

The discovery of two new species of *Lithopagurus* Provenzano, 1968 (Crustacea, Decapoda, Anomura, Paguroidea, Paguridae) and the first records of the genus in the western Pacific

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ABSTRACT

Two new species of the hermit crab genus *Lithopagurus* Provenzano, 1968 are described and illustrated together with an illustrated and detailed diagnosis of the type species, *L. yucatanicus* Provenzano, 1968 that is included for comparative purposes. This genus, heretofore monotypic and known only from off the Atlantic coast of Mexico, is now reported from two widely separated Pacific areas, the Indonesian Kai Islands and the Fiji Islands. In having 13 pairs of gills and one pair of pleopods modified as gonopods, *Lithopagurus* is included in the *Pylopaguropsis* group within the family Paguridae, and would appear most closely allied to the monotypic *Tomopaguroides* Balss, 1912. Species of *Lithopagurus* are very characteristic, with large operculate or semioperculate right chelipeds, reduced and somewhat bulbous pleons; males with paired and modified second pleopods, but lacking all unpaired pleopods; females with only unpaired pleopods 2-4; and telsons without lateral indentations and with terminal margins lacking median clefts. *Lithopagurus boucheti* n. sp., from the Fiji Islands, is morphologically quite similar to its Atlantic counterpart, *L. yucatanicus*, whereas *L. tribulomanus* n. sp., from the Kai Islands, is very distinctive. All three now recognized species have been collected from relatively deep water, 146-540 m, but little is known about their habitats other than one specimen of *L. yucatanicus* reportedly was occupying a piece of lithistid sponge at the time of collection.

KEY WORDS

Crustacea,
Decapoda,
Anomura,
Paguridae,
Lithopagurus,
western Pacific,
new species.

RÉSUMÉ

Découverte de deux nouvelles espèces de Lithopagurus Provenzano, 1968 (Crustacea, Decapoda, Anomura, Paguroidea, Paguridae) et première mention du genre dans le Pacifique occidental.

Deux nouvelles espèces de Bernard-l'ermite du genre *Lithopagurus* Provenzano, 1968 sont décrites et illustrées. Une diagnose détaillée et des illustrations de l'espèce type, *L. yucatanicus* Provenzano, 1968, sont incluses pour comparaison. Ce genre, jusqu'ici monotypique et uniquement connu du large de la côte atlantique du Mexique, est maintenant mentionné de deux zones largement distantes dans le Pacifique, les îles indonésiennes Kai et les Îles Fidji. La présence de 13 paires de branchies et d'une paire de pléopodes modifiés en gonopodes permet de placer *Lithopagurus* dans le groupe *Pylopaguropsis* dans la famille des Paguridae, et de le rapprocher du genre monotypique *Tomopaguroides* Balss, 1912. Les espèces de *Lithopagurus* sont très caractéristiques, avec de grands chélipèdes droits operculés ou semi-operculés, des pléons réduits et quelque peu bulbeux ; les mâles avec des seconds pléopodes pairs et modifiés, mais ne possédant pas de pléopodes impairs ; les femelles avec des pléopodes 2-4 uniquement impairs ; et les telsons sans indentations latérales et avec des marges terminales sans fissures médianes. *Lithopagurus boucheti* n. sp., des Îles Fidji, est morphologiquement assez similaire à son équivalent atlantique, *L. yucatanicus*, alors que *L. tribulomanus* n. sp., des Îles Kai, est très particulier. Les trois espèces maintenant reconnues ont été récoltées à des profondeurs relativement importantes, 146-540 m, mais on sait peu de choses sur leur habitat hormis le fait qu'un spécimen de *L. yucatanicus* a été récolté dans un morceau d'éponge lithistide.

MOTS CLÉS

Crustacea,
Decapoda,
Anomura,
Paguridae,
Lithopagurus,
Pacifique ouest,
nouvelles espèces.

INTRODUCTION

The hermit crab genus *Lithopagurus* Provenzano, 1968 was established for the very distinctive species, *Lithopagurus yucatanicus* Provenzano, 1968, described from three specimens collected in the northwestern Caribbean Sea off the coast of the Yucatan peninsula, Mexico. Although no subsequent specimens of *L. yucatanicus* have been reported, this monotypic genus is sufficiently singular as to permit prompt recognition. Thus it was with true astonishment that during the preliminary sorting of hermit crabs from the recent MUSORSTOM cruises to the Fiji Islands we recognized a single male specimen as attributable to *Lithopagurus*. A second species, also represented by a single male, was subsequently discovered among earlier MUSORSTOM materials.

Lithopagurus boucheti n. sp., and *L. tribulomanus* n. sp., representing the second and third species

of the genus, are described and illustrated. Additionally, a more detailed diagnosis of *L. yucatanicus* than was provided in the original description is presented for comparative purposes.

Although *Lithopagurus* is not the first presumably endemic Atlantic genus to be found in the western Pacific, it is the first previously monotypic genus to be recognized in the region. A similarly uncommon, albeit not monotypic genus, *Nematopaguroides* Forest & de Saint Laurent, 1968, described for two species from the Atlantic waters off Brazil, was also believed to be endemic to the western Atlantic. However, a new species of this genus was recently described by Wang & McLaughlin (2000) from the East China Sea. Similarly, the genus *Xylopagurus* A. Milne-Edwards, 1880, until recently thought to be endemic to the Americas (Lemaitre 1995), was found to have representatives in the Philippines Islands and New Caledonia (Forest 1997). The phylogenetic

position of *Lithopagurus* proposed by Provenzano (1968) and briefly discussed by Provenzano (1971) and Lemaitre (1995) is reexamined in the light of more recent advances in our knowledge and understanding of pagurid diversity.

