguished from the latter by the lack of a dorsomedian crest on the palm of the left cheliped (cf. Komai 1999).

Other genera characterized by the combination of the possession of 11 pairs of biserial gills, the presence of paired first pleopods in females, and the development of male sexual tube(s) include *Cycetopagurus* McLaughlin, 2004 and *Nematopagurus* A. Milne-Edwards and Bouvier, 1892. These two genera are primarily differentiated from *Pliopagurus* gen. nov. by the possession of a long right sexual tube with a filiform distal part and subequal chelipeds (cf. McLaughlin 2004a, 2004b). *Goreopagurus* McLaughlin, 1988 was also originally diagnosed by the same combination of characters, but the subsequent discovery of *G. poorei* Lemaitre and McLaughlin, 2003, which is characterized by 11 pairs of distally quadriserial gills and the lack of male sexual tubes, led Lemaitre and McLaughlin (2003b) to emend the diagnosis of the genus. *Goreopagurus* is easily distinguished from the present new genus by an unusual, sexually dimorphic expansion of the carpus of the right cheliped (Lemaitre and McLaughlin 2003b).

Etymology. From the Greek prefix “*plio-*”, derived from *pleion* (=more), and the generic name *Pagurus*, alluding to the discovery of one additional new genus closely related to the “*Pylopagurus-Tomopagurus*” group of McLaughlin (1981a).

Pliopagurus curvimanus sp. nov.

Figs 1–5

Material examined. Holotype: PANGLAO 2004, stn L42, Balicasag Island, Bohol Sea, 09°31.2'N, 123°40.7'E, 80–90 m, 2 July 2004, male (sl 2.5 mm), NMCR 39083.

Paratypes: same data as holotype, 1 ovigerous female (sl 1.3 mm), ZRC 2013.0578; same data as holotype, 1 ovigerous female (sl 1.5 mm), CBM-ZC 11571.

Description. Shield (Fig. 1A) about 1.1 times as long as wide; anterior margin between rostrum and lateral projections concave; dorsal surface with some tufts of short setae laterally, paragastric grooves delimited only on posterior parts; anterolateral margins sloping. Rostrum broadly triangular, subacutely pointed, extending beyond lateral projections. Lateral projections broadly rounded, moderately separated from rostrum, each with 1 submarginal spinule.

Ocular peduncles (Fig. 1A) about 0.8 times as long as shield, moderately slender, faintly constricted at mid-length, each with longitudinal row of tufts of short setae on dorsal surface; cornea slightly dilated; basal width of peduncle subequal to corneal width. Ocular acicles narrowly triangular, separated basally by about basal width of 1 acicle, each with acutely or subacutely pointed tip, without submarginal spine distally; distal part of ocular acicle nearly flat on dorsal surface. Interocular lobe clearly visible.

Antennular peduncles (Fig. 1A) slightly overreaching distal corneal margins. Ultimate segment with single short seta near dorsolateral distal angle, dorsal surface with few additional short setae. Basal segment with moderately inflated statocyst lobe bearing small lateral spine; ventrodiscal angle slightly produced.

Antennal peduncles (Fig. 1A) slightly overreaching distal corneal margins. Fifth segment with row of short, stiff setae on mesial margin. Fourth segment with some short, stiff setae. Third segment with tiny spine at ventromesial distal angle, although this spine not visible in dorsal view. Second segment with dorsolateral distal angle produced into strong spine not reaching midlength of fourth segment, mesial margin without additional spinules; dorsomesial distal angle with tiny spine. First segment unarmed on lateral surface; ventrodiscal margin strongly produced, with minute terminal spine. Antennal acicle slightly arcuate, reaching distal corneal margin, terminating in tiny spine, with row of short setae dorsomesially (right antennal acicle of holotype abnormally short, only reaching corneal base). Antennal flagellum about 5 times as long as shield, overreaching extended right cheliped; each article with 1–3 short setae, with 1 additional mesial long setae every 2 articles.

Mandible without distinguishing characters. Maxillule (Fig. 2A) with proximal endite subquadrate; distal endite slightly widened distally, mesial margin truncate; endopod with obsolete inner lobe bearing 2 bristle-like setae and slender, non-recurved outer lobe. Maxilla (Fig. 2B) with anterior lobe of scaphognathite not reaching level of distal margin of distal endite. First maxilliped (Fig. 2C) with exopod moderately expanded proximolaterally. Second maxilliped (Fig. 2D) with endopod relatively short; exopod long.

