CONTRIBUTIONS IN SCIENCE

THE IDENTITY OF *Pagurus lepidus* (Bouvier) (Decapoda, Anomura, Paguridae) AND DESCRIPTION OF A NEW EASTERN PACIFIC INSULAR SPECIES

Janet Haig and Patsy A. McLaughlin

TWO NEW HERMIT CRABS OF THE GENUS *Pagurus* (Provenzanoi Group) (Crustacea, Anomura, Paguridae) FROM THE EASTERN PACIFIC, WITH NOTES ON THEIR ECOLOGY

Alan W. Harvey and Patsy A. McLaughlin
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THE IDENTITY OF *PAGURUS LEPIDUS* (BOUVIER) (DECAPODA, ANOMURA, PAGURIDAE) AND DESCRIPTION OF A NEW EASTERN PACIFIC INSULAR SPECIES

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ABSTRACT. The name *Pagurus lepidus* (Bouvier) has been assigned to several small closely allied hermit crab species in the Eastern Pacific. *Pagurus lepidus* is a member of the *provensanoi* group of *Pagurus*, an informal group of the genus that has both Western Atlantic and Eastern Pacific representatives. Because species from the Pacific have not received the systematic attention afforded their Atlantic relatives, several species of the group from the Gulf of California, Mexico, western Central America, and Eastern Pacific atolls and archipelagos have been commonly referred to only as the *Pagurus lepidus* species complex.

*Pagurus lepidus*, herein redescribed and illustrated, is a geographically variable species, whose range is now documented from the Gulf of California, Mexico, to Peru. Certain specimens previously assigned questionably to *P. lepidus* are also described and illustrated as a new insular species, *P. nesotes*, distributed from Clipperton Island to the Galapagos Archipelago.

INTRODUCTION

*Pagurus lepidus* (Bouvier) is one of the few named pagurids occurring in the shallow waters of the Gulf of California, Mexico, and as a result this name has been applied, at one time or another, to virtually all of the region's small hermit crabs with striped walking legs. Although it was Bouvier (1898) that first described *Pagurus lepidus* (as *Eupagurus*) from a collection made in the Gulf of California, the first documented capture of this species is from the Bay of Panama by J.G.H. Kinberg, zoologist aboard the Royal Swedish frigate "Eugenie", under the command of C.A. Virgin, during her circumnavigation of the world from 1851 to 1853. It remained, cataloged only as *Eupagurus sp.*, in the collections of the Naturhistoriska Riksmuseet, Stockholm, until its recent rediscovery.

Some years ago one of us (JH) began to notice distinct, albeit subtle, differences in the color patterns among the Gulf of California pagurids. Subsequent examinations revealed certain morphological differences as well. One character in particular, the lateral marginal plate of the telson, was found to differ among specimens. For example, in certain specimens the lateral margin was simply a weakly calcified or chitinous plate (Fig. 1A). In others this plate was terminated anteriorly by a prominent spine (Fig. 1B). In still others, this plate was composed of distinct individual spinules (Fig. 1C) or spines (Fig. 1D). These differences were found to correlate with some of the observed differences in color patterns.

Bouvier's description of *P. lepidus* was based on two specimens collected at "Baie de la Paz, Basse Californie", Mexico, and whereas his description was relatively detailed, it dealt with general characters and color patterns that have since proved to be analogous among several species. *Pagurus lepidus* is a moderately common intertidal to shallow subtidal species in the Gulf of California; however, it is not alone in exhibiting a preference for this habitat. Several additional, but undescribed, taxa have been confounded with this species (e.g., Haig *et al.*, 1970; Ball and Haig, 1974; Snyder-Conn, 1980). We have now had an opportunity to examine the syntypes of *Pagurus lepidus* and have found that only two of the subsequently published reports of this species (i.e., Glassell, 1937; Forest and de

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Saint Laurent, 1968) referred exclusively to this taxon. Specimens included in these other reports, as well as supplemental collections, represent new species that will be described in forthcoming publications.