MATERIALS AND METHODS

The holotype and one of the female paratypes of *Lithopagurus yucatanicus* are deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM) under catalogue numbers USNM 122636 and 122637. The remaining paratype, a female collected with the holotype, is deposited in the Muséum national d'Histoire naturelle, Paris (MNHN) and also has been reexamined. The holotypes of both new species are deposited in the collections of the MNHN. Terminology and the generic diagnosis are after McLaughlin (2003b, a, respectively), except for the change of references from abdomen to pleon (cf. Schram & Koenemann 2004). Station data for the MUSORSTOM cruises were taken from Crosnier *et al.* (1997) and Richer de Forges *et al.* (2000). The abbreviation DW refers to Warén dredge, stn to station, and ovig. to ovigerous. The shield length in millimeters, measured from the tip of the rostrum to the midpoint of the posterior margin of the shield, provides an indication of animal size.

SYSTEMATICS

Family PAGURIDAE Latreille, 1802

Genus *Lithopagurus* Provenzano, 1968

Lithopagurus Provenzano, 1968: 629. — McLaughlin & Lemaitre 1997: 112. — McLaughlin 2003a: 123.

TYPE SPECIES. — *Lithopagurus yucatanicus* Provenzano, 1968, by original designation; gender masculine.

SPECIES INCLUDED. — *Lithopagurus yucatanicus* Provenzano, 1968; *Lithopagurus boucheti* n. sp.; *Lithopagurus tribulomanus* n. sp.

DISTRIBUTION. — Northern Caribbean Sea; Fiji and Kai Islands, southwestern Pacific Ocean.

DIAGNOSIS. — Thirteen pairs of biserial gills. Rostrum triangular. Ocular acicles simple or multifid. Crista dentata with one accessory tooth. Chelipeds grossly unequal; right chela operculate or semioperate. Sternite of third pereopods with subquadrate, subtriangular or obsolete anterior lobe. Fourth pereopods semichelate; propodal rasp with several rows of corneous scales; no preungual process. Fifth pereopods minutely chelate. Male with second pleopods paired, modified; no unpaired pleopods. Female with unpaired left pleopods 2-4. Pleon somewhat to considerably reduced. Uropods symmetrical or nearly so. Telson without lateral indentations; terminal margin entire.

REMARKS

McLaughlin & Lemaitre (1997), in their discussion of male paired pleopods modified as gonopods, incorrectly reported that it was the first pleopods in *Lithopagurus* that were paired rather than the second. Provenzano (1968) had considered *Lithopagurus* to be part of de Saint Laurent-Dehancé's (1966) *Pylopaguropsis* group, and most closely allied to *Tomopaguroides* Balss, 1912, primarily because of the paired second pleopods, a character shared by species of both genera. Provenzano's comparative information was taken from Balss' (1912) description of the pair of known males of *T. valdiviae* (Balss, 1911) and unpublished information on the female provided by M. de Saint Laurent (Provenzano 1968: 642). Although McLaughlin (2004) questioned the accuracy of M. de Saint Laurent's identification, she concurred that the male paired second pleopods was a character shared only by species of those two genera.

Lithopagurus yucatanicus Provenzano, 1968
(Fig. 1)

Lithopagurus yucatanicus Provenzano, 1968: 629, figs 1-4; 1971: 237.

TYPE MATERIAL. — **Caribbean Sea.** Pillsbury, stn P-584, 21°02'N, 86°24'W, 353-347 m, 23.V.1967, holotype ♂ 2.8 mm (USNM 122636), paratype ovig. ♀ 2.6 mm (USNM 122637); stn P-581, 21°05'N, 86°23'W, 146-265 m, 22.V.1967, paratype ♀ 2.8 mm (MNHN-Pg 458).

TYPE LOCALITY. — Caribbean Sea, 21°05'N, 86°23'W, 146-265 m.