Third maxilliped (Fig. 1B) moderately stout. Ischium (Fig. 1C) bearing well-developed crista dentata consisting of row of small corneous teeth increasing in size proximally and 1 accessory tooth. Merus and carpus unarmed. Exopod overreaching distal margin of ischium.

Chelipeds appreciably unequal and dissimilar. Right cheliped (Fig. 3A–D) thick, suboperculariform; angle of articulation of chela and carpus about 30°. Dactylus distinctly shorter than palm, strongly curved ventrally; dorsal surface with distinct median ridge accompanied by shallow sulcus mesially, otherwise almost smooth; dorsomesial margin carinate, with row of small blunt denticles decreasing in size distally; mesial surface with broad, shallow sulcus medially, flanked by rows of short setae; cutting edge with row of rounded calcareous teeth, terminating in small corneous claw. Palm slightly widened distally, slightly longer than carpus; dorsal surface gently convex, unarmed, with sparse single setae or tufts of short setae; dorsolateral margin with tuberculate carina extending to midlength of fixed finger but not to proximal margin of palm; dorsomesial margin slightly elevated, with single row of small spines or tubercles proximally decreasing in size and acuteness and with row of moderately long stiff setae, dorsomesial distal angle slightly produced; lateral surface almost glabrous, slightly rugose with scattered short, oblique ridges; mesial surface nearly flat, with scattered granules and sparse setae, and with low, oblique ridge proximovertrally; ventral surface almost glabrous, with shallow concavity at base of fixed finger. Fixed finger with large, subtriangular tooth on median part of cutting edge, terminating in small corneous claw. Carpus subequal in length to merus, distinctly widened distally; dorsomesial margin with row of long setae and small spines at least in distal half; dorsal midline slightly elevated, with 4–6 tiny to moderately small spines and 2 irregular rows of long setae; dorsolateral surface sloping, almost glabrous; mesial surface shallowly depressed distally, with long setae dorsally and ventrally; ventral surface strongly convex, with scattered short to long setae. Merus unarmed on dorsodistal margin; dorsal surface also unarmed, with moderately long setae in distal half; lateral surface glabrous, distal half of ventrolateral margin slightly concave and with row of some tiny spines; mesial surface also almost glabrous, distal half of ventromesial margin with row of small spines; ventral surface convex in proximal half, with numerous long setae, distal half forming concavity accommodating proximal part of carpus when entire cheliped flexed. Ischium unarmed, with short setae dorsally and ventrally.

Left cheliped (Fig. 4A–D) with chela curving laterally and ventrally, like a bird beak in general shape, subequal in length to carpus and merus combined; angle of articulation of chela and carpus about 45°. Dactylus about twice as long as palm, surfaces unarmed, bearing scattered long setae; dorsal surface with shallow median sulcus extending beyond midlength; cutting edge with row of closely-set corneous teeth (several teeth partially fused), terminating in small corneous claw. Palm short, about half length of carpus; dorsomesial margin with row of 4 or 5 small spines; dorsal surface sloping to lateral surface, with row of long setae