Not only does *P. lepidus* exhibit the sexual dimorphism common to other members of the *provenzanoi* group of *Pagurus* (see McLaughlin, 1975), it has been found to also exhibit morphological variations correlated to its geographic distribution. Consequently, only a few characters and specific differences in color patterns can be used to separate *P. lepidus* from the other sympatric species of the subtropical and tropical Eastern Pacific. From the material available we have found that inspecific variation in *P. lepidus* considerably exceeds that of most Western Atlantic species of the group as described by Lemaire et al. (1982).

Chace (1962) reported ?*Pagurus lepidus* from Clipperton Island, noting that his specimens agreed in most characters with Bouvier’s (1898) description but differed in the shape of the ocular acicles. We have reexamined the Clipperton Island specimens, and although clearly belonging to the *provenzanoi* group, they are distinct from all of the Gulf of California species of the *lepidus* complex and are herein described as *Pagurus nesiotes* new species.

**MATERIALS**

Materials for this study have come from the Crustacea collections formerly of the Allan Hancock Foundation (AHF) (now part of the Crustacea collection of the Natural History Museum of Los Angeles County), American Museum of Natural History (AMNH), Muséum National d’Histoire Naturelle, Paris (MNHN), National Museum of Natural History, Smithsonian Institution (USNM), Natural History Museum of Los Angeles County (LACM), Naturhistoriska Riksmuseet, Stockholm (NHRM), Smithsonian Oceanographic Sorting Center (SOSC), and from individual collectors. Specimens will be returned to their repositories of origin and/or deposited in these museums and the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH). Material formerly belonging to the Allan Hancock Foundation is indicated by an original AHF catalog number in addition to its current LACM number, which follows the AHF number in parentheses. One measurement, shield length (SL), provides an indication of size ranges of the specimens examined.

**SYSTEMATICS**

*Pagurus lepidus* (Bouvier, 1898)

FIGURES 2A–G, 3A–G

_Esopagurus lepidus_ Bouvier, 1898:381.

*Pagurus lepidus*: Glassell, 1937:256; Chace, 1962:623 by implication (in part, see discussion); Forest and de Saint Laurent, 1968:116; Haig et al., 1970:19 (in part, see discussion); Ball and Haig, 1974:102 (in part, see discussion); Snyder-Conn, 1980:283 (in part, see discussion).

*Pagurus* (?) _lepidus*: Moran, 1984:76, fig. 5.


LECTOTYPE (herein selected). δ (SL = 2.2 mm), MNHN, Paris, Pg 246, 1898. _Type locality._ Baie de la Paz, Basse Californie [Baja California Sur], Mexico.

PARALECTOTYPE. δ (SL = 2.2 mm), MNHN, Paris, Pg 246, 1898.