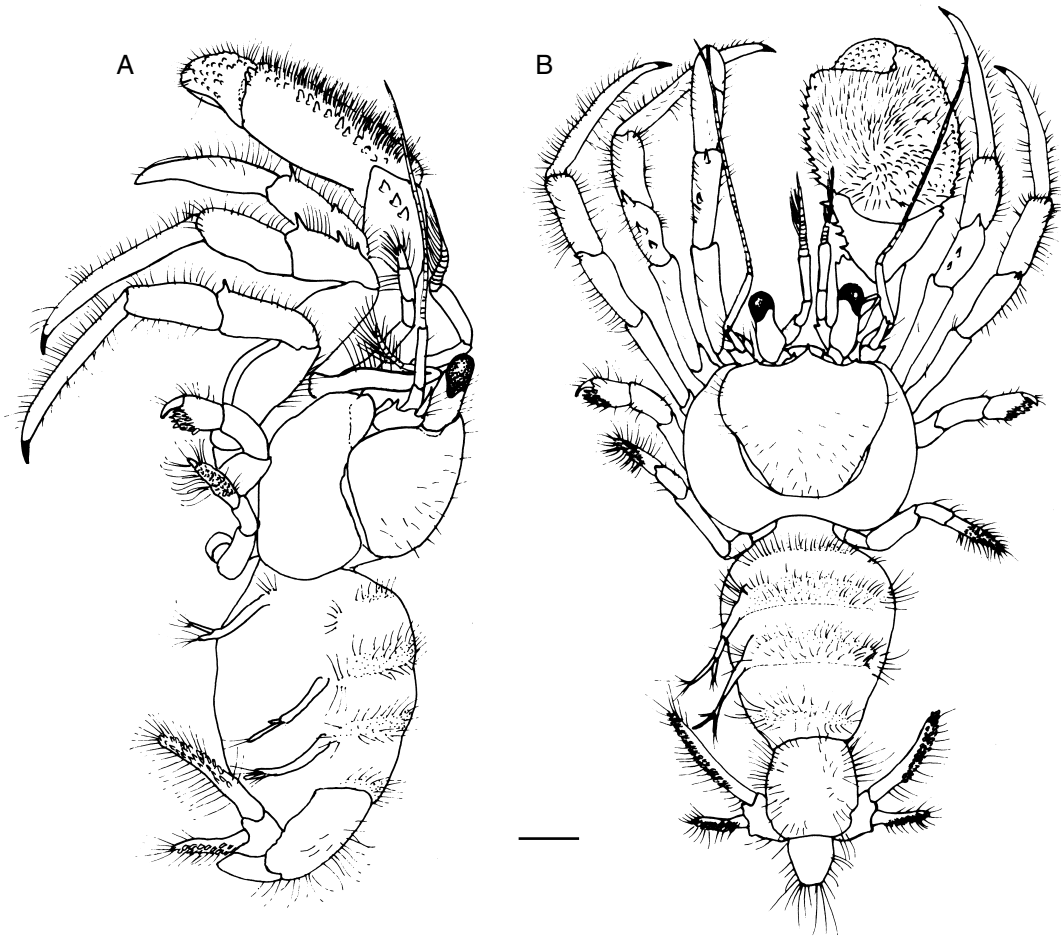


FIG. 1. — *Lithopagurus yucatanicus* Provenzano, 1968, paratype ♀ (MNHN-Pg 458), Caribbean Sea, Pillsbury, stn P-581, 21°05'N, 86°23'W, 146-265 m, 22.V.1967; **A**, whole animal, lateral view; **B**, whole animal, dorsal view (after Provenzano 1968). Scale bar: 1 mm.

DISTRIBUTION. — Arrowsmith Bank, off the Yucatan Peninsula, Mexico.

DESCRIPTION

Shield (Fig. 1A) considerably broader than long, distinctly vaulted, surface with few simple setae laterally. Rostrum prominently produced, overreaching spines of ocular acicles, broadly triangular, with short, rounded, median keel, terminating in acute small spine. Lateral projections weakly produced, but each with acute terminal spine. Ocular peduncles short, approximately 0.6 length of shield, swollen basally,

concave medially; corneal diameter approximate 0.3 of peduncular length; ocular acicles quite small, triangular, each with terminal spine. Antennular peduncles overreaching distal margins of corneas by full length of ultimate peduncular segments. Antennal peduncles overreaching corneas and reaching to proximal halves of ultimate segments of antennular peduncles; second segments each with dorsolateral distal angle produced, terminating in simple spine and with few short, simple setae; antennal acicles reaching to proximal margins of ultimate peduncular segments, each with simple terminal spine and few moderately short, marginal setae.

Chelipeds grossly unequal (Fig. 1), right operculate; dactyl and fixed finger with distinct hiatus, both terminating in corneous claws. Dactyl with dorsomesial margin not delimited, dorsal and dorsomesial surfaces both with covering of moderately long, stiff setae arising from low protuberances. Dorsal surfaces of palm and fixed finger with similar setation and low protuberances, dorsomesial margin of palm with row of very small spines. Carpus with four spines in distal half of dorsomesial margin, distal margin with numerous moderately long stiff setae. Left cheliped very slender; unarmed but segments covered with moderately dense, stiff setae; carpus unarmed or with two or three spines on dorsal surface.

Ambulatory legs detached, but appear to be approximately as long as right cheliped. Dactyls of second pereopods approximately twice length of propodi, dactyls of third about 1.5 length of propodi; dorsal, lateral and mesial faces each with numerous, moderately long, stiff setae; ventral margins each with eight to 10 corneous spines. Propodi unarmed but surfaces all with scattered short to moderately long, stiff setae. Dorsal margins of carpi of second pereopods each with prominent dorsodistal spine and two smaller spines in posterior half; third pereopods with only dorsodistal spine or with one small spine on dorsal surface in addition to dorsodistal spine; with scattered short to moderately long, stiff setae. Meri each with sparse dorsal and ventral setae. Fourth pereopods semichelate, dactyls very short; propodi each with multiple rows of scales in rasp. Fifth pereopods weakly chelate. Sternite of third pereopods with reduced subquadrate anterior lobe, concealed by setae.

Pleon reduced (Fig. 1); tergites 2-5 well defined, entire but membranous and provided with scattered short, stiff setae, tergite 6 well calcified, subquadrate, also with covering of moderately short, stiff setae. Female with pleopods 2-4 on left, with second somewhat smaller than others; right side sometimes with rudimentary, very weakly biramous second pleopod. Uropods very large, generally symmetrical; both rami with elongate rasps of small corneous scales.