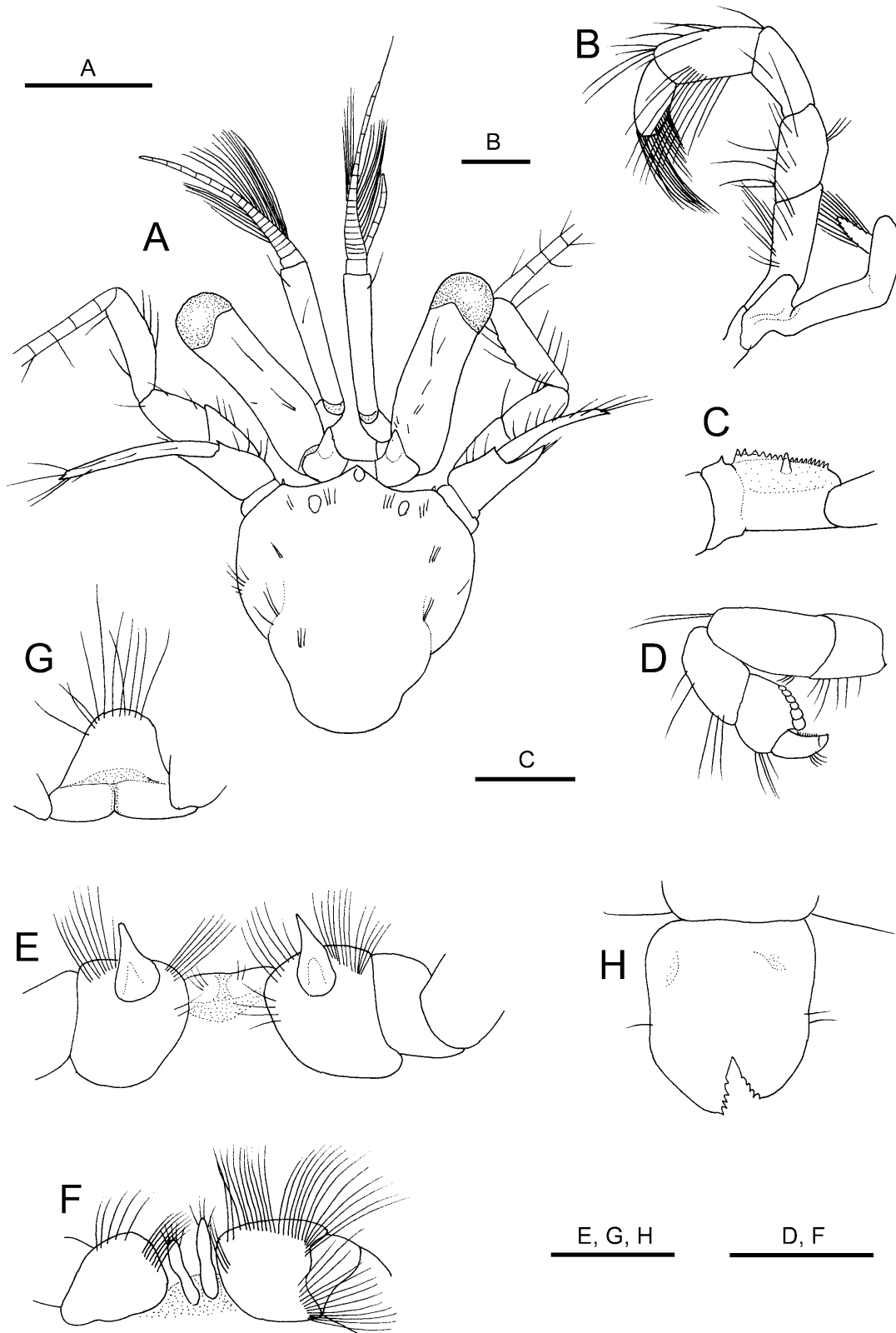


Fig. 1. *Pliopagurus curvimanus* gen. nov., sp. nov. A–C, E, G, H, holotype, male (sl 2.5 mm), PANGLAO 2004, stn L42, NMCR 39083; D, paratype, ovigerous female (sl 1.3 mm), same station, ZRC 39083; F, paratype, ovigerous female (sl 1.5 mm), same station, CBM-ZC 11571. A, shield and cephalic appendages, dorsal view; B, left third maxilliped, lateral view; C, same, ischium and basis, ventral view; D, left fourth pereopod, lateral view; E, coxae of fifth pereopods and eighth thoracic sternite, ventral view; F, coxae of fifth pereopods and first pleopods, ventral view; G, sixth thoracic sternite, ventral view; H, telson, dorsal view. Scale bars: 1 mm for A; 0.5 mm for B–H.

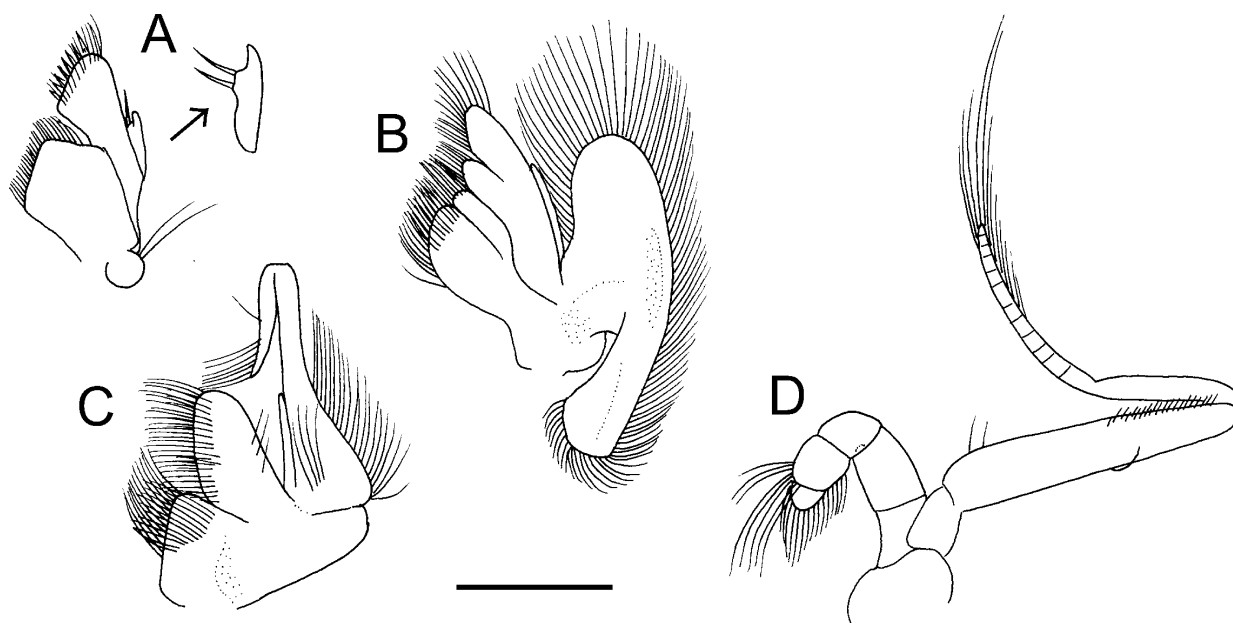


Fig. 2. *Pliopagurus curvimanus* gen. nov., sp. nov., holotype, male (sl 2.5 mm), PANGLAO 2004, stn L42, NMCR 39083, left mouthparts. A, maxillule, ventral view; inset, endopod, lateral view; B, maxilla, ventral view; C, first maxilliped, ventral view; D, second maxilliped, ventral view. Scale bar: 0.5 mm.

on midline; lateral and mesial faces with sparse short setae; ventral surface slightly convex, with few short setae; fixed finger with scattered tufts of long setae, cutting edge with row of small corneous teeth, terminating in small corneous claw. Carpus subequal in length to merus; dorsolateral margin with row of 3 or 4 spines (dorsodistal spine strong, other 2 spines small) in distal half, dorsomesial margin with row of 4 or 5 spines decreasing in size proximally, each margin also bearing row of long, stiff setae; dorsodistal margin with 1 additional minute spine laterally; lateral surface with short to long setae dorsally, otherwise glabrous, ventrolateral distal angle with minute spine; mesial surface smooth, with long setae dorsally and ventrally; ventral surface convex, with several long setae. Merus unarmed on dorsodistal margin; dorsal surface with row of short setae; lateral surface nearly glabrous, generally convex ventrolateral margin with row of prominent spines in distal half; mesial surface also smooth, with few setae dorsally and ventrally, ventromesial margin with row of tiny spines or tubercles in distal two-thirds; ventral surface with numerous setae. Ischium unarmed, with short setae dorsally and ventrally.

Ambulatory legs (Fig. 5A, D) generally similar on right and left. Dactyli slightly curved ventrally in lateral view, nearly straight in dorsal view, 1.5–1.6 times as long as propodi; dorsal margins each with row of sparse tufts of moderately long setae decreasing in length distally; lateral and mesial surfaces without sulcus or groove, mesial surfaces each with 2 min corneous spinules adjacent to dorsal margin in distal half (second; Fig. 5B) or double row of 6 or 7 min corneous spinules adjacent to dorsal margin (third; Fig. 5D); ventral margins each with row of 8–11 slender corneous spines. Propodi with numerous tufts of long setae on dorsal margins and fewer tufts of long setae on ventral margins; lateral and mesial faces with few tufts of short setae ventrally; ventrodistal margins each with 1 slender corneous

spine. Carpi each with tiny dorsodistal spine; dorsal surfaces each with row of long setae; ventral surfaces with few short and long setae (second) or almost glabrous (third). Meri with tufts of moderately long setae on dorsal margins; lateral and mesial faces smooth, bearing row of short or very short setae ventrally; ventral margins each with tufts of long setae (second) or few short to long setae (third), ventrolateral distal margin slightly concave and armed with tiny subterminal spine (second) or straight and unarmed (third). Ischia about half length of meri (second) or subequal in length to it (third). Female with paired gonopores on coxae of third pereopods.

Fourth pereopods (Fig. 1D) semichelate. Dactyli each with row of minute corneous teeth on ventral margins; no preungual process. Propodi with rasp consisting of single row of corneous scales.

Coxae of fifth pereopods in male (Fig. 1E) symmetrical, bearing tufts of moderately short setae at anterolateral and anteromesial angles, each with very short, abruptly tapering sexual tube directed anteroventrally. Coxae of female fifth pereopods (Fig. 1F) unequal with left larger, right with tufts of setae at anterolateral and anteromesial angles, left with numerous longer setae extending from anterior margin to posterolateral angle.

Third thoracic sternite unarmed on anterior margin. Sixth thoracic sternite (Fig. 1G) with anterior lobe subtrapezoidal; anterior margin rounded, with several long setae. Eighth thoracic sternite (Fig. 1E) slightly bilobed, with few short setae.

Pleon dextrally twisted. Male with 3 (third to fifth) unpaired left pleopods, decreasing in size posteriorly, third unequally biramous, fourth and fifth uniramous. Female with paired first pleopods modified as gonopods, each indistinctly bi-articulated (Fig. 1F); unpaired, left second to fifth pleopods present, second and third subequally biramous, fourth