OTHER MATERIAL EXAMINED. Gulf of California, Sonora, Mexico: Puerto Peñasco, 1 δ (SL = 1.1 mm), November 23–26, 1955, collector E.P. Chace, USNM 99802; Puerto Peñasco, 1 δ (SL = 2.4 mm), intertidal, July 17, 1967, collector P. Pickens, AHF 2791-01 (LACM 67-241.1); NORSE Beach, 3 δ, 1 ovigerous δ (SL = 1.7–2.6 mm), Choya Bay Survey station 66033, shore, August 15, 1966, collectors T. & B. Burch, AHF 2789-01 (LACM 66-354.1); Norse Beach, 3 δ, 2ovigerous δ (SL = 1.2–2.4 mm), shore, December 2, 1967, collector A. Havens, AHF 2790-01 (LACM 67-198.2); Coquina Reef, 1 δ, 4 ovigerous δ (SL = 2.0–2.8 mm), lower intertidal, June 1973, collectors A. Kuris, M. Brody, E. Snyder, AHF 2792-01 (LACM 73-215.1); Station Beach, 3 δ, 1 ovigerous δ (SL = 2.0–2.4 mm), intertidal, July 27, 1988, collector A. Harvey, NHRM, RMNH D 38112; Station Beach, 9 ovigerous δ (SL = 1.4–2.1 mm), intertidal, December 1988, collector A. Harvey, USNM 244080; Turner’s Island south of Tiburon Island, 3 δ (SL = 1.7–2.0 mm), "Veleri III" station 1042–40, shore, January 24, 1940, AHF 2787-01 (LACM 40-14.5). Bahia La Paz, Baja California Sur, Mexico,
26°50'45"N, 111°54'20"W, 3 δ, 2 ovigerous ♀ (SL = 1.4–2.0 mm), Templeton Crocker Expedition “Zaca” station 144 D-1, 2 m, April 15, 1936, AMNH 12574. South Bay, Isla Cedros, W. Baja California Sur, Mexico, 1 ♀ (SL = 2.1 mm), “Velero III” station 287-34, 20–30 m, March 10, 1934, AHF 2786-01 (LACM 34-161.3). Punta Pequeña, Bahía de San Juanico, W. Baja California Sur, Mexico, 2 δ, 1 ♀ (SL = 1.6–2.7 mm), “Magbay” Expedition, 3.5 m, February 8, 1964, collectors T. Hopkins, T. Scanland, AHF 2788-01 (LACM 64-176.1). Outside Bahía Magdalena, W. Baja California Sur, Mexico, 1 δ (SL = 2.2 mm), “Magbay” Expedition, 20 m, February 1, 1964, collectors T. Hopkins, T. Scanland, AHF 2795-01 (LACM 64-177.1). Bahía Tenacatita, Jalisco, Mexico, 19°17'N, 104°50'W, 1 δ (SL = 1.7 mm), “Te Vega” Expedition station 18-22, 1.5–3.5 m, May 27, 1968, collector P. Smith, AHF 2629-03 (LACM 68-372.1). Mizata, Depto. La Libertad, El Salvador, 2 δ (SL = 1.5, 1.7 mm), shore, December 6, 1978, collector D. Moran, AHF 1623-01 (LACM 78-212.1). Gulf of Panama, 1 δ (SL = 1.5 mm), “Eugenie” Expedition, 1852, NHRM 7177. Panama Bay, Panama, 1 δ, 1 ♀, 1 ovigerous ♀ (SL = 1.2–1.3 mm), December 12, 1981, collector T. Spight, AHF 2793-01 (LACM 81-129.1). Punta Paitilla, Panama, 8°58.1'N, 79°31'W, 1 ovigerous ♀ (SL = 1.5 mm), “Te Vega” Expedition station 18-14b, 2 m, May 6, 1968, collector E. Ball, AHF 2616-05 (LACM 68-373.1). Atacames Reef, Ecuador, 1 ♀ (SL = 1.2 mm), “Te Vega” Expedition station 18-8, 8 m, April 23, 1968, collectors M. Younghbluth, P. Smith, AHF 2607-03 (LACM 68-377.1). Manta, Ecuador, 0°56'S, 80°43'W, 1 δ (SL = 1.7 mm), “Te Vega” Expedition station 18-5, 6.3 m, April 19, 1968, collectors E. Ball, P. Smith, AHF 2605-06 (LACM 68-374.1). Punta Mancinga, Salinas, Ecuador, 2°11'S, 80°43'W, 2 δ, 2 ovigerous ♀ (SL = 0.8–1.4 mm), “Te Vega” Expedition station 18-4, intertidal, April 16, 1968, collector E. Ball, AHF 2604-03 (LACM 68-376.1). Talara, Peru, 4°34'S, 81°07'W, 4 δ, 4 ovigerous ♀ (SL = 1.3–1.8 mm), “Te Vega” Expedition station 18-2, 5 m, April 9, 1968, collector E. Ball, AHF 2602-02 (LACM 68-375.1).