Telson roundly subrectangular, without lateral incisions or indentations; terminal margin entire, unarmed.

REMARKS

Provenzano (1968) described the carpus of the left cheliped as having two or three large spines on the dorsal surface. Only one spine is illustrated for the female paratype from station P 581, but no spine was observed when the specimen was reexamined; it possibly had been broken off. Other discrepancies between the present diagnosis and the original description reflect morphological variations between the described male holotype and the female paratypes and/or semantics.

No mention was made by Provenzano (1968) about the rudimentary right second pleopod present on the female paratype in the MNHN; no similar right second pleopod occurs in the other female paratype. Whether incomplete loss of this pleopod is an anomaly or a variable condition in this genus cannot be determined at present. Both new species are known only from their male holotypes.

Lithopagurus boucheti n. sp.

(Fig. 2)

TYPE MATERIAL. — Fiji. BORDAU 1, stn DW 1486, 19°01'S, 178°26'W, 385-540 m, 10.III.1999, holotype ♂ 2.0 mm (MNHN-Pg 7079).

ETYMOLOGY. — This species is dedicated to Philippe Boucher (MNHN) whose enthusiasm for exploring the mysteries of the western Pacific marine environment is inspirational.

TYPE LOCALITY. — Fiji, 19°01'S, 178°26'W, 385-540 m.

DISTRIBUTION. — Known only from the type locality.

DESCRIPTION

Shield (Fig. 2A, B) somewhat vaulted; as broad as long; anterior margin between rostrum and lateral projections concave; anterolateral margins sloping, each with posterolaterally directed slender spine; posterior margin roundly truncate; dorsal surface well calcified, glabrous. Rostrum as broadly subtriangular lobe with prominent supra-marginal spine produced well beyond level of