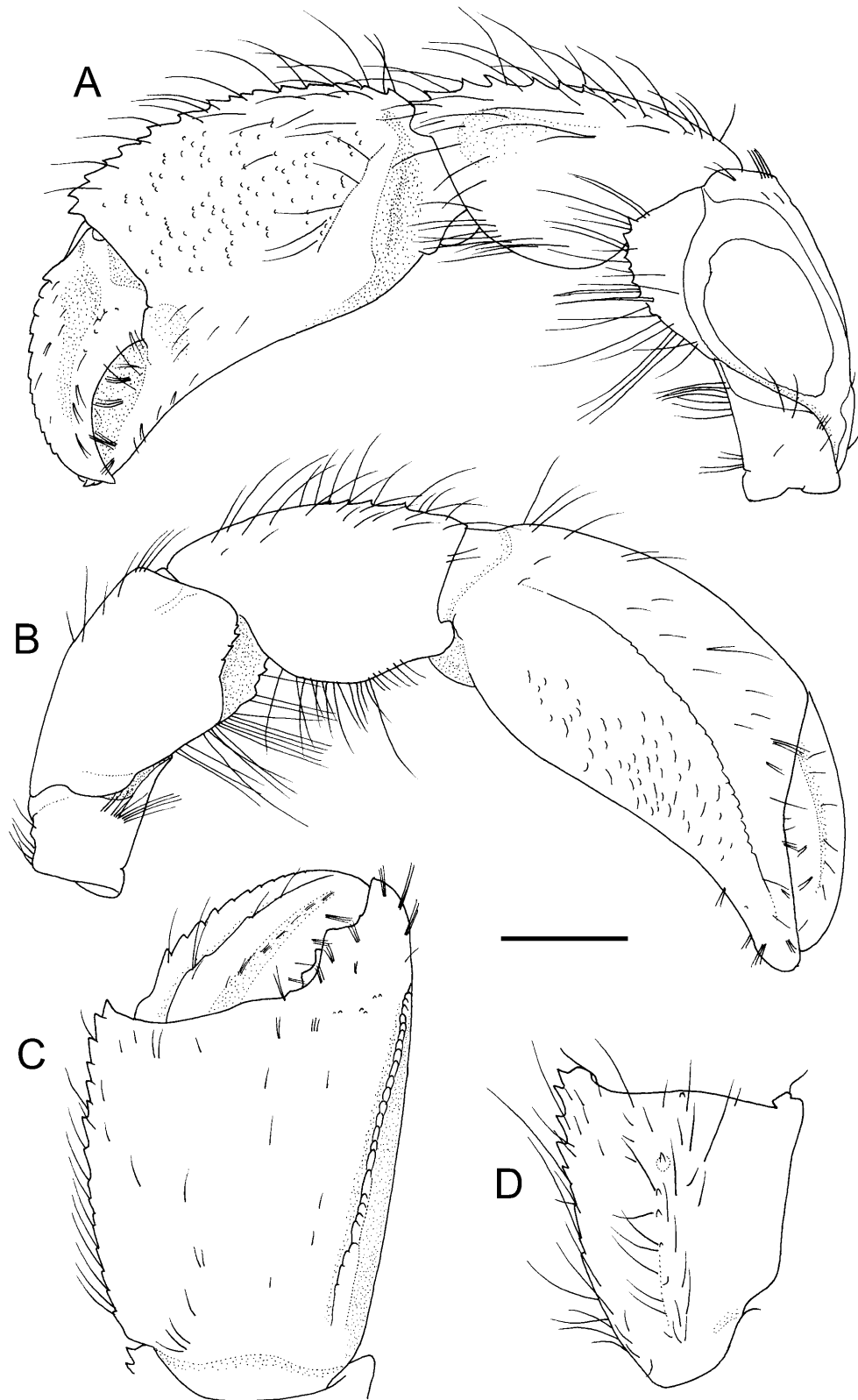


Fig. 3. *Pliopagurus curvimanus* gen. nov., sp. nov., holotype, male (sl 2.5 mm), PANGLAO 2004, stn L42, NMCR 39083. A, right cheliped, mesial view; B, same, lateral view; C, same, chela, dorsal view; D, same, carpus, dorsal view. Scale bar: 1 mm.

slightly unequally biramous, and fifth strongly unequally biramous. Uropods strongly asymmetrical.

Telson (Fig. 1H) with faint (holotype) or shallow (paratypes) lateral indentations; posterior lobes slightly asymmetrical, subtriangular, each with few short setae proximally on

lateral margin; terminal margins strongly oblique, each with some spinules.

Coloration in preservative. No distinct markings seen on shield, antennae, chelipeds, or ambulatory legs. Ocular peduncle with orange and white stripes, white stripes on

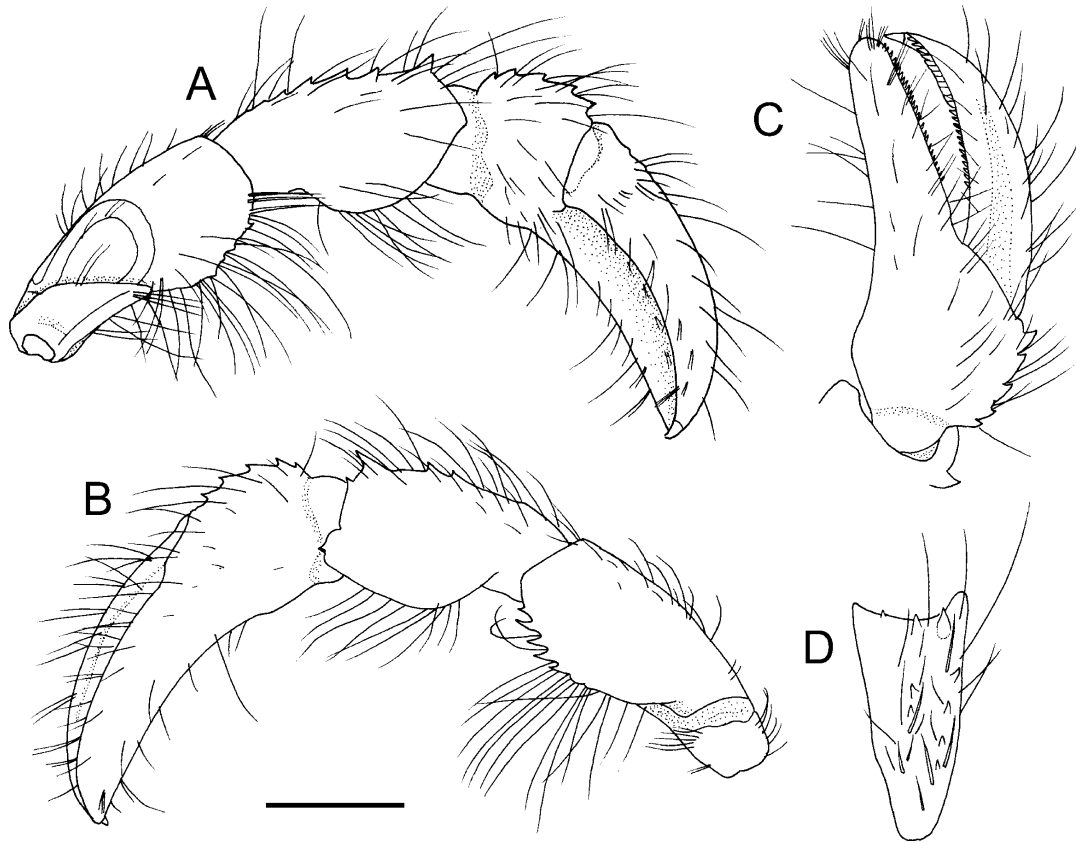


Fig. 4. *Pliopagurus curvimanus* gen. nov., sp. nov., holotype, male (sl 2.5 mm), PANGLAO 2004, stn L42, NMCR 39083. A, left cheliped, mesial view; B, same, lateral view; C, same, chela, dorsal view; D, same, carpus, dorsal view. Scale bar: 1 mm.

dorsal and ventral midline and on lateral and mesial faces, white stripe on dorsal mid-line much narrower than orange stripes.

Distribution. Known only from the type locality, Balicasag Island, Bohol Sea, the Philippines, 80–90 m deep.

Habitat. Gastropod shells.

Etymology. From the combination of the Latin, *curvatis* (=curved) and *manus* (=hand), in reference to the noticeably curved left chela. Used as a noun in apposition.

Key to genera of the “*Pylopagurus-Tomopagurus*” group [emended from Lemaitre and McLaughlin (2003a)]

- 1. Pleon reduced; males without unpaired pleopods; females with unpaired second to fourth pleopods. *Protoniopagurus*
- Pleon not reduced; males with some unpaired pleopods; females with unpaired second to fifth pleopods. 2
- 2. Protopods of uropods prominently produced posteriorly; dorsal surface of right chela commonly with characteristic covering of mushroom-shaped tubercles *Agaricochirus*
- Protopods of uropods not prominently produced posteriorly; dorsal surface of right chela usually without characteristic covering of mushroom-shaped tubercles 3
- 3. Spines on dorsal surfaces of chelae with basal rosettes *Rhodochirus*

- Spines on dorsal surfaces of chelae without basal rosettes 4
- 4. Propodal rasps of fourth pereopods each with more than one row of corneous scales 5
- Propodal rasps of fourth pereopods each with only one row of corneous scales 7
- 5. Left chela triangular or subtriangular in cross-section, dactylus and fixed finger not dorsoventrally flattened. 6
- Left chela not triangular or subtriangular in cross-section, dactylus and fixed finger dorsoventrally flattened. *Manucomplanus*
- 6. Telson with lateral indentations suggesting division into anterior and posterior portions. *Anisopagurus*
- Telson without lateral indentations suggesting division into anterior and posterior portions. *Enallopaguropsis*
- 7. Ocular acicles multispinose; coxae of male fifth pereopods asymmetrical *Pylopaguridium*
- Ocular acicles simple; coxae of male fifth pereopods symmetrical 8
- 8. Telson with lateral indentations suggesting division into anterior and posterior portions. 9
- Telson without lateral indentations suggesting division into anterior and posterior portions. *Enallopagurus*
- 9. Chela of right cheliped subovate to subcircular, margins unarmed, weakly tuberculate or minutely crenulate and/or serrate, but never armed with prominent, blunt or acute spines 10
- Chela of right cheliped variable, margins armed with

- berculate *Lophopagurus (Lophopagurus)*
 – Left chela with midline slightly elevated, but not into prominent keel or crest, lateral margin strongly spinose *Haigiopagurus*

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