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

Patsy A. MCLAUGHLIN
Shannon Point Marine Center, Western Washington University, 1900 Shannon Point Road, Anacortes, WA 98221-9081B (USA) hermit@fidalgo.net

Rafael LEMAITRE
Department of Systematic Biology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20013-7012 (USA) lemaître.rafael@nmnh.si.edu

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.
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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
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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 Waren dredge, stn to station, and ovig. to ovi-generous. 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


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.

Lithopagurus yucatanicus Provenzano, 1968

(Fig. 1)


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.
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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, over-reaching 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 over-reaching distal margins of corneas by full length of ultimate peduncular segments. Antennal peduncles over-reaching 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.
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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. Carpus 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. Carpus of second pereopods each with 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 raps 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.

\textit{Lithopagurus boucheti} n. sp.

(Fig. 2)

\textbf{Type Material.} — Fiji. BORDAU 1, stn DW 1486, 19°01'S, 178°26'W, 385-540 m, 10.III.1999, holotype $\delta$ 2.0 mm (MNHN-Pg 7079).

\textbf{Etymology.} — This species is dedicated to Philippe Bouchet (MNHN) whose enthusiasm for exploring the mysteries of the western Pacific marine environment is inspirational.

\textbf{Type Locality.} — Fiji, 19°01'S, 178°26'W, 385-540 m.

\textbf{Distribution.} — Known only from the type locality.

\textbf{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.
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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 approxima-
tely 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 pedun-
cular segments. Segments all with scattered short
setae, basal segment also with small spine on
dorsolateral margin.
Antennal peduncles overreaching distal cornual
margins by approximately 0.5 length of fifth seg-
ments. Fifth and fourth segments each with few
scattered setae. Third segment with small spine at
ventrodistal angle. Second segment with dorsolat-
eral distal angle produced, terminating in small
bifid spine, also with small subdistal spine; dorso-
nal 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 moderate-
ly large, calcareous teeth, terminating in small
conical claw; dorsal surface flat, with numerous
long setae and small tubercles, dorsomodal mar-
gin not delimited, rounded surface with abun-
dance of long setae and small tubercles, two more
prominent, teardrop-shaped small spines proxim-
ally; rounded ventromesial surface with low
tubercles or granules becoming obsolete toward
cutting edge. Palm approximately 1.3 length of
carpus; dorsomodal 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 conical
claw. Carpus approximately half length of merus,
broadly subtriangular in dorsal view; dorsodistal
margin unarmed but with row of moderately
long setae, dorsomodal margin with prominent,
acute spines and few long setae, dorsal surface
with scattered short setae and stiff bristles, dorso-
nal distal 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 ventral 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 ventrodistal mar-
gin 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 dorsomodal and dorsolateral
margins, dorsodistal margin also with one spine
proximally and spinule at distal margin, dorso-
nal distal margin with two small spines proximally.
Merus with small spine at dorsodistal margin,
dorsal surface with sparse tufts of fine setae; late-
nodistal margin with small spine ventrally; ven-
tromesial margin with two spines in proximal
half. Ischium with three widely-spaced spines on
ventromesial margin. Coxa with one spine on
ventrodistal margin.
Second and third pereopods (Fig. 2E, F) general-
ly 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 dorsoangular 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 6 2.0 mm (MNHN-Pg7080).

**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.
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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 over-reaching 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; dorsomesial 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, posteriorly-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.
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(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 para-types of L. yucatanicus was occupying a fragment of lithistid sponge at the time of capture.

DISCUSSION
Provenzano (1968) assigned Lithopagurus to the Pylapaguropsis 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 Pylapaguropsis group at the time included the five genera, Pylapaguropsis Alcock, 1905, Munidopagurus A. Milne-Edwards & Bouvier, 1893 (authorship incorrectly credited to A. Milne-Edwards, 1880 by McLaughlin 2003a), Tomopaguropsis 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 Bathypaguropsis McLaughlin, 1994, Bythiopagurus McLaughlin, 2003, Chanopagurus Lemaitre, 2003, and Propagurus McLaughlin & de Saint Laurent, 1998, to the Pylapaguropsis group, those differences have been amplified, and the unifying characters of the group eroded. For example, Bythiopagurus males do develop very short sexual tubes; Bathypaguropsis 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 pleurobranchs 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 Pylapaguropsis 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 Pylapaguropsis 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 Pyltopaguropsis 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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