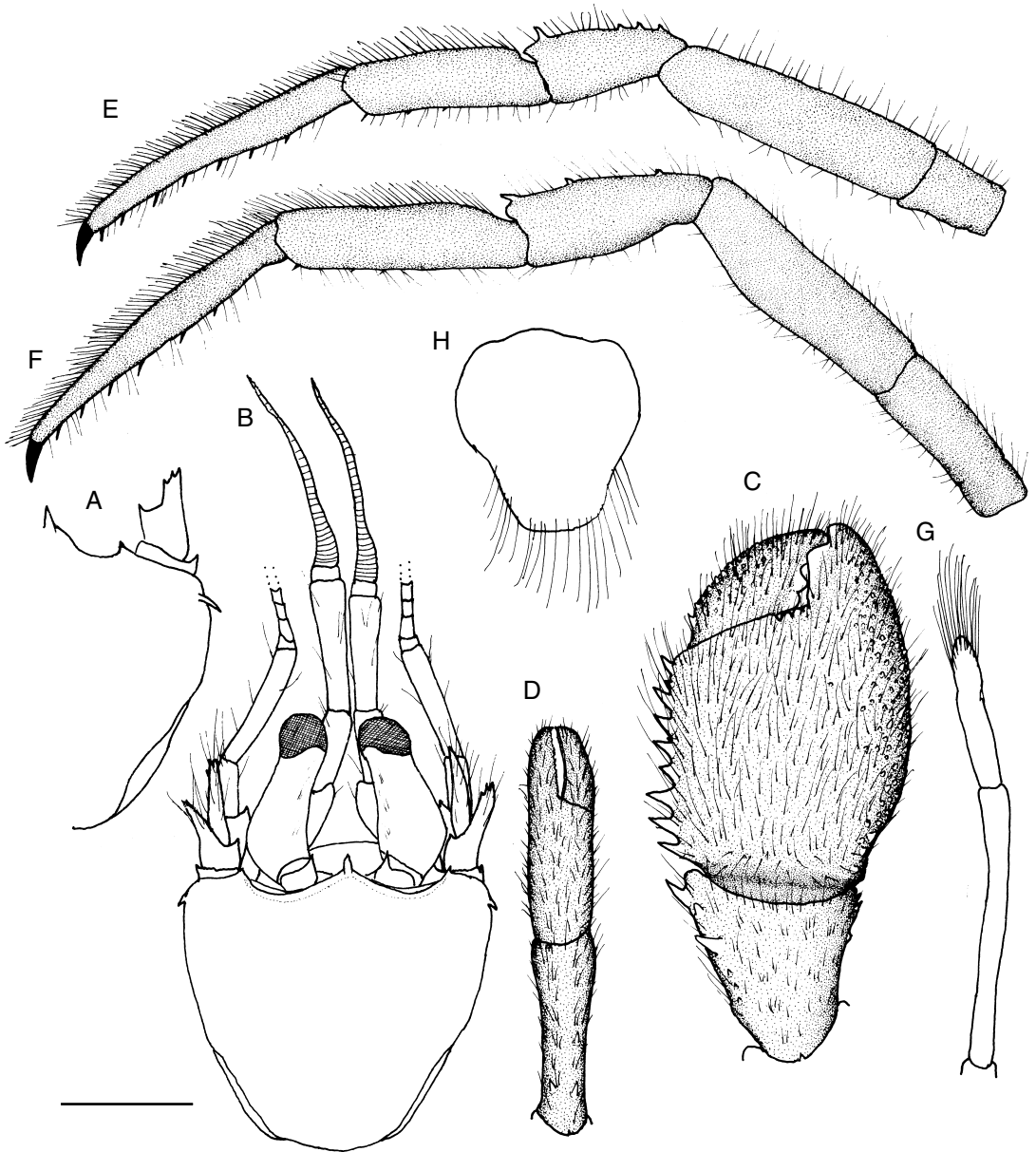


FIG. 2. — *Lithopagurus boucheti* n. sp., holotype ♂ (MNHN-Pg 7079), Fiji, BORDAU 1, stn DW 1486, 19°01'S, 178°26'W, 385-540 m, 10.III.1999; **A**, right side of shield, dorsolateral view; **B**, shield and cephalic appendages (aesthetascs omitted); **C**, chela and carpus of right cheliped, dorsal view; **D**, chela and carpus of left cheliped, dorsal view; **E**, left second pereopod, lateral view; **F**, left third pereopod, lateral view; **G**, right second pleopod; **H**, telson. Scale bar: A-F, 1.0 mm; G, H, 0.5 mm.

lateral projections. Lateral projections weakly developed, broadly subtriangular, each with small marginal spine.

Ocular peduncles 0.6 shield length, swollen in proximal half, each with row of sparse tufts of setae dorsomesially; corneal diameter approximately 0.3 of peduncular length. Ocular acicles moderately small, narrowly triangular, each with prominent terminal spine; separated basally by more than basal width of one acicle.

Antennular peduncles overreaching distal margins of corneas by entire length of ultimate peduncular segments. Segments all with scattered short setae, basal segment also with small spine on dorsolateral margin.

Antennal peduncles overreaching distal corneal margins by approximately 0.5 length of fifth segments. Fifth and fourth segments each with few scattered setae. Third segment with small spine at ventrodiscal angle. Second segment with dorsolateral distal angle produced, terminating in small bifid spine, also with small subdistal spine; dorsomesial distal angle with small spine. First segment with prominent spine on laterodistal margin, small spine laterally on produced ventral margin. Antennal acicles reaching to or slightly beyond proximal margins of fifth peduncular segments; terminating in simple or bifid spine and with few moderately long setae. Antennal flagella reaching full length of right cheliped; each article with irregularly set, short to moderately long (1 or 2 article-length) setae.

Right cheliped (Fig. 2C) very much larger than left, semioperculate. Dactyl approximately 0.8 length of palm; cutting edge with row of moderately large, calcareous teeth, terminating in small corneous claw; dorsal surface flat, with numerous long setae and small tubercles, dorsomesial margin not delimited, rounded surface with abundance of long setae and small tubercles, two more prominent, teardrop-shaped small spines proximally; rounded ventromesial surface with low tubercles or granules becoming obsolete toward cutting edge. Palm approximately 1.3 length of carpus; dorsomesial margin with row of prominent spines, accompanied by long, simple setae, flat dorsal surface with covering of moderately long

and stiff, simple setae, dorsolateral margin not delimited; rounded dorsolateral surface with short setae, closely-spaced spinulose tubercles and tuberculate spines extending almost full length of fixed finger; rounded mesial and lateral surfaces with closely-spaced tubercles becoming obsolete on ventral surface; cutting edge of fixed finger with one prominent tooth and row of fused calcareous teeth, terminating in small corneous claw. Carpus approximately half length of merus, broadly subtriangular in dorsal view; dorsodistal margin unarmed but with row of moderately long setae, dorsomesial margin with prominent, acute spines and few long setae, dorsal surface with scattered short setae and stiff bristles, dorsolateral margin not delimited; ventrolateral margin with row of small spines; lateral, mesial and ventral surfaces unarmed. Merus roundly subtriangular; dorsodistal margin with small spine, dorsal margin with few tufts of fine setae; ventromesial and ventrolateral margins each with row of small, acute spines; ventral surface with few minute granules. Ischium with row of very small spines on ventromesial margin, ventral surface with few minute spinules. Coxa with one large and two smaller spines on ventrodiscal margin and two small spines on ventromesial margin. Left cheliped (Fig. 2D) short, slender. Dactyl approximately 0.8 as long as palm. Dactyl, palm and fixed finger all unarmed, but with irregular rows of stiff bristles. Carpus with row of very stiff bristles on both dorsomesial and dorsolateral margins, dorsolateral margin also with one spine proximally and spinule at distal margin, dorsomesial margin with two small spines proximally. Merus with small spine at dorsodistal margin, dorsal surface with sparse tufts of fine setae; laterodistal margin with small spine ventrally; ventromesial margin with two spines in proximal half. Ischium with three widely-spaced spines on ventromesial margin. Coxa with one spine on ventrodiscal margin.

Second and third pereopods (Fig. 2E, F) generally similar (right second missing). Dactyls 1.3-1.4 length of propodi; dorsal surfaces each with row of tufts of moderately long, stiff setae; mesial faces each with numerous but randomly set,

moderately short, stiff bristles; ventral margins each with row of six or seven corneous spines and few setae. Propodi each with tufts of moderately long setae dorsally; mesial faces with randomly scattered, moderately short, stiff bristles; ventrodistal margins each with one or two corneous spinules and one or two additional corneous spinules in distal half. Carpi each with spine at dorsodistal angle, dorsal surface with or without one smaller spine at midlength and one to three small spines in proximal half. Meri with scattered setae on dorsal and ventral margins. Ischia unarmed. Coxae each with four or five prominent spines on ventromesial margin (second) or unarmed (third). Fourth pereopods with propodal rasp consisting of three or four rows of sharp corneous scales; dactyl with small terminal claw. Anterior lobe of sternite of third pereopods subtriangular. Pleon moderately short. Distal segments of two-segmented male paired second pleopods (Fig. 2G) each with terminal tuft of long setae. Tergite of sixth pleomere divided unequally by incomplete, transverse suture; both portions well calcified with moderately dense covering of short setae. Uropods symmetrical. Telson (Fig. 2H) longer than broad, subtrapezoidal, unarmed, terminal margin with row of setae.

AFFINITIES

In the shape of the shield and cephalic appendages *L. boucheti* n. sp. more closely resembles *L. yucatanicus* than *L. tribulomanus* n. sp. However, in place of the short rostral keel of *L. yucatanicus*, *L. boucheti* n. sp. has a very distinctive rostral spine that actually arises from the dorsal surface of the shield rather than from the anterior margin. The anterolateral margins of the shield are also distinctive in the new species in that they each carry a prominent, posterolaterally directed spine. The general shapes of the right and left chelipeds are similar in *L. yucatanicus* and *L. boucheti* n. sp., although the armature appears to be variable in *L. yucatanicus*. For example, Provenzano (1968) described the carpus of the right cheliped as having spines on both the [dorso]lateral and [dorso]medial (mesial) margins; however, no dorsolateral spines were

illustrated for the female paratype (Provenzano 1968: fig. 3, left and center), nor did we find such spines in the MNHN paratype. Similarly, and as previously mentioned, Provenzano described the left cheliped of the western Atlantic species as having two or three large spines on the dorsal surface of the carpus, whereas one spine, in addition to the dorsodistal spine, was illustrated for the female paratype (1968: fig. 2, upper left). We found no spines on the carpus of that paratype.

Lithopagurus tribulomanus n. sp.

(Fig. 3)

TYPE MATERIAL. — Indonesia. Kai Islands, KARUBAR, stn DW 18, 05°18'S, 133°10'E, 205-212 m, 24.X.1991, holotype ♂ 2.0 mm (MNHN-Pg 7080).

ETYMOLOGY. — The specific epithet is from the Latin *tribulosus* meaning thorny, and *manus* meaning hand, forming a compound name used as an adjective and reflecting the spiny or thorny armature of the right chela of this species.

TYPE LOCALITY. — Kai Islands, Indonesia, 05°18'S, 133°10'E, 205-212 m.

DISTRIBUTION. — Known only from the type locality.

DESCRIPTION

Shield (Fig. 3A) somewhat vaulted; considerably longer than broad; anterior margin between rostrum and lateral projections weakly concave; unarmed anterolateral margins sloping; posterior margin truncate; dorsal surface well calcified, glabrous. Rostrum triangular, produced to nearly midlength of ocular acicles and well beyond level of lateral projections, terminating in prominent spine. Lateral projections weakly developed, subacute, each with tiny marginal spinule.

Ocular peduncles long, 0.8 shield length, slightly swollen basally; corneal diameter approximately 0.2 of peduncular length. Ocular acicles acutely triangular, reaching beyond proximomesial margins of ocular peduncles, each with prominent terminal spine; left with one and right with two accessory spinules on lateral margin; separated basally by more than basal width of one acicle.

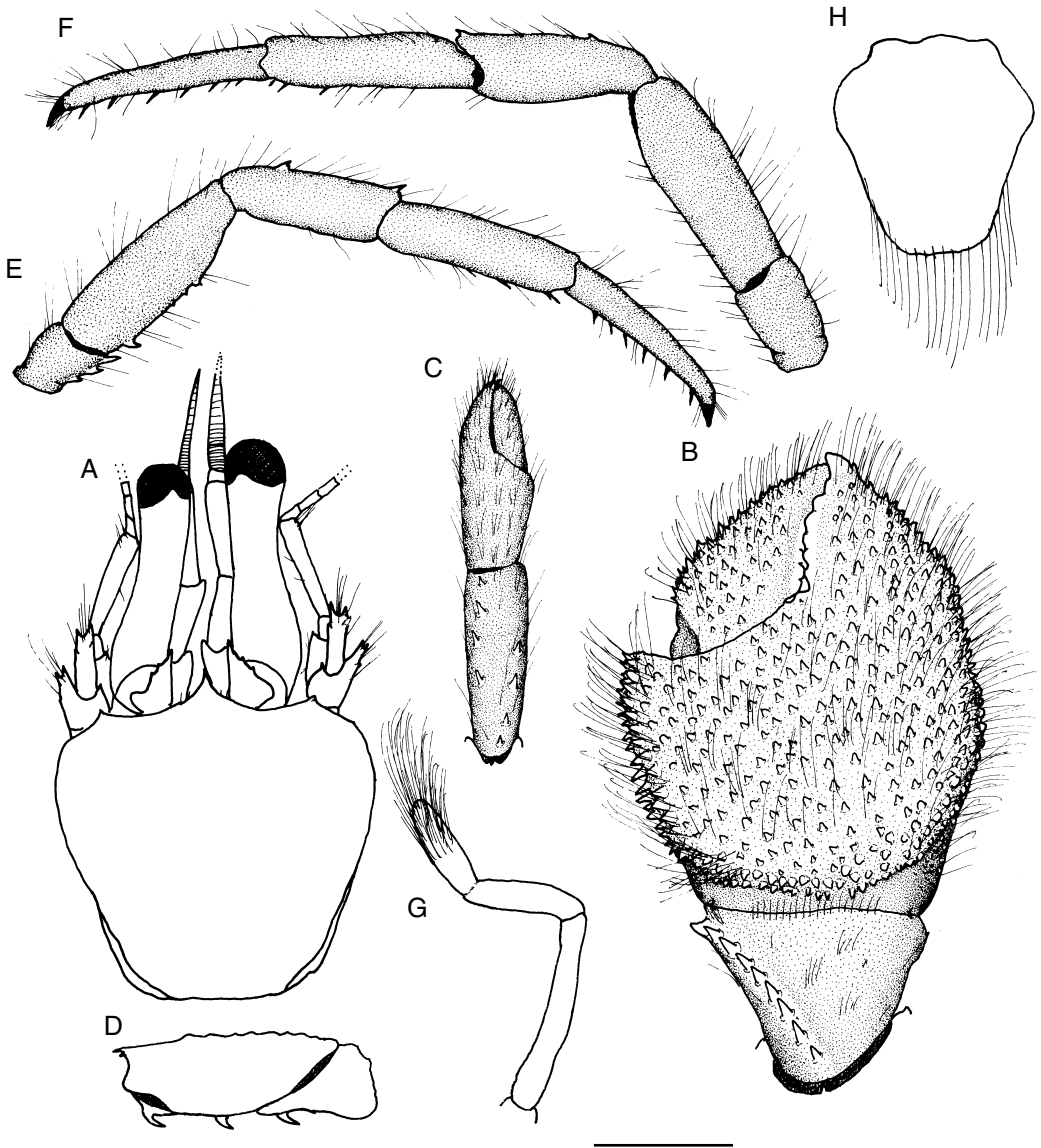


FIG. 3. — *Lithopagurus tribulomanus* n. sp., holotype ♂ (MNHN-Pg 7080), Indonesia, KARUBAR, stn DW 18, 05°18'S, 133°10'E, 205-212 m, 24.X.1991; **A**, shield and cephalic appendages (aesthetascs omitted); **B**, chela and carpus of right cheliped, dorsal view; **C**, chela and carpus of left cheliped, dorsal view; **D**, merus and ischium of left cheliped, lateral view; **E**, left second pereopod, lateral view; **F**, left third pereopod, lateral view; **G**, right second pleopod; **H**, telson. Scale bar: A-F, 1.0 mm; G, H, 0.5 mm.

Antennular peduncles when fully extended overreaching ocular peduncles by approximately 0.3 length of ultimate segments. All segments unarmed, glabrous.

Antennal peduncles reaching beyond proximal halves of ocular peduncles, but not reaching to basal margins of corneas. Fifth and fourth segments each with few scattered setae. Third segment with sparse tuft of setae and tiny spinule at ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in bifid spine, lateral margin with subdistal spinule, dorsomesial distal angle with well developed spine. First segment unarmed. Antennal acicles approximately reaching proximal 0.3 ocular peduncles; terminating in bifid spine, and with lateral and mesial subdistal spinules, smallest on left. Antennal flagella short, only slightly longer than carapace; each article with irregularly set, short to moderately long (2-4 article-length) setae.

Right cheliped (Fig. 3B) very much larger than left, operculate. Dactyl broad, slightly shorter than palm; articulation with chela somewhat oblique; cutting edge with row of moderately small, calcareous teeth, terminating in calcareous claw; dorsal surface flat, with scattered short setae and numerous small, acute or rounded tubercles, dorsomesial margin with abundance of long setae not concealing irregular double row of small spines in proximal half becoming rounded tubercles and decreasing in size distally; rounded ventromesial surface with low tubercles or granules becoming obsolete toward cutting edge. Palm approximately twice length of carpus; circumscribed marginally by double row of small, slender spines accompanied by long, simple setae, flat dorsal surface with covering of short to moderately long, simple setae and rounded, sometimes spinulose tubercles and small spines; rounded mesial and lateral surfaces tuberculate, with closely-spaced tubercles becoming obsolete on ventral surface; cutting edge of fixed finger with row of fused calcareous teeth, terminating in large, upturned, calcareous claw. Carpus approximately equal to length of merus, broadly subtriangular in dorsal view; dorsodistal margin unarmed but with row

of moderately short setae, dorsomesial margin with row of prominent, acute spines and few long setae, dorsal surface with scattered short setae, dorsolateral margin not delimited; lateral surface with short row of three small spines dorsodistally (not readily visible in dorsal view), remainder of surface unarmed; mesial and ventral surfaces unarmed. Merus roundly subtriangular; dorsodistal margin with small spine, dorsal surface with widely-spaced, very sparse tufts of setae; ventromesial margin with one prominent, forward-directed spine distally; ventrolateral margin with row of small, acute spines; ventral surface unarmed. Ischium with one prominent, proximally-directed spine on ventromesial margin. Coxa with row of five small spines on ventrodistal margin. Left cheliped (Fig. 3C, D) short, slender. Combined length of dactyl and palm approximately equal to individual lengths of carpus and merus. Dactyl, palm and fixed finger all unarmed, but with irregular rows of sparse tufts of long setae. Carpus with row of spines on dorsomesial margin in proximal half, dorsolateral margin with row of spines in distal 0.6. Merus with pair of small spines at dorsodistal margin, dorsal surface with widely-spaced sparse tufts of setae; two prominent, slender, posteriorly-directed spines on ventromesial margin. Ischium with one prominent, posteriorly-directed spine on ventromesial margin. Coxa unarmed.