**DIAGNOSIS.** Shield longer than broad. Ocular acicles multispinose. Antennal flagellum with 1–3 short setae each article and scattered longer setae. Carpus of right cheliped with 4 or 5 spines on dorsomesial margin. Left cheliped with dorsomesial surface of palm horizontal, margin with row of protuberances or spines. Dactyli of ambulatory legs...
each with 5–9 corneous spines on ventral margin; carpi each with spine at dorso-distal margin and P$_2$ also with dorsal surface usually slightly spinulose or with 1 small spine proximally. Posterior lobes of telson with terminal margins oblique, lateral margins with narrow, undifferentiated plate and without delimiting spine anteriorly. In life, chelifeds with distal four-fifths of fingers greenish-white or white; meri with pinkish-white band distally. Ambulatory legs with greenish-brown longitudinal stripes.

**REDESCRIPTION.** Shield longer than broad, anterior margin between rostrum and lateral projections concave, posterior margin roundly truncate. Rostrum obsolete, unarmed; lateral projections unarmed or with minute terminal spinule. Dorsal surface of shield with scattered tufts of setae.

Ocular peduncles one-half to four-fifths length of shield, broadened basally and with cornesae slightly dilated, with longitudinal row of tufts of setae on dorsosomal face. Ocular acicles somewhat subquadrate, with 3–6 terminal marginal spines; separated basally by approximately one-half basal width of 1 acicle.

Antennular peduncles overreaching ocular peduncles by one-fourth to one-half length of ultimate segment. Ultimate segment with scattered setae dorsally and ventrally. Penultimate segment with few setae ventrally. Basal segment with 1 acute spine on dorsolateral face.

Antennal peduncles slightly overreaching cornesae. Fifth and 4th segments with few tufts of setae. Third segment unarmed or with very small spinule at ventro-distal margin. Second segment with dorsolateral distal angle produced, terminating in acute spine, lateral and mesial margins occasionally with accessory small spine and with long or moderately long setae; dorsosomalial distal angle unarmed or with small spine, mesial face with long setae. First segment with small spine on lateral face distally, particularly apparent in small individuals, ventral margin produced and armed with 1 spine laterally. Antennal acicle somewhat arcuate, terminating in small spine, mesial margin with moderately long setae. Antennal flagellum with 1–3 short setae or bristles on every article and frequently also with scattered longer setae (1–2 articles in length).

Right chelifed with dactylus equal to or as much as one-half again as long as palm. Slight hiatus be-
tween dactylus and fixed finger. Cutting edge of dactylus varying from 1 strong calcareous tooth in proximal half and small calcareous teeth distally to 1-3 small calcareous teeth proximally and row of concomous teeth distally, terminating in concomous tip. Cutting edge of fixed finger with 1 strong and several small calcareous teeth in proximal half and row of small concomous teeth interspersed with small calcareous teeth in distal half or only with alternating calcareous and concomous teeth, terminating in small calcareous or concomous claw. Dactylus overlapped by fixed finger. Dorsomesial margin of dactylus with row of small acute spines and long setae, dorsal surface slightly elevated in midline and also armed with row of small spines and tufts of long stiff setae, ventral surface with tufts of long stiff setae. Palm one-half to two-thirds length of carpus; dorsomesial margin with irregularly double row of spines, strongest proximally, dorsal surface with numerous tufts of long stiff setae and varying in armature from scattered spinules or small spines and median inverted V-shaped row of stronger spines to only few scattered spinules, dorsolateral margin with low protuberances proximally becoming row of small spines on fixed finger or row of spines increasing in size on fixed finger. Fixed finger often with irregular row of small spines. Carpus slightly shorter to slightly longer than merus; dorsomesial margin with row of 4 or 5 rather widely spaced spines, 1 or 2 spines on or near distal margin, dorsal surface unarmed or slightly spinulose and with tufts of long setae, dorsolateral margin unarmed or with row of spines, distolateral margin sometimes with small spine and ventrolateral distal angle usually with acute spine, lateral and mesial faces with scattered setae. Merus subtriangular; dorsal margin with few tufts of setae and often small spine on distal margin, ventromesial and ventrolateral margins unarmed or with 1 small spine on ventromesial margin and short row of small spines on ventrolateral margin in distal half. Ischium unarmed.

Left cheliped with dactylus and fixed finger somewhat spoon-shaped. Cutting edge of dactylus with row of concomous teeth, terminating in concomous claw; dorsal surface with row of stiff setae near cutting edge, midline with row of spines and frequently 2nd row of longer setae, dorsomesial margin with low protuberances or row of small spines; mesial margin and ventral surface also with tufts of long setae. Palm one-half to two-thirds length of carpus; midline armed with irregular double row of spines, extending onto the fixed finger as single row adjacent to cutting edge, dorsolateral face strongly sloping ventrally, with row of tufts of long setae and usually row of small spines in ventral half and 2nd row of protuberances or spines and tufts of long setae marginally, dorsomesial face horizontal with margin marked by row of protuberances or moderate to strong spines and tufts of setae, mesial face with low protuberances and tufts of setae. Carpus usually equaling merus in length; dorsomesial and dorsolateral margins each with row of strong spines and tufts of long setae, dorsodistal margin with 1 strong spine, dorsal surface and mesial and lateral faces with scattered setae. Merus triangular; dorsal margin with tufts of setae, ventrolateral margin with row of acute spines in distal half, ventromesial margin with row of spines, usually only on proximal half in large males, ventral surface with long setae laterally. Ischium with acute spine at ventrolateral distal angle and often also with row of small spines on ventromesial margin.

Second and 3rd pereopods with dactyli and propodi varying in length and width; 3rd right usually longest and most slender, 3rd left shortest and broadest. Dactyli slightly less than half to almost equaling length of propodi, approximately one-third to one-fifth as broad (proximally) as long, terminating in strong curved concomous claws; dorsal, mesial, and lateral surfaces all with tufts of moderate to long setae, ventral margins each with row of 5-9 concomous spines and long stiff setae. Propodi exceeding length of carpi by one-fourth to one-third own length; dorsal surfaces with tufts of long stiff setae, ventral surfaces each with pair of concomous spines at distal margin and 1 additional spine in distal third (2nd) or 1st, 2nd, or 1st and 2nd paired spines followed by row of widely spaced concomous spines proximally (3rd). Carpi approximately equaling length of meri; dorsodistal margins each with 1 small spine, dorsal surfaces with low protuberances, 2nd usually slightly spinulose and/or with small spine developed proximally, also with tufts of long setae, mesial and lateral faces and ventral surface with scattered setae. Meri with tufts of long setae on dorsal margins; ventral margins with low protuberances and tufts of long setae or with small spine on ventrolateral margin distally (2nd). Ischia with row of long setae on ventral margins.

Anterior lobe of sternite of 3rd pereopods subrectangular to subsemicircular, unarmed. Fourth pereopods with small preungual process at base of claw; propodal raps with 5-8 rows of concomous scales; dorsomesial of dactyli, propodi, carpi, and meri (distally) with very long dense setae.

Exopod of left uropod with row of 6-10 thick setae on inner margin. Telson with terminal margins oblique, each armed with row of spines, 1 or 2 usually stronger and sometimes concomous-tipped; lateral margins delimited by narrow plate, no anterior spine.

COLOR. Northern Populations in Life. Antennal flagellum with 2 transparent articles proximally followed by greenish-brown articles interrupted every 3 articles by 1 white or transparent article. Shield transparent centrally with mottled green flecked with yellow marginally and posteriorly. Ocular peduncles mottled greenish-brown on white with flecks of pink distally and dorsal patch of pink proximally, concomae crimson; acicles with reddish-brown flecks on greenish-white background, distal margin with out flecks. Antennular peduncles with ultimate and penultimate segments greenish-white with red flecks, basal segment greenish-white in distal half and pink.
in proximal half. Chelipeds greenish-brown or olive with white spines often tinged with dark red-brown basally on palms and carpi, distal four-fifths of fingers white or greenish-white, meri with distal pinkish-white band and remainder mottled greenish or olive flecked with reddish-brown. Ambulatory legs with dactyli greenish-white distally and greenish-brown with short darker greenish-brown longitudinal stripes proximally; propodi with pink patch on lateral face near distal margin and pink band proximally, greenish-brown longitudinal stripes on greenish or grayish-white background centrally; carpi with light pink distally and dark greenish-brown longitudinal stripes on greenish or grayish-white background in proximal two-thirds; meri pink proximally and distally with dark greenish-brown longitudinal stripes on light green or gray background centrally (PAMcL, unpublished data).

**Southern Population in Life.** Antennal flagellum usually with 3 olive drab articles interrupted by 1 white article. Shield mottled olive drab and white. Ocular peduncle mottled white and olive drab, cornice red. Antennal peduncles with white patch dorsally and green bands proximally on ultimate segment and dark green band distally on penultimate segment. Chelipeds with white dactyli, and fixed fingers, palms, carpi, and meri mottled olive drab and white. Ambulatory legs with distal halves of dactyli white, proximal halves with short brown stripes; propodi with longitudinal brown stripes on pale background, with yellow spots between stripes; carpi and meri with dark brown longitudinal stripes on pale background (E.E. Ball, field notes).

**In Preservative.** Palms and carpi of chelipeds red-orange, fingers white. Stripes of ambulatory legs reddish-orange. All color fading with time to straw yellow.

**DISTRIBUTION.** West Pacific coastal Baja California, Baja California Sur, and Gulf of California, Mexico to Peru; intertidal to 20 m.

**AFFINITIES.** As previously indicated, *Pagurus lepidus* is the name that has been applied to at least six small hermit species occurring in the shallow waters of the Eastern Pacific. All of these species are similar in morphology and color patterns. Distinctions among the species can only be made by careful structural examination or comparisons of colors in living animals. These structural characters include the multispine condition of the ocular acicles, as opposed to the simple, single-spined condition; the presence of short setae on the articles of the antennal flagellum rather than long (more than three articles in length), randomly placed or serially paired setae; and the horizontal as opposed to sloping dorsomesial face of the left chela. Although *P. lepidus* exhibits considerable variations over its geographic range, it can be distinguished from the majority of similarly striped species by the absence of an anterior spine on the lateral margin of the posterior telsional margin plates and by the almost horizontal dorsomesial surface of the left chela. The setation of the antennal flagellum, consisting of short and scattered moderately long (one to two articles in length) in *P. lepidus* is diagnostic only when compared with species having truly long and serially paired setae.

**VARIATIONS.** There are distinct differences between the specimens of *P. lepidus* collected in the Gulf of California and the outer coast of the Baja California Peninsula and those from Central and South America. If specimens from the extremes of the range are examined, these differences appear significant enough to suggest that two distinct taxa may be involved. However, despite the relative paucity of material from the central portion of the range (southern Mexico and northern Central America), we have observed enough character clines to convince us that we are dealing with one highly variable species.

The Puerto Peñasco, Sonora, Mexico, region was the source of more than half of the specimens examined. A characteristic of *P. lepidus* from this region is a difference in the length–width ratios of the dactyli of the left and right 3rd pereopods, regardless of overall body size. Proximally the 3rd left dactylus is one-third to one-fourth as broad as long, whereas the 3rd right is usually one-fourth to one-fifth as broad as long. At this apparent northern end of its range, *P. lepidus* reaches a large overall size (shield length in excess of 2.5 mm), and with increasing size additional morphological changes in the ambulatory legs usually occur that have not often been observed in the Central and South American population. This is particularly apparent in the length relationships of the dactyli to their respective propodi. In small individuals (shield lengths less than 1.7 mm) within this northern population, the dactyli, especially the 3rd left, usually are from three-fourths to nine-tenths the length of the propodi; both segments are visually quite short. With increasing size, the dactylