

## Generic reassignment and redescription of *Pagurus gladius* (Benedict, 1892), and description of a new species of *Pagurus* Fabricius, 1775 (Crustacea: Paguroidea: Paguridae) from the Mexican Pacific

Manuel Ayón Parente<sup>1</sup>  [orcid.org/0000-0002-2043-0142](https://orcid.org/0000-0002-2043-0142)

Michel E. Hendrickx<sup>2</sup>  [orcid.org/0000-0001-9187-6080](https://orcid.org/0000-0001-9187-6080)

Rafael Lemaitre<sup>3</sup>  [orcid.org/0000-0003-2828-612X](https://orcid.org/0000-0003-2828-612X)

**1** Universidad de Guadalajara, Departamento de Ecología, CUCBA. Carretera a Nogales km. 15.5, Las Agujas Nextipac, Zapopan, Jalisco, C.P. 45110, Mexico.  
**MAP** E-mail: manuel\_aparente@hotmail.com

**2** Universidad Nacional Autónoma de México, Instituto de Ciencias del Mar y Limnología, Laboratorio de Invertebrados Bentónicos, Unidad Académica Mazatlán. P.O. Box 811, Mazatlán, Sinaloa, 82000, Mexico.  
**MEH** E-mail: michel@ola.icmyl.unam.mx

**3** Smithsonian Institution, National Museum of Natural History, Department of Invertebrate Zoology. 4210 Silver Hill Road, Suitland, Maryland 20746, U.S.A.  
**RL** E-mail: lemaitrr@si.edu

**ZOOBANK:** <http://zoobank.org/urn:lsid:zoobank.org:pub:C16CB355-3BD1-4F39-B0ED-2F023D370346>

### ABSTRACT

After a study of the type specimens, as well as supplementary materials of the eastern Pacific hermit crab *Pagurus gladius* (Benedict, 1892), this taxon is transferred to the genus *Spathapagurus* Lemaitre and Felder, 2011, and a full redescription and illustrations are presented. Morphological similarities of Benedict's taxon with three other eastern Pacific species (*Pagurus albus* (Benedict, 1892), *Pagurus perlatus* H. Milne Edwards, 1848, and *Pagurus pseudoalbus* Ayón-Parente and Wehrtmann, 2019) are summarized. While examining museum specimens during this study, one female specimen representing a new species of *Pagurus* Fabricius, 1775, was discovered. This new species, named *Pagurus marysolae* sp. nov., is fully described and illustrated, and is assigned to Group II ("exilis") of *Pagurus*.

### KEYWORDS

Hermit crabs, Mexican Pacific, new species, *Pagurus*, taxonomy

Editor-in-chief  
Christopher Tudge

Associate Editor:  
Kareen Schnabel

Corresponding Author  
Manuel Ayón Parente  
[manuel\\_aparente@hotmail.com](mailto:manuel_aparente@hotmail.com)

SUBMITTED 3 February 2022  
ACCEPTED 2 May 2022  
PUBLISHED 16 December 2022

DOI 10.1590/2358-2936e2022039



All content of the journal, except where identified, is licensed under a Creative Commons attribution-type BY.

Nauplius, 30: e2022039

## INTRODUCTION

With 89 genera and about 550 species known worldwide, the hermit crab family Paguridae is the most diverse among the Paguroidea. The genus *Pagurus* Fabricius, 1775 contains about 180 described species and is by far the largest in number of species in this family (WoRMS Editorial Board, 2021). In the eastern tropical Pacific, *Pagurus* is represented by 18 species of which 14 have been recorded from the Pacific coast of Mexico (Hendrickx and Harvey, 1999; Lemaitre and Cruz-Castaño, 2004; Ayón-Parente and Hendrickx, 2012; Ayón-Parente and Wehrtmann, 2019).

While examining hermit crab specimens collected in the tropical eastern Pacific, mostly by the R/V “El Puma”, of the Universidad Nacional Autónoma de México, and deposited in the Regional Collection of Invertebrates (ICML-EMU), in Mazatlán, Mexico, we found numerous specimens assigned to *Pagurus gladius* (Benedict, 1892), and one of *Pagurus* that did not match any of the known species of this genus from the region. A thorough review of the morphology of this material revealed that *P. gladius* should be transferred to the genus *Spathapagurus* Lemaitre and Felder, 2011, while the specimen of *Pagurus* represents a new species. As Benedict’s (1892) description of *Eupagurus gladius* was brief and lacked illustrations, we herein provide a redescription of this taxon and formally reassign it to *Spathapagurus*. The type specimens used by Benedict as well as additional material collected since then, and deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), have also been studied and added to the present report. We present herein a full description with illustrations of the new species of *Pagurus*, making it the fifteenth of this genus known from the eastern Pacific.

General terminology for the descriptive text follows McLaughlin (2003). Measurements in millimeters (mm) indicated in the material examined sections are of shield length, measured from the midpoint of the rostral lobe to the midpoint of the posterior margin of the shield. The length of the ocular peduncle was obtained by measuring the total length of the ultimate peduncular segment along the lateral face, including the cornea. Geographic names are used with their

original spelling. In the material examined section stations are listed North to South. Other abbreviations used: AHF, Allan Hancock Foundation; NS, not sexed; NM, not measured; ovig, ovigerous; sta, station; USFC United States Fish Commission; CORTES, series of three cruises in the Gulf of California; BBMAZ, series of cruises in the Bay of Mazatlán SW, Gulf of California; B/E FC1, “Buque Escuela Ferro-cemento 1”.

## SYSTEMATICS

### Infraorder Anomura MacLeay, 1838

### Superfamily Paguroidea Latreille, 1802

### Family Paguridae Latreille, 1802

### Genus *Spathapagurus* Lemaitre and Felder, 2011

### *Spathapagurus gladius* (Benedict, 1892) **comb. nov.** (Figs. 1A–E, 2A–F, 3A–G, 4A–F)

*Eupagurus gladius* Benedict, 1892: 7 [type locality: USFC Albatross sta 2823, Isla Cerralvo, Gulf of California]. — Nobili, 1901: 22.

*Pagurus gladius*. — Rathbun, 1910: 597. — Haig et al., 1970: 21. — Snyder-Conn, 1980: 283. — Brusca, 1980: 283, fig. 18.12. — Hendrickx, 1993: 309. — Hendrickx and Harvey, 1999: 372. — Boschi, 2000: 105. — Lemaitre and Cruz-Castaño, 2004: 78. — Hendrickx et al., 2006: 38. — Vargas and Cortés, 2006: 482. — McLaughlin et al., 2010: 33. — Olguín and Mantelatto, 2013: 439, figs. 1, 2.

*Type material*. Lectotype herein selected, male (5.4 mm), USNM 16723, USFC “Albatross” sta 2823, Isla Cerralvo, Gulf of California, 24°18’00”N 110°22’00”W, 48.5 m depth, 30 April 1888. Paralectotypes, 2 males (4.0 mm and 4.9 mm), USNM 108262, same station data as lectotype.

*Other material*. Eastern Pacific: 1 ovig female (4.3 mm), USNM 110944, USFC “Albatross” sta 3026, 31°22’00”N 114°07’45”W, Gulf of California, Sonora, west of Adair Bay, 31 m, 25 March 1889; 4 males (3.7–4.8 mm), 1 ovig female (4.5 mm),

USNM 16728, USFC “Albatross”, same station data as previous lot; 1 male (4.4 mm), ICML-EMU 4115C, off Rocas Consag, Gulf of California, Mexico, R/V “El Puma”, CORTES 2 sta 37, 31°16'12"N 114°22'06"W, 32 m, 16 March 1985; 2 males (5.9–6.0 mm), 3 ovig females (4.2–4.8 mm), ICML-EMU 4050A, off Rocas Consag, Mexico, R/V “El Puma”, CORTES 1 sta 37, 31°16'12"N 114°22'30"W, 35 m, 9 May 1982; 1 female (3.9 mm), 1 ovig female (4.2 mm), ICML-EMU 4051, off Rocas Consag, Mexico, R/V “El Puma”, CORTES 2 sta 38, 31°09'18"N 114°15'30"W, 65 m, 16 March 1985; 8 males (5.6–6.7 mm), 10 ovig females (4.7–5.3 mm), ICML-EMU 4050B, off Rocas Consag, Mexico, R/V “El Puma”, CORTES 1 sta 38, 31°09'N 114°15'18"W, 60 m, 9 May 1982; 3 males (3.3–4.0 mm), USNM 16727, USFC “Albatross” sta 3022, Gulf of California, Sonora, San Jorge Bay, 30°58'30"N 113°17'15"W, 20 m, 24 March 1889; 1 male (5.6 mm), USNM 16726, USFC “Albatross” sta 3020, Gulf of California, Sonora, Cape Tepoca, El Desemboque, 30°37'30"N 113°07'00"W, 13 m, 24 March 1889; 2 males (3.7–4.5 mm), ICML-EMU 4115B, N. of Isla Tiburón, Gulf of California, Mexico, R/V “El Puma”, CORTES 2 sta 27, 29°28'N 112°29'12"W, 41 m, 14 March 1985; 1 male (3.9 mm), 2 ovig females (3.6–4.5 mm), ICML-EMU 4069, Tiburón Island, Gulf of California, Mexico, R/V “El Puma”, CORTES 1 sta 27, 29°26'00"N 112°26'00"W, 14 March 1985; 4 males (3.7–4.9 mm), 1 female (3.0 mm), 1 ovig female (5.4 mm), USNM 16725, USFC “Albatross” sta 3014, Gulf of California, south of Tiburón Island, Sonora, 28°28'00"N 112°04'30"W, 53 m, 23 March 1889; 1 male (3.7 mm), 1 ovig female (3.1 mm), USNM 16724, USFC “Albatross” sta 3013, Gulf of California, south of Tiburón Island, Sonora, 28°23'45"N 111°58'00"W, 26 m, 23 March 1889; 6 males (4.7–5.7 mm), ICML-EMU 4115A, off Cabo San Miguel, Gulf of California, Mexico, R/V “El Puma”, CORTES 2 sta 20, 28°08'12"N 112°45'24"W, 55 m, 13 March 1985; 1 ovig female (2.8 mm), ICML-EMU 4116B, off Punta Arboleda, Gulf of California, Mexico, R/V “El Puma”, CORTES 1 sta 16, 26°55'36"N 110°05'06"W, 23 m, 5 May 1982; 1 male (4.5 mm), USNM 16729, USFC “Albatross” sta 3037, Gulf of California, Sonora, south of Guaymas, 27°45'00"N 110°45'00"W, 37 m, 31 March 1889; 1 female (1.8 mm), USNM 1289682, AHFR/V “Velero III”, sta 520–36, 24°23'N 111°33'W, Baja California