Second and third pereopods (Fig. 3E, F) generally similar. Dactyls only slightly longer than propodi; dorsal surfaces each with row of sparse tufts of moderately long setae; ventral margins each with row of five or six corneous spines. Propodi each with tufts of long setae dorsally, ventrodistal margins each with one or two corneous spinules and additional one or two similar spinules in distal halves. Carpi each with spine at dorsodistal angle and one small spine in proximal half. Meri with scattered setae on dorsal margins; ventral margins each with row of small spines (second) or unarmed (third). Ischia each with two or three, anteriorly or posteriorly-directed, spines on ventromesial margins (second) or unarmed (third). Coxae each with one posteriorly-directed spine on ventromesial distal margin (second) or unarmed

(third). Fourth pereopods with propodal rasp consisting of three or four rows of sharp corneous scales; dactyl with small terminal claw. Anterior lobe of sternite of third pereopods subquadrate, with three small marginal spines.

Pleon short, bulbous. Distal segments of apparently three-segmented male paired second pleopods (Fig. 3G) each with terminal tuft of long setae. Tergite of sixth pleomere divided unequally by incomplete, transverse suture; both portions well calcified with moderately dense covering of short setae. Uropods symmetrical. Telson (Fig. 3H) longer than broad, subtrapezoidal, unarmed, terminal margin with row of setae.

AFFINITIES

In addition to generic characters, *Lithopagurus tribulomanus* n. sp. shares with *L. yucatanicus* the short bulbous pleon, but little else. *Lithopagurus tribulomanus* n. sp. is set apart from both *L. yucatanicus* and *L. boucheti* n. sp. by several characters. These include the longer rostrum and ocular peduncles, more operculate right chela, the dorsal surface of which is circumscribed by a double row of acute spines, very prominent and posteriorly-directed spines on the ventromesial margin of the merus of the left cheliped, and the apparently three-segmented paired second pleopods.

REMARKS

The operculate right cheliped and reduced pleon characteristic of all three species of *Lithopagurus* suggests more specialized habitats than the typical gastropod shells. The habitats of *L. boucheti* n. sp. and *L. tribulomanus* n. sp. are unknown, but Provenzano (1968) reported that one of the paratypes of *L. yucatanicus* was occupying a fragment of lithistid sponge at the time of capture.

DISCUSSION

Provenzano (1968) assigned *Lithopagurus* to the *Pylopaguroopsis* group defined by de Saint Laurent-Dechancé (1966) as those pagurid species having 13 pairs of gills, an accessory tooth on the crista dentata of the third maxilliped, at least one pair

of pleopods modified as gonopods in one or the other sex, and no development of male sexual tubes. Her *Pylopaguroopsis* group at the time included the five genera, *Pylopaguroopsis* Alcock, 1905, *Munidopagurus* A. Milne-Edwards & Bouvier, 1893 (authorship incorrectly credited to A. Milne-Edwards, 1880 by McLaughlin 2003a), *Tomopaguroopsis* Alcock, 1905, *Tomopaguroides* Balss, 1912, and *Xylopagurus* A. Milne-Edwards, 1880. Because both *L. yucatanicus* and *Tomopaguroides valdiviae* (Balss, 1911), representing monotypic genera, had male paired second pleopods, Provenzano (1968) expressed the view that on the basis of present knowledge, *Lithopagurus* was probably most closely related to *Tomopaguroides*. However, he emphasized the major morphological differences exhibited among members of the individual genera within the group. Following the addition of *Bathypaguroopsis* McLaughlin, 1994, *Bythiopagurus* McLaughlin, 2003, *Chanopagurus* Lemaitre, 2003, and *Propagurus* McLaughlin & de Saint Laurent, 1998, to the *Pylopaguroopsis* group, those differences have been amplified, and the unifying characters of the group eroded. For example, *Bythiopagurus* males do develop very short sexual tubes; *Bathypaguroopsis* and *Propagurus* species do not have at least one pair of sexually modified appendages in one or the other sex, and *Propagurus* and *Chanopagurus* species, while still having pleurobranches on the thoracic walls above the second, third and fourth pereopods, those above the second are often reduced and those above the third consistently are rudimentary. In her discussion of the *Pylopaguroopsis* group, McLaughlin (2003b) pointed out that the only mutually shared character was the 13 pairs of gills, and even those appeared to be undergoing reduction. Following a similar line of reasoning, McLaughlin (2004) proposed that the paired second pleopods characteristic of *Lithopagurus* and *Tomopaguroides* reflected a transitional phase between the primitive condition of paired first and second male pleopods seen in *Xylopagurus* and the absence of all paired pleopods seen in males of the remaining seven genera of the *Pylopaguroopsis* group. The absence of all unpaired male pleopods characteristic of *Lithopagurus*,

Munidopagurus and *Xylopagurus* is an unusual character, but one that is also found in genera with 14, 13 and 11 pairs of gills. *Lithopagurus* is retained in the *Pylopaguropsis* group for the present; however, it should be emphasized that this placement is based on “key” character convenience (cf. McLaughlin 2003a) rather than on substantiated phylogenetic relationships.

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