Sur, Agua Verde Bay, 9–18 m, 27 February 1936; 3 males (4.2–5.5 mm), 1 female (3.2 mm), ICML-EMU 4116A, off Santa María Bay, Gulf of California, Mexico, R/V “El Puma”, CORTES 1 sta 3, 25°02'42"N 108°31'30"W, 28 m, 3 May 1985; several disintegrated dried specimens, USNM 16722, USFC “Albatross”, sta 2822, Gulf of California, Baja California, Cerralvo Island, 24°16'0"N 110°22'00"W, 28 m, 30 April 1888; 1 male (2.4 mm), USNM 1289681, USFC “Albatross”, Lower California cruise, [no sta number or other data]; 2 males (2.8 mm and 4.3 mm), 3 females (2.2–2.7 mm), USNM 1156044, Baja California Sur, Santa Maria Bay, 18.3–36.6 m, 22 January 1938, coll. S.A. Glassell; 1 male (4.1 mm), ICML-EMU 1347, Mazatlán Bay, Gulf of California, Mexico, B/E FC1 BBMAZ cruise 13 sta 5, 23°12'06"N 106°28'56"W, 18 m, 26 June 1980; 1 male (4.9 mm), ICML-EMU 0928, Mazatlán Bay, Gulf of California, Mexico, B/E FC1, BBMAZ cruise 18 sta 18, 23°10'53"N 106°26'11"W, 13 m, 14 March 1981; 1 ovig female (4.4 mm), ICML-EMU 4116C, off Banco Gordo, Gulf of California, Mexico, R/V “El Puma”, CORTES 1 sta 55, 23°08'30"N 109°27'24"W, 38 m, 13 May 1982; 1 female (1.9 mm), 1 ovig female (2.2 mm), USNM 1289685, Mexico, Tenacatita Bay, AHFR/V “Velero III”, sta 485–35, 19°18'N 104°50'W, 9 m, 15 February 1935; 1 male (2.5 mm), 2 ovig females (2.2 mm and 2.3 mm), USNM 1289686, Mexico, Tenacatita Bay, AHFR/V “Velero III”, same station data as previous; 1 female (2.2 mm), USNM 1289677, Mexico, Acapulco Bay, 16°50'N 99°53'W, April 1930, coll. H. Lowe; 1 male (3.3 mm), 2 females (2.8 mm and 3.3 mm), USNM 1289687, Mexico, Tangola-Tangola Bay, Santa Cruz Bay, AHFR/V “Velero III”, sta 259–34, 15°45'N 96°06'12"W, 27–37 m, 28 February 1934; 15 males (1.6–3.1 mm), 2 females (2.2 mm and 2.3 mm), 5 ovig females (1.8–3.4 mm), USNM 1289674, Costa Rica, Salinas Bay, AHFR/V “Velero III”, sta 480–35, 11°04'10"N 85°44'40"W, 22 m, 11 February 1935; 1 male (1.9 mm), USNM 1289688, Costa Rica, Salinas Bay, AHFR/V “Velero III”, sta 478–35, 11°03'13"N 85°44'10"W, 2.7 m, 11 February 1935; 1 male (4.0 mm), USNM 1289684, Costa Rica, Port Parker, AHFR/V “Velero III”, sta 472–35, 10°57'50"N 85°48'45"W, 55 m, 9 February 1935; 2 males (2.8 mm and 4.6 mm), 1 female (1.8 mm), 1 ovig female (3.0 mm), USNM 1289676, Ecuador, Santa Elena Bay, 02°10'S 80°52'W,

[no depth], 9 February 1934; 1 male (3.7 mm), 3 females (1.9–2.8 mm), USNM 1289675, R/V “Stranger” sta 15, Ecuador, Santa Elena, La Libertad, 02°12’S 80°54’W, 15 m, 21 February 1939, coll. Fred E. Lewis.

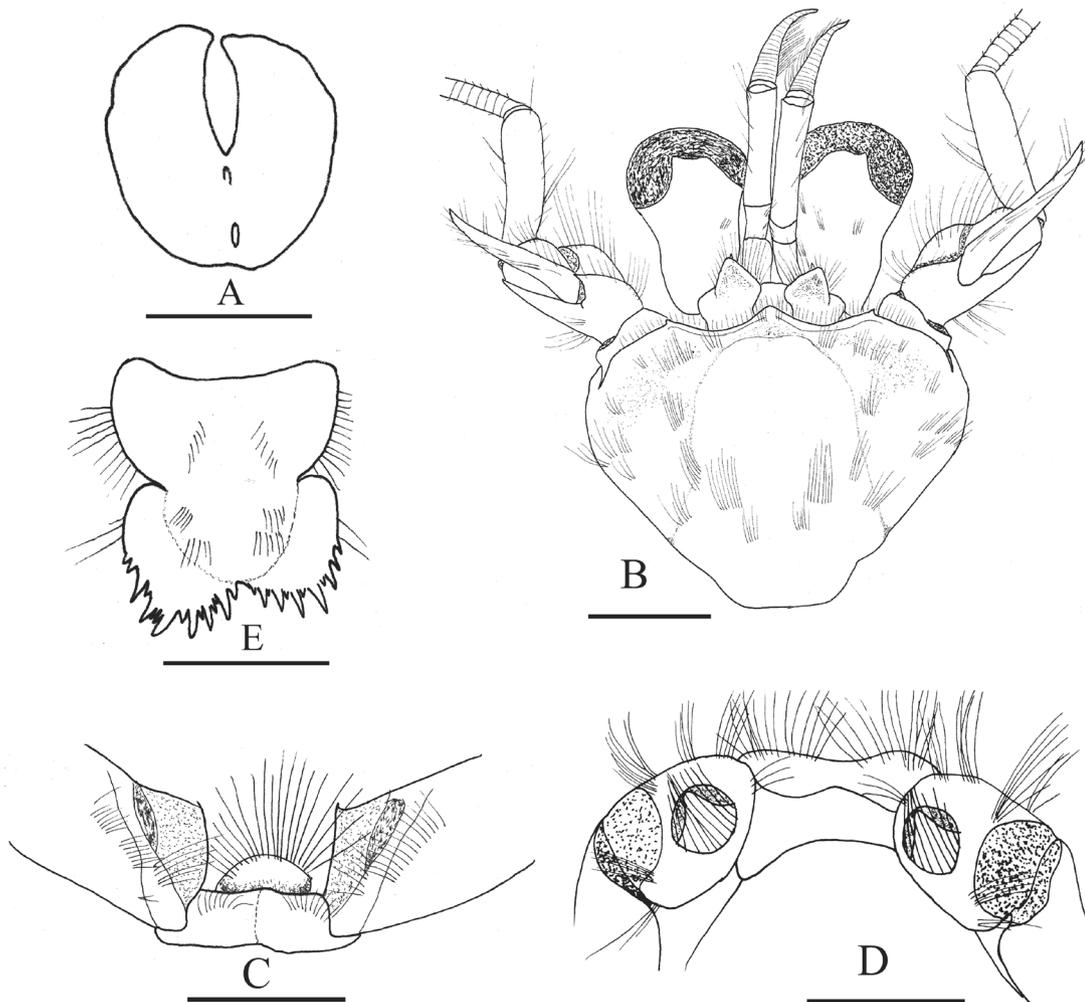
**Redescription.** Eleven pairs of biserial gills (Fig. 1A) at most weakly divided distally. Shield (Fig. 1B) about 1.3 times as broad as long; anterolateral margins sloping; anterior margin between rostrum and lateral projections concave, fringed by short setae; anterolateral angle with slit; posterior margin roundly truncate; dorsal surface flattened, with numerous tufts of short setae. Rostrum obtusely triangular, length slightly exceeding lateral projections in distal extension; lateral projections obtusely triangular, armed with small terminal spine.

Ocular peduncles (Fig. 1B) stout, short, approximately 0.6 length of shield, slightly constricted

medially, dorsal surface with few tufts of short setae. Cornea dilated, width about 0.7 length of ocular peduncle. Ocular acicles bluntly subtriangular, weakly concave dorsally, tip subacute, with small, submarginal spine, and moderately long setae, acicles separated basally by about basal width of one acicle.

Antennular peduncle (Fig. 1B), when extended, exceeding ocular peduncles by 0.7 length of ultimate segment; ultimate and penultimate segments both with few short setae on dorsal surface; basal segment with moderately strong spines on laterosubdistal margin.

Antennal peduncle (Fig. 1B) moderately long, when extended, exceeding ocular peduncle by 0.5 length of ultimate segment. Fifth segment unarmed, with scattered setae on dorsal and ventral margins. Fourth segment unarmed, with scattered setae. Third segment with small spine on ventrodistal margin,

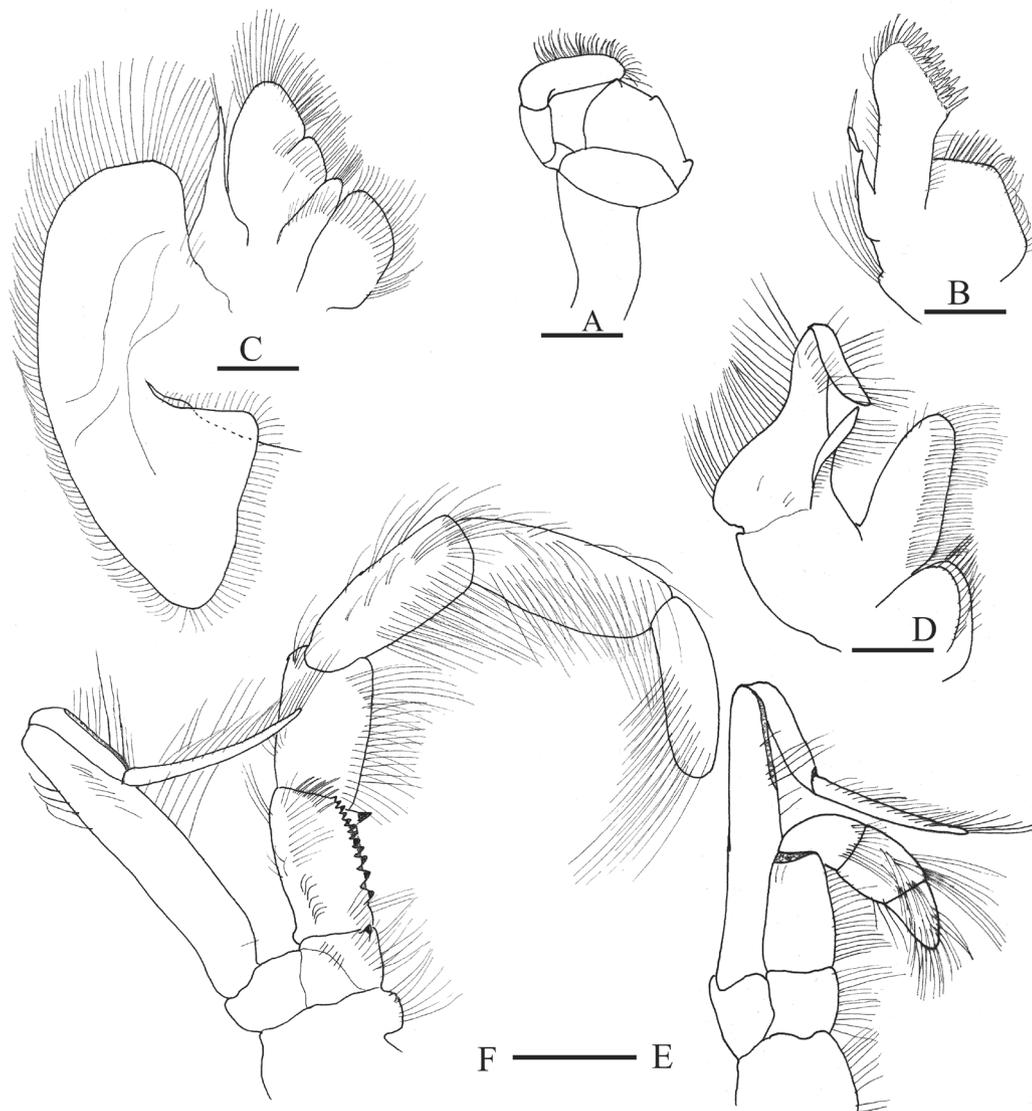


**Figure 1.** *Spathapagurus gladius* (Benedict, 1892) comb. nov., male 4.9 mm, Mazatlán Bay, Gulf of California (ICML-EMU 928). **A**, Gill lamella; **B**, shield and cephalic appendages, dorsal view; **C**, thoracic sternite XII, ventral view; **D**, thoracic sternite XIV, coxae of fifth pereopods, and gonopores with sexual tubes, ventral view; **E**, telson, dorsal view. Scale bars: 1 mm (A, E), 2 mm (B–D).

partially obscured by tufts of setae. Second segment with dorsolateral distal angle reaching about 0.4 of antennal acicle, terminating in strong spine; lateral margin unarmed; dorsomesial distal angle with strong spine; mesial margin with short setae. First segment lateral margin unarmed; ventral margin produced, with 1 small laterodistal spine. Antennal acicles moderately long, exceeding length of ocular peduncles by 0.3 times their length, terminating in spine; dorsal surface and mesial margin with tufts of short setae. Antennal flagella long, reaching to distal third of right cheliped; each article with few bristles less than 1 article length.

Mandible (Fig. 2A) with upper and lower incisor edges calcareous; palp 3-segmented, ultimate segment

setose, slightly longer than combined length of penultimate and basal segments. Maxillule (Fig. 2B) with proximal endite subquadrate, distal endite subrectangular, enlarged distally; endopod with external lobe moderately developed, not recurved; internal lobe with long terminal bristle. Maxilla (Fig. 2C) with endopodite inflated basally, exceeding scaphognathite by 0.3 in distal extension. First maxilliped (Fig. 2D) with endopodite approximately 0.6 length of exopodite; basal segment of exopodite inflated. Second maxilliped (Fig. 2E) without distinguishing characters. Basis of third maxilliped (Fig. 2F) with 1 strong spine; ischium with well-developed crista dentata, consisting of 9–12 corneous-tipped teeth and 1 accessory tooth; merus unarmed.



**Figure 2.** *Spathapagurus gladius* (Benedict, 1892) comb. nov., male 4.9 mm, Mazatlán Bay, Gulf of California (ICML-EMU 928). Left mouthparts, internal view: **A**, Mandible; **B**, maxillule; **C**, maxilla; **D**, first maxilliped; **E**, second maxilliped; **F**, third maxilliped. Scale bar: 1 mm.

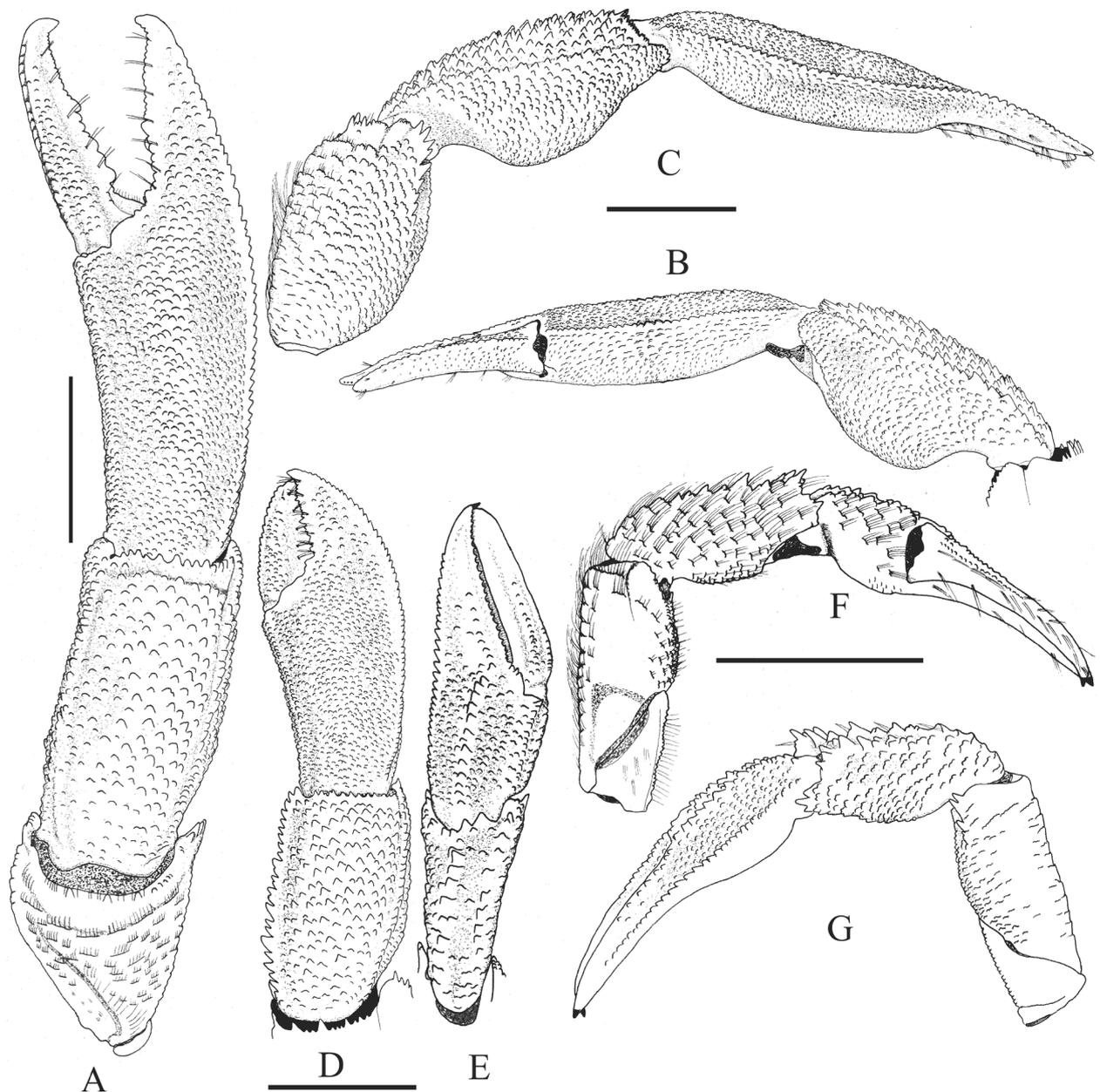
Chelipeds unequal, right (Fig. 3A–D) long and slender, twice as long as left cheliped; chela 2 (female) to 3 (males) times longer than broad; palm, fixed finger and dactyl slender, dorsoventrally compressed. Fingers each with dorsal and ventral row of tufts of setae parallel to and near cutting edges; dorsal surfaces somewhat flattened, with numerous small tubercles or protuberances, each terminating in calcareous claw, often worn. Dactyl moderately long, about 0.8 length of propodus; cutting edge with row of 6 or 7 strong calcareous teeth on proximal half, and row of small calcareous teeth on distal half; dorsomesial margin delimited by row of small tubercles decreasing in size distally. Fixed finger broader than dactyl, broader in females (Fig. 3D) than in males (Fig. 3A); lateral margin delimited by row of tubercles decreasing in size distally; cutting edge with moderately prominent calcareous tooth at midlength, 5–7 smaller calcareous teeth on proximal half, and row of small calcareous teeth on distal half. Palm slightly shorter than carpus, dorsomesial margin distinctly delimited by row of small granules or tubercles; mesial face rounded, sloping, covered with numerous small tubercles; dorsolateral margin well delimited by row of spines or tubercles, dorsal surface moderately elevated along midline, covered with numerous small granules or tubercles. Carpus distinctly longer than merus, with dorsal surface convex, and moderately produced ventrally, 1.8–2.1 times longer than broad, broader in females than in males; dorsomesial margin weakly expanded, armed with row of small spines of different size; dorsodistal margin with row of strong or moderately strong spines; dorsal surface with numerous spiny granules or tubercles and scattered setae; dorsolateral margin delimited by row of spiny granules or tubercles; mesial, lateral, and ventral surfaces with small granules or tubercles; mesial face strongly sloping, nearly perpendicular to dorsal face. Merus subtriangular; dorsodistal margin with 3–5 well-spaced, small spines; dorsal and ventrolateral surfaces with transverse, sparsely setose furrows; ventromesial and ventrolateral margins each with row of spines, ventrolateral angle with several spiny teeth, ventral surface usually with few scattered granules and sparse, moderately long setae. Ischium unarmed or with inconspicuous small protuberances on dorsal and ventral surfaces.

Left cheliped (Fig. 3E–G) slender, scarcely reaching base of right cheliped palm; dactyl and fixed finger weakly arched ventrally; fingers with ventral row of setal tufts parallel to and near cutting edges, each finger terminating in inwardly directed corneous claw. Dactyl 1.8–2.0 length of palm; cutting edge with row of small corneous teeth; dorsal surface slightly elevated in midline, with row of small granules or tubercles on proximal half; dorsomesial margin not well defined, with row of small spine-like tubercles extending on proximal half, mesial surface with row of long setal tufts. Fixed finger broader than dactyl, somewhat expanded laterally, dorsal surface with few small tubercles or granules on proximal half; cutting edge with row of small calcareous teeth interspersed with small corneous teeth. Palm 0.6–0.7 length of carpus; dorsomesial margin with row of small granules or tubercles; mesial surface with scattered small tubercles and short setae; dorsal surface with numerous minute granules or tubercles, and distinctly elevated on midline and armed with longitudinal row of small spine-like tubercles; dorsolateral margin with row of small spinules or granules; ventral surface with scattered tufts of long setae. Carpus slightly shorter than merus; dorsal surface somewhat flattened, with dorsomesial and dorsolateral rows of spine-like tubercles; dorsodistal margin with row of spine-like tubercles; mesial face with numerous small tubercles and short setae; lateral face covered with small spine-like tubercles, ventrolateral margin produced in moderately strong spine. Merus subtriangular; dorsal surface with transverse, sparsely setose furrows; mesial surface with few small tubercles and with tufts near to ventral margin; ventrolateral margin with row of spines largest distally; ventral surface granulose and tufts of short setae. Ischium with row of small calcareous spines on ventromesial margin.

Second and third pereopods similar left from right, slender, of similar length (Fig. 4A–D). Dactyls curved, twisted, 1.5–1.7 times length of propodi; dorsal margins each with few spines on proximal half, and sparse row of short stiff setae; ventromesial margins each with row of 20–22 small corneous spinules; mesial faces each with row of small corneous spines near dorsal margin, and weak median longitudinal sulcus; lateral faces each with weak longitudinal sulcus. Propodi about 1.3 times length of carpi; dorsal

margin each with row of small spines or spine-like tubercles and sparse short setae; dorsomesial and dorsolateral faces each with numerous small spine-like tubercles or tubercles fringed with very short stiff setae; ventral margin with small spines or granules; ventromesial and ventrolateral faces with numerous small spine-like tubercles or tubercles, fringed with very short setae. Carpi each with row of spines and sparse setae on dorsal margin, and 1 or 2 spines on dorsodistal angle; mesial surfaces each with few small

granules near dorsal margin; dorsolateral faces each with few spine-like tubercles fringed distally with short stiff setae; ventral margin unarmed. Meri with low protuberances and tufts of setae on dorsal surfaces; lateral and mesial faces glabrous; ventral margin with few minute spines or tubercles, at least distally. Ischia unarmed or with minute granules on ventromesial margin and stiff setae or bristles dorsally. Anterior lobe of thoracic sternite XII (of third pereopods) (Fig. 1C) subcircular, with long stiff bristles.



**Figure 3.** *Spathapagurus gladius* (Benedict, 1892) comb. nov., male 4.9 mm, Mazatlán Bay, Gulf of California (ICML-EMU 928), A–C, E–G; ovig female 4.0 mm, off Rocas Consag, Gulf of California (ICML-EMU 4050-A), D. A, Right cheliped, dorsal view; B, palm and propodus of right cheliped, mesial view; C, right cheliped, outer view; D, palm and propodus of right cheliped, dorsal view; E, palm and propodus of left cheliped, dorsal view; F, left cheliped, mesial view; G, left cheliped, outer view. Scale bar: 5 mm.

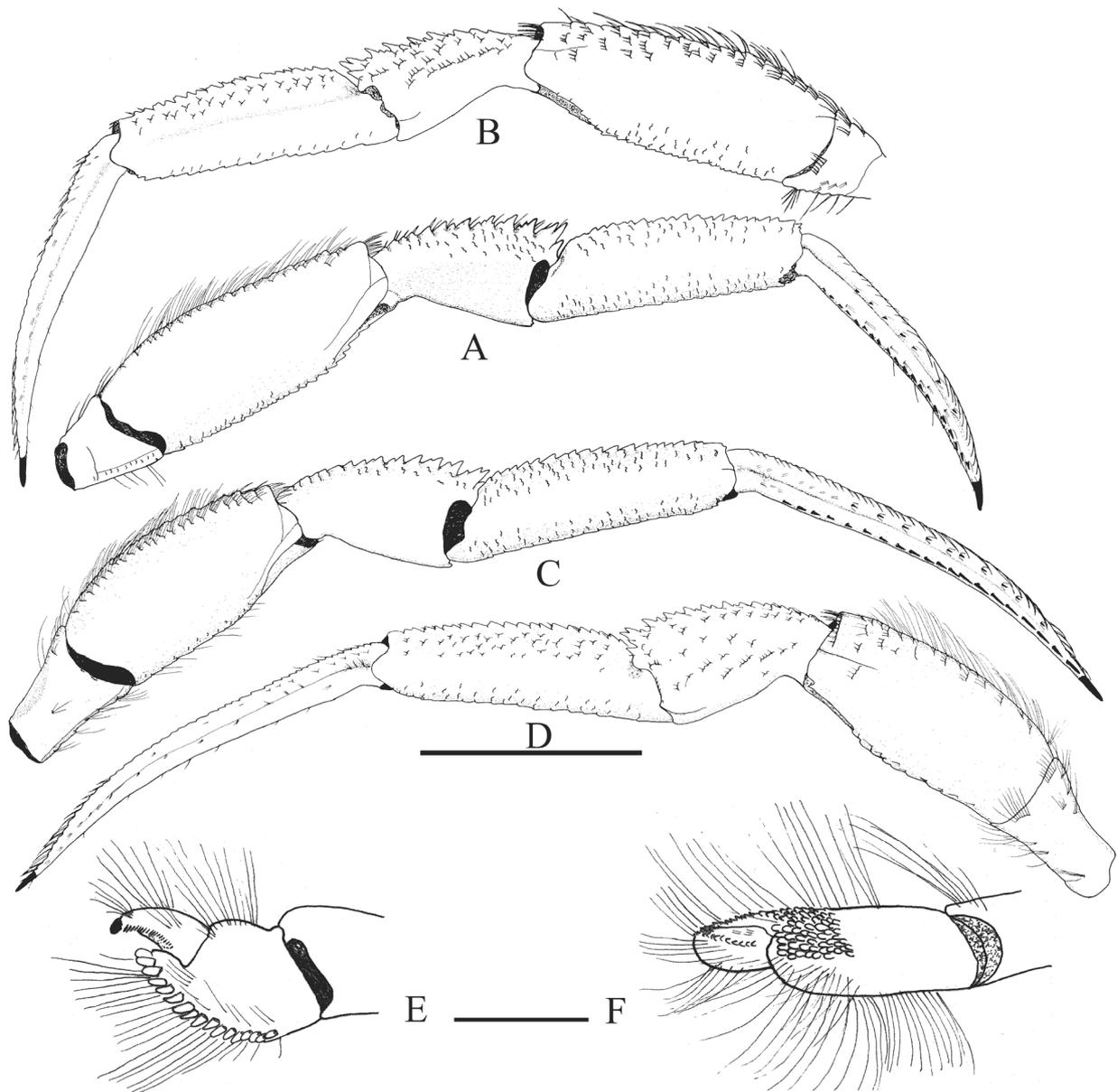
Fourth pereopods (Fig. 4E) without preungual process at base of claw on lateral face of dactyl; propodal rasp with single row of lanceolate scales.

Fifth pereopod (Fig. 4F) chelate. Dactyls with one row of small ovate scales. Propodal rasp with 8–9 rows of lanceolate scales, extending posteriorly nearly to midlength of propodus. Coxae weakly asymmetrical.

Males with paired, short sexual tubes consisting of slight protrusions of vas deferens partially masked by stiff, long, forwardly directed setae on coxae around margins of gonopores (Fig. 1D); unpaired left pleopods 3–5 with exopods well developed and

endopods rudimentary. Females without paired pleopods 1; pleopods 2–4 with endopods stout, exopods long, slender; pleopod 5 weakly developed, uniramous.

Uropods markedly asymmetrical. Telson (Fig. 1E) subquadrate, with transverse indentation; anterior lobes each with tuft of long setae; posterior lobes asymmetrical, left slightly longer than right, separated by small round cleft in inverted U-shaped; posterior half of lateral margins and terminal margins armed with spines (strongest on left lobe) interspersed with small spines, terminal margins slightly convex.



**Figure 4.** *Spathapagurus gladius* (Benedict, 1892) comb. nov., male 4.9 mm, Mazatlán Bay, Gulf of California (ICML-EMU 928). **A**, Left second pereopod, mesial view; **B**, left second pereopod, outer view; **C**, left third pereopod, mesial view; **D**, left third pereopod, outer view; **E**, propodus and dactyl, left fourth pereopod, outer view; **F**, propodus and dactyl, left fifth pereopod, outer view. Scale bars: 5 mm (A–D), 1 mm (E, F).

*Color.* According to Brusca (1980: 283): “In life the carapace is orange to red, lightly speckled with pale green. Abdomen slightly lighter in color. Chelae pinkish-buff, with a light purplish tinge and speckled with pale brown and red small blotches. Eystalks pale orange, cornea dark green to black. Walking legs pale gray with two orange bands and a bright red band on the merus (not distinct in all specimens), and vague red or purple bands on the propodus. Entire ventral side of the hermit crab pinkish-buff, except on the frontal portion, which is scarlet red”. According to Glassell (1937: 258): “In alcohol the carapace is a dark cream maculated with red and purple. Chelipeds and ambulatories with a purple tinge and red spots; a dark purple stain on hand near dactyl; propodus and dactyli of ambulatories banded with purple. Eye-stalks mottled”.

*Habitat.* On sandy substrates, at a depth range of 2.7 to 65 m, although mostly in less than 55 m. In waters ranging in temperatures of 13.6–25 °C, and oxygen concentration of 2.56–5.4 ml/l (Hendrickx et al., 2006). Glassell (1937) mentioned that this species uses shells partially disintegrated by the action of bryozoans or polyps. The unidentified polypoid growth can form a large, flexible, spiral home for the crab.

*Geographic distribution.* Eastern Pacific: from Tosca Point, west coast of Baja California Sur, the Gulf of California and further south on the coasts of Mexico, Costa Rica, and Ecuador (Nobili, 1901; Rathbun, 1910; Haig et al., 1970; Hendrickx and Harvey, 1999; this report).

*Morphological variations.* The rostrum can be broadly rounded and unarmed or terminate in a small spine. The right cheliped in larger males (shield length > 4 mm) is longer and more slender than in females (Fig. 3A, D).

*Remarks.* The study of Benedict’s (1892) types of *Pagurus gladius* has shown that this species clearly exhibits all diagnostic characters of *Spathapagurus*, and is therefore reassigned to that genus along with the other two congeneric species, the eastern Pacific *Spathapagurus collinae* Lemaitre and Felder, 2011, and

the western Atlantic *Spathapagurus longimanus* (Wass, 1963). Most striking in species of *Spathapagurus* are the grossly unequal chelipeds, the right being twice, or more, as long as the left and with a flattened, spatulate chela. Other primary characters of these species include: 11 pairs of phyllobranch gills, absence of preungual process on the fourth pereopod, and in males, paired, short sexual tubes that slightly protrude from the gonopores and are masked by forwardly directed setae.

*Spathapagurus gladius* comb. nov. can be distinguished from the other congeners by several characters. The relative length of the antennular and antennal peduncles are proportionally shorter in *S. gladius* comb. nov. than in *S. collinae*, but longer than in *S. longimanus*. The antennal acicles are proportionally longer relative to the ocular peduncles in *S. gladius* comb. nov. than in the two other congeners. The length/width ratio of the right chela is proportionally greater in *S. longimanus* than in *S. collinae* and *S. gladius* comb. nov., reaching 3 in females and 4 in males of the former, whereas in the latter two species it reaches 2 in females and 3 in males. The armature of the palm of the right and left chelipeds of *S. gladius* comb. nov. is more granulose than in *S. collinae* and *S. longimanus*. The ambulatory legs in *S. gladius* comb. nov. have dactyls that each bear a longitudinal row of small corneous spines on the mesial surface, and the propodi and carpi have numerous spine-like tubercles on mesial and lateral surfaces, whereas in *S. collinae* and *S. longimanus* those segments are unarmed.

*Phylogenetic relationships.* Benedict (1892) noted, without providing any details, that his *Eupagurus gladius* (= *Pagurus gladius*) “is closely allied to *longicarpus* [= *Pagurus longicarpus* (Say, 1817), a western Atlantic species] and related species”. Both *P. gladius* and *P. longicarpus* have an elongated right cheliped, a similarity that possibly led Benedict to suggest a relationship between these two species. However, the chela of the right cheliped in *P. longicarpus* is not flattened as in *P. gladius*, and other characters exhibited by *P. longicarpus* also do not conform with the morphology that defines the species of *Spathapagurus*.

In a recent study using molecular data, Olguín and Mantelatto (2013) evaluated the phylogenetic

position of species of *Pagurus* from the Pacific and Atlantic coasts of South America that several authors had previously placed in three groups (“provenzanoï” group, “comptus” group, and “exilis” group) of the 11 groups that informally have been proposed for several species of this genus (see Forest and de Saint Laurent, 1968; McLaughlin, 1974; Ingle, 1985). In addition to *P. gladius*, the “exilis” group originally included five other species, three of which, *P. perlatus*, *Pagurus exilis* (Benedict, 1892), and *P. longicarpus*, occur in South America. Olguín and Mantelatto (2013) added *Pagurus pollicaris* Say, 1817, a western Atlantic species known from the eastern coast of the United States and the Gulf of Mexico to the Florida Keys, to the “exilis” group. *Pagurus longimanus*, a western Atlantic species originally placed in the “exilis” group, was removed from that group and reassigned by Lemaitre and Felder (2011) to *Spathapagurus*. Olguín and Mantelatto’s (2013) analysis of the molecular data showed that *P. gladius*, *P. exilis*, *P. perlatus*, and *P. longicarpus*, form a stable and well supported grouping or clade. With *P. gladius* now reassigned to *Spathapagurus* based on clear morphological grounds, it seems desirable to expand Olguín and Mantelatto’s (2013) analysis to include more taxa of *Pagurus* (not just the ones that occur in South America) in order to ascertain more accurately the relationships of the species that have been included in the “exilis” group.

***Pagurus marysolae* sp. nov.**  
(Figs. 5A–H, 6A–E)

Zoobank: [urn:lsid:zoobank.org:act:D44075F5-8539-4208-9051-E1151C64FB3A](https://zoobank.org/urn:lsid:zoobank.org:act:D44075F5-8539-4208-9051-E1151C64FB3A)

*Material examined.* Holotype: female (5.1 mm), ICML-EMU 13284, off Altata, Sinaloa, Gulf of California, Mexico, 24°27'00"N 107°44'17"W, trawl, 16 m, 23 July 2010.

*Description.* Eleven pairs of biserial gills at most weakly divided distally (Fig. 5A). Shield (Fig. 5B) about 1.1 times as broad as long; anterolateral margins sloping; anterior margin between rostrum

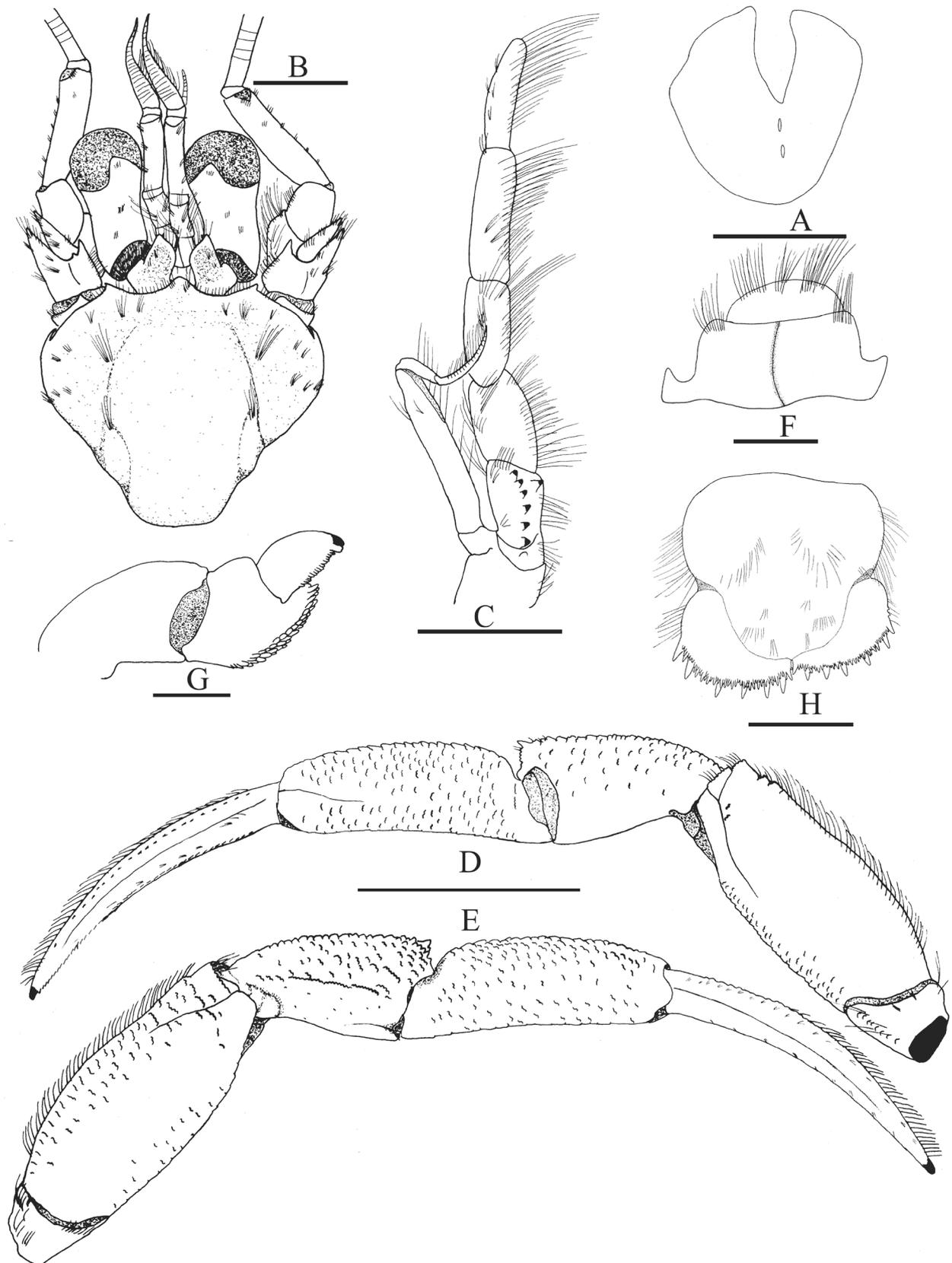
and lateral projections concave; anterolateral angle with slit; posterior margin roundly truncate; dorsal surface flattened, with numerous tufts of short setae. Rostrum obtusely triangular, slightly exceeding lateral projections in forward extension; lateral projections obtusely triangular, armed with small terminal spine.

Ocular peduncles (Fig. 5B) stout, short, approximately 0.6 length of shield; slightly constricted medially, dorsal surface with few tufts of short setae. Cornea dilated, width about 0.5 length of ocular peduncle. Ocular acicles bluntly subtriangular, concave dorsally, tip rounded, with small, submarginal spine barely visible in dorsal view, moderately long setae distally; acicles separated basally by about 0.5 basal width of 1 acicle.

Antennular peduncle (Fig. 5B), when totally extended, exceeding ocular peduncle by 0.5 length of ultimate segment; ultimate and penultimate segments both with few short, dorsal setae; basal segment with moderately strong spines on latero-subdistal margin.

Antennal peduncle (Fig. 5B) moderately long, when totally extended exceeding ocular peduncle by 0.7 length of ultimate segment. Fifth segment unarmed, scattered setae on dorsal and ventral margins. Fourth segment unarmed, with scattered setae. Third segment unarmed; ventral margin with tufts of setae. Second segment with dorsolateral distal angle produced, almost reaching distal margin of antennal acicle, terminating in strong spine; lateral margin unarmed; dorsomesial distal angle with strong spine, and small median spine dorsodistally on left side (at least on holotype); mesial margin with short setae. First segment with 1 small ventrolateral distal spine. Antennal acicles short, almost straight, reaching 0.5 length of the fourth antennal segment, terminating in small spine; dorsal surface and mesial margin with tufts of short setae. Antennal flagella long, exceeding tip of right cheliped; each article with few short bristles.

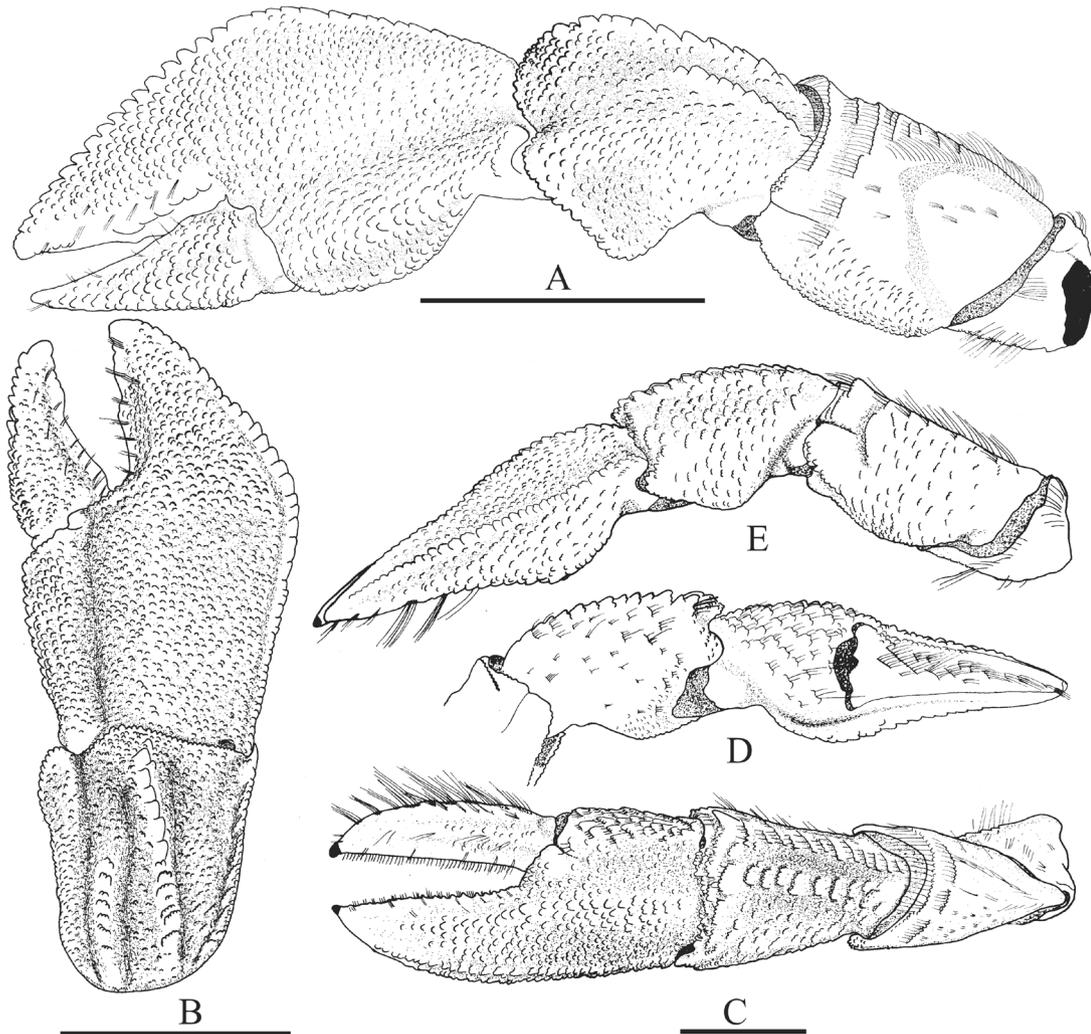
Third maxilliped (Fig. 5C) with basis-ischium fusion incomplete; basis with 1 small spine; ischium with crista dentata well developed, consisting of 6 corneous-tipped teeth and 1 accessory tooth; merus unarmed. Sternite with small spine and tuft of long setae on each side of midline.



**Figure 5.** *Pagurus marysolae* sp. nov., holotype, female 5.1 mm (ICML-EMU 13284). **A**, Gill lamella; **B**, shield and cephalic appendages, dorsal view; **C**, left third maxilliped; **D**, second right pereiopod, mesial view; **E**, same, outer view; **F**, thoracic sternite XII, ventral view; **G**, dactyl, propodus and carpus of fourth right pereiopod, outer view; **H**, telson, dorsal view. Scale bars: 1 mm (**A**, **E-H**), 2 mm (**B**), 5 mm (**C**, **D**).

Chelipeds unequal (Fig. 6A–E), right longer than left. Right cheliped long, stout (Fig. 6A, B). Dactyl moderately long, as long as propodus; mesial and dorsal surfaces with small conical spines or granules, and row of short setae near cutting edge; mesial margin with row of small conical spines increasing in size distally; cutting edge with row of small calcareous teeth on distal third, ending in calcareous claw. Palm broader than long, slightly bent upward; dorsal, mesial, lateral, and ventral surfaces thickly set with flattened granules, more prominent distally and on fixed finger, a weak longitudinal depression near dorsomesial margin; dorsomesial margin not well delimited, rounded, with numerous small granules or tubercles; mesial surface weakly concave medially; dorsolateral margin with prominent conical calcareous teeth or rounded granules, decreasing in size proximally and distally.

Fixed finger broadest proximally, cutting edge bearing few calcareous teeth and row of short setae near cutting edge, ending in calcareous claw. Carpus as long as palm; mesial surface flattened; upper face granulated and with 2 longitudinal granulated crests, inner the longest; dorsomesial margin not well defined; proximal 2/3 of dorsolateral margin with granulated crest; mesial, lateral and ventral surfaces with small granules. Merus armed with very small conical spines or granules on distal margin, numerous small conical spines or granules on mesial and lateral margins; dorsal margin with rows of small granules extending on mesial and lateral surface, tufts of long setae on proximal half; ventromesial margin somewhat inflated, bearing small tubercles; ventrolateral margin with small spines or denticles; ventral surface with small tubercles. Ischium with row of small denticles or spines on ventromesial margin.



**Figure 6.** *Pagurus marysolae* sp. nov., holotype, female 5.1 mm (ICML-EMU 13284). **A**, Right cheliped, mesiodorsal view; **B**, right cheliped, claw and carpus, dorsal view; **C**, left cheliped, dorsal view; **D**, left cheliped, claw and carpus, mesial view; **E**, left cheliped, outer view. Scale bars: 5 mm (A, B), 2 mm (C–E).

Left cheliped (Fig. 6C–E) enlarged, reaching to proximal 0.5 of palm of major cheliped, dactyl and fixed finger slightly curved ventrally. Dactyl about 1.5 times length of palm, dorsal surface weakly convex with few small granules or spine-like tubercles on proximal half; dorsomesial margin not well defined, with tufts of long setae; mesial surface with few flattened tubercles, with tufts of long setae proximally; cutting edge with corneous teeth, ending in large corneous claw. Palm slightly broader than long, 0.67 times length of carpus; dorsal surface convex and weakly elevated in middle, covered with rounded tubercles or granules, larger medially and on anterior half of fixed finger; dorsomesial margin not well delimited; dorsolateral margin with prominent rounded tubercles; ventral surface convex; mesial and lateral surfaces with tubercles, larger on mesial surface, fringed distally with short setae. Carpus as long as merus, subrectangular in dorsal view, mid-dorsal surface and dorsomesial margin with row of prominent tubercles fringed with small granules and short setae distally; mesial surface with flattened tubercles, with tufts of short, stiff setae; lateral and ventral surfaces covered with small, rounded tubercles; dorsodistal margin with granulated tubercles distally. Merus subtriangular in cross-section, dorsodistal and subdistal margins with numerous small, calcareous teeth or granules extending on lateral surfaces; mesial and outer surfaces with numerous short rows of small calcareous teeth; ventral surface covered with small granules; ventrolateral distal margin with few small calcareous teeth. Ischium with row of small calcareous spines on ventromesial margin; ventral surface with small, flattened granules.

Second (Fig. 5E, F) and third pereopods similar left from right, long, reaching 0.5 length of fixed finger of right cheliped. Dactyl slender, long and slightly curved ventrally, 1.3–1.6 times length of propodus, ending in sharp corneous claw; dorsal margins with row of minute granules on proximal third, decreasing in size distally and with long stiff setae; mesial faces with longitudinal groove medially, shallower distally; dorsomesial margin with row of corneous spines; lateral faces with narrow longitudinal groove medially, shallowest distally, flanked dorsally by tufts of very short setae; ventral margins each with

row of very slender spines. Propodus elongated, 1.3 times length of carpus; dorsal surfaces with short transverse rows of small protuberances fringed distally by short setae; mesial and lateral faces with numerous flattened protuberances or scale-like tubercles fringed with short setae. Carpus with numerous scale-like tubercles fringed with short setae on dorsal and outer surfaces, dorsodistal margin with strong spine; outer surface somewhat inflated, with few granules on distal margin; mesial surfaces with few flattened tubercles; ventral surfaces smooth. Merus 1.3–1.5 times length of carpus, dorsal surface with row of small protuberances becoming scale-like tubercles distally; distal margin fringed with small calcareous teeth; mesial surface smooth with longitudinal row of moderately long setae near dorsal margin, ventromesial margin with small, simple or toothed tubercles; outer surface and ventrolateral margin with numerous flattened protuberances or scale-like tubercles. Ischium with row of minute spines or spine-like tubercles on ventromesial margin. Anterior lobe of thoracic sternite XII (third pereopods) subovate (Fig. 5F), with long stiff setae on anterior margin.

Fourth pereopods (Fig. 5G) semichelate. Dactyl with preungual process at base of claw, with ventrolateral row of 15–17 closely set, small, corneous spines. Propodal rasp with 2 or 3 rows of lanceolate scales.

Fifth pereopods chelate. Dactyls with 4 rows of small ovate scales on proximal half and one row on distal half. Propodal rasp with 9 or 10 rows of lanceolate scales, extending posteriorly to nearly midpoint of segment. Coxae almost symmetrical.

Female with paired gonopores and unpaired pleopods 2–5. Pleopods 2–4 biramous, rami moderately developed; pleopod 5 with rudimentary endopod.

Uropods asymmetrical. Telson (Fig. 5H) subrectangular, posterior lobes asymmetrical, left slightly longer than right, separated by median cleft; terminal margins almost straight, each with 2 or 3 rows of calcareous spines; marginal spines longer than submarginal ones; anterior lobes unarmed, lateral margins with long setae.

*Color.* Live color unknown.

*Habitat.* Sandy substrate.

*Distribution.* Only known from the type locality in the Gulf of California, off Altata, Sinaloa, Mexico, at a depth of 16 m.

*Etymology.* The species is dedicated to Montserrat Marysol Ayón, daughter of the first author, using the middle name Marysol.

*Remarks.* *Pagurus marysolae* sp. nov. exhibits all the diagnostic characters of Group II (“exilis” group) of *Pagurus* proposed by Forest and Saint Laurent (1968) and subsequently emended by McLaughlin (1974), and thus can be included in that group. Among species of *Pagurus* from the eastern tropical Pacific, *P. marysolae* sp. nov. most closely resembles *Pagurus albus* (Benedict, 1892), *Pagurus pseudoalbus* Ayón-Parente and Wehrtmann, 2019, and to some extent *P. perlatus*. *Pagurus marysolae* sp. nov. does differ, however, in several characters. A comparison of these three species follows (Tab. 1).

In *P. marysolae* sp. nov. the antennal acicles are short, only reaching to 0.5 the length of the fourth antennal segment, whereas in *P. pseudoalbus* they reach the distal margin of the fourth antennal segment, and in *P. albus* and *P. perlatus* the antennal acicles exceed the fourth antennal segment. On the major cheliped, the proportion of the palm is 1.1 times broader than long in *P. marysolae* sp. nov., in lieu of as long as broad in *P. albus* and 1.3 times as long as broad in *P. perlatus*; in *P. marysolae* sp. nov. the carpus is subrectangular to subquadrate (vs. subtriangular in *P. albus*), the dorsomesial margin is not well defined (vs. well defined in *P. albus*), and there is a toothed crest near this margin

(absent in *P. albus*) extending up to 0.5 the proximal length; and the merus bears only minute denticles on the dorsodistal margin (vs. armed with 6 or 7 stout conical spines in *P. albus*). In *P. marysolae* sp. nov. the dactyl of the fourth pereopod has a preungual process, whereas the process is absent in *P. albus*.

In *P. marysolae* sp. nov. the antennal acicles reach to 0.5 of the fourth antennal segment, the merus and carpus of the third maxilliped are unarmed, whereas in *P. pseudoalbus* the antennal acicle reaches the distal margin of the fourth antennal segment, and the merus and carpus of the third maxilliped are both armed with small spines. In *P. marysolae* sp. nov. the dactyl of the major cheliped is as long as palm, and the palm is broader than long, the cutting edge of the fingers is armed distally with small, rounded teeth, whereas in *P. pseudoalbus* the dactyl of the major cheliped is shorter than palm, the palm is longer than broad, and the cutting edge of the fingers is armed with more numerous, sharper teeth. In *P. marysolae* sp. nov. there are two prominent longitudinal crests on the upper surface of the carpus of the major cheliped, whereas in *P. pseudoalbus* the upper surface of the carpus is slightly convex in the middle and covered with granules. In *P. pseudoalbus*, the cutting edge of the fixed and mobile fingers of the major cheliped bears sharper and more numerous teeth than in *P. marysolae* sp. nov. In *P. marysolae* sp. nov. the anterior lobe of thoracic sternite XII is subovate, and the fourth pereopod has a preungual process, whereas in *P. pseudoalbus* the anterior lobe of thoracic sternite XII is weakly bilobed, and the fourth pereopod lacks a preungual process.

**Table 1.** Comparison of morphological features of some species of *Pagurus* from the eastern tropical Pacific.

	<i>Pagurus marysolae</i> sp. nov.	<i>P. albus</i>	<i>P. perlatus</i>	<i>P. pseudoalbus</i>
Shield	1.1 times as broad as long	1.1 times as broad as long	As long as broad	1.2 times as broad as long
Antennal acicle	Reaching half length of the fourth antennal segment	Exceeding the fourth antennal segment	Exceeding the fourth antennal segment	Reaching the distal margin of the fourth antennal segment
Merus and carpus of third maxilliped	Unarmed	Armed with small spines	Unarmed	Armed with small spines
Palm of major cheliped	1.1 times broader than long	As long as broad	1.3 times as long as broad	1.3 times as long as broad
Anterior lobe of thoracic sternite XII	Subovate	Subrectangular	Subcircular	Subrectangular
Preungual process of the fourth pereopod	Present	Absent	Absent	Absent

Finally, *Pagurus marysolae* sp. nov. does show some resemblance to *P. perlatus*, although the two can be distinguished by a combination of characters. In both species the rostrum is obtusely triangular and longer than the lateral projections, but in *P. marysolae* sp. nov. the projections end in a small spine, whereas in *P. perlatus* the projections are unarmed. In *P. marysolae* sp. nov. the shield is broader than long, whereas it is as long as broad in *P. perlatus*. In *P. marysolae* sp. nov. the antennular peduncles exceeds the ocular peduncles by 0.5 length of the ultimate segment, whereas in *P. perlatus* the antennular peduncles are shorter than the ocular peduncles. In *P. marysolae* sp. nov. the antennal acicles do not exceed 0.5 the length of the fourth antennal segment, whereas they overreach the fourth antennal segment in *P. perlatus*. In *P. marysolae* sp. nov. the palm of the major cheliped is broader than long, whereas it is longer than broad in *P. perlatus*. In *P. marysolae* sp. nov. a preungual process is present on the fourth pereopod, whereas in *P. perlatus* this process is absent. In *P. marysolae* sp. nov. the posterior lobes of the telson are asymmetrical and convex, armed with 2 or 3 rows of calcareous teeth, whereas the posterior lobes are symmetrical and straight, armed with one row of calcareous teeth in *P. perlatus*.

## ACKNOWLEDGEMENTS

We greatly appreciate the support and help provided by Mercedes Cordero Ruiz (ICML, UNAM) and R. Gulledge (USNM) when inspecting the material deposited in the collections.

## ADDITIONAL INFORMATION AND DECLARATIONS

### Author Contributions

Conceptualization and Design: MAP, MEH, RL. Performed research: MAP, MEH, RL. Acquisition of data: MAP, MEH, RL. Analysis and interpretation of data: MAP, MEH, RL. Preparation of figures/tables/maps: MAP. Writing - original draft: MAP, MEH, RL. Writing - critical review & editing: MAP, MEH, RL.

### Consent for publication

All authors declare that they have reviewed the content of the manuscript and gave their consent to submit the document.

### Competing interests

The authors declare no competing interest.

### Data availability

All study data are included in the article.

### Funding and grant disclosures

The CORTES 2 cruise was partly supported by CONACyT (project PCCBBNA-02196). The BBMAZ project was partly supported by CONACyT (project PCMANAL79001) and by the Escuela Técnica Pesquera, Mazatlán, Mexico. CORTES 1 and 2 cruises aboard the R/V “El Puma” were partly financed by the Instituto de Ciencias del Mar y Limnología, UNAM, Mexico

### Study permits

No collection permit was required, because the material is deposited in the Regional Collection of Invertebrates, Mazatlán, Mexico (ICML-EMU) and in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

## REFERENCES

- Ayón-Parente M and Hendrickx ME 2012. A new species of *Pagurus* (Crustacea: Decapoda: Paguridae), new records and a redescription of the hermit crabs from the Mexican Pacific. *Scientia Marina*, 76(3): 489–506. DOI: 10.3989/scimar.03407.09A
- Ayón-Parente M and Wehrtmann IS 2019. Description of a new species of *Pagurus* Fabricius, 1775 (Crustacea: Paguroidea: Paguridae) from the Pacific coast of Costa Rica, Central America, with notes on *Pagurus albus* (Benedict, 1892). *Zootaxa*, 4712(1): 101–13. DOI: 10.11646/zootaxa.4712.1.7
- Benedict JE 1892. Preliminary descriptions of thirty-seven new species of hermit crabs of the genus *Eupagurus* in the U.S. National Museum. *Proceedings of the United States National Museum*, 15: 1–26. DOI: 10.5479/si.00963801.15-887.1
- Boschi EE 2000. Species of decapod crustaceans and their distribution in the American marine zoogeographic provinces.

- Revista de Investigación y Desarrollo Pesquero*, 13: 7–56. <https://aquadocs.org/handle/1834/2606>
- Brusca RC 1980. Common Intertidal Invertebrates of the Gulf of California. 2<sup>nd</sup> Edition. Tucson, University of Arizona, 513p. [https://www.researchgate.net/publication/305490017\\_Common\\_Intertidal\\_Invertebrates\\_of\\_the\\_Gulf\\_of\\_California\\_2nd\\_ed\\_fullTextFileContent](https://www.researchgate.net/publication/305490017_Common_Intertidal_Invertebrates_of_the_Gulf_of_California_2nd_ed_fullTextFileContent)
- Fabricius JC 1775. Systema entomologiae, sistens insectorum classes, ordines, genera, species, adiectis, synonymis, locis, descriptionibus, observationibus. Flensburgi et Lipsiae, Officina Libraria Kortii, 832p. DOI: 10.5962/bhl.title.36510
- Forest J and de Saint Laurent M 1968. Résultats scientifiques des campagnes de la “Calypso”, Part VII. Campagne de la Calypso au large des côtes Atlantiques de l’Amérique du Sud (1961–1962). 6. Crustacés Décapodes: Pagurides. *Annales de l’Institut Océanographique de Monaco, New Series*, 45(2): 45–172. <https://decapoda.nhm.org/pdfs/32207/32207.pdf>
- Glassell SA 1937. The Templeton Crocker Expedition. 11. Hermit Crabs from the Gulf of California and the West Coast of Lower California. *Zoologica*, 22(3): 241–263. <https://www.biodiversitylibrary.org/page/50969709-page/299/mode/1up>
- Haig J; Hopkins TS and Scanland T 1970. The shallow water anomuran crab fauna of southwestern Baja California, Mexico. *Transactions of the San Diego Society of Natural History*, 16(2): 13–32. DOI: 10.5962/bhl.part.15453
- Hendrickx ME 1993. Crustáceos decápodos del Pacífico Mexicano. p. 271–318. In: Salazar-Vallejo SI and González NE (Eds.), Biodiversidad Marina y Costera de México. México, D.F., Comisión Nacional para el Estudio y Uso de la Biodiversidad y CIQRO. <https://decapoda.nhm.org/pdfs/29674/29674.pdf>
- Hendrickx ME and Harvey AW 1999. Checklist of anomuran crabs (Crustacea: Decapoda) from the Eastern tropical Pacific. *Belgian Journal of Zoology*, 129(2): 363–389. <https://decapoda.nhm.org/pdfs/29678/29678.pdf>
- Hendrickx ME; Landa-Jaime V and Ayón-Parente M 2006. Distribution and ecology of *Pagurus gladius* (Benedict, 1892), *Pagurus smithi* (Benedict, 1892) and *Paguristes bakeri* Holmes, 1900 (Decapoda: Anomura: Paguridae and Diogenidae) off the coast of western Mexico. *Biology of Anomura II. Crustacean Research*, Special Number 6: 33–43. DOI: 10.18353/crustacean.Special2006.6\_33
- Ingle RW 1985. Northeastern Atlantic and Mediterranean hermit crabs (Crustacea: Anomura: Paguroidea: Paguridae). 1. The genus *Pagurus* Fabricius, 1775. *Journal of Natural History (London)*, 19: 745–759. DOI: 10.1080/00222938500770461.
- Lemaitre R and Cruz-Castaño N 2004. A new species of *Pagurus* Fabricius, 1775 from the Pacific coast of Colombia, with a checklist of eastern Pacific species of the genus. *Nauplius*, 12(2): 71–82. <https://repository.si.edu/handle/10088/7339>
- Lemaitre R and Felder DL 2011. A new genus of Paguridae (Crustacea: Decapoda: Anomura) for a new species from the tropical eastern Pacific and *Pagurus longimanus* Wass, 1963 from the tropical western Atlantic. *Zootaxa*, 3125(1): 39–50. DOI: 10.11646/zootaxa.3125.1.3
- McLaughlin PA 1974. The hermit crabs (Crustacea Decapoda, Paguroidea) of northwestern North America. *Zoologische Verhandelingen*, 130: 1–396, pl. 1. <https://repository.naturalis.nl/pub/317891/ZV1974130001.pdf>
- McLaughlin PA 2003. Illustrated keys to families and genera of the superfamily Paguroidea (Crustacea: Decapoda: Anomura), with diagnoses of genera of Paguridae. *Memoirs of Museum Victoria*, 60: 111–144. DOI: 10.24199/j.mmv.2003.60.16
- McLaughlin PA; Komai T; Lemaitre R and Rahayu DL 2010. Annotated checklist of anomuran decapod crustaceans of the world (exclusive of the Kiwaoidea and families Chirostyliidae and Galatheidae of the Galatheoidea). Part I—Lithodoidea, Lomisoidea and Paguroidea. *Raffles Bulletin of Zoology*, 23 (Supplement): 5–107. [https://profiles.si.edu/display/sro\\_106331](https://profiles.si.edu/display/sro_106331)
- Milne Edwards H. 1848. Note sur quelques nouvelles espèces du genre *Pagure*. *Annales des Sciences Naturelles Zoologie, Paris*, ser. 3. 10: 59–64. <https://www.biodiversitylibrary.org/item/108329-page/7/mode/1up>
- Nobili G 1901. Viaggio del Dr. Enrico Festa nella Repubblica dell’Ecuador e regioni vicine. 23. Decapodi e Stomatopodi. *Bollettino Musei di Zoologia ed Anatomia comparata della R. Università di Torino*, 16(415): 9–58. <https://decapoda.nhm.org/pdfs/27394/27394.pdf>
- Olguín N and Mantelatto F. 2013. Molecular analysis validates of some informal morphological groups of *Pagurus* (Fabricius, 1775) (Anomura: Paguridae) from South America. *Zootaxa*, 3666(4): 436–448. DOI: 10.11646/zootaxa.3666.4.2
- Rathbun MJ 1910. The stalk-eyed Crustacea of Peru and the adjacent coast. *Proceedings of the United States National Museum*, 38: 531–620, pls. 36–56. DOI: 10.5479/si.00963801.38-1766.351
- Say T 1817. An account of the Crustacea of the United States. *Journal of the Academy of Natural Sciences of Philadelphia*, 1(1): 155–169. <https://www.biodiversitylibrary.org/part/244400>
- Snyder-Conn E 1980. Arthropoda Crustacea Paguroidea and Coenobitoidea (hermit crabs). p. 275–285. In: Brusca RC (Ed.), Common intertidal invertebrates of the Gulf of California. University of Arizona Press, Tucson, Arizona. <https://www.researchgate.net/publication/305490017>
- Vargas R and Cortés J 2006. Biodiversidad Marina de Costa Rica: Crustacea: Infraorden Anomura. *Revista de Biología Tropical*, 54(2): 461–488. <https://www.scielo.sa.cr/pdf/rbt/v54n2/3837.pdf>
- Wass, M.L. 1963. New species of hermit crabs (Decapoda, Paguridae) from the western Atlantic. *Crustaceana*, 6(2): 133–157. DOI: 10.1163/156854063X00525
- WoRMS Editorial Board 2021. World Register of Marine Species. Available from <http://www.marinespecies.org> at VLIZ. Accessed on 03 November 2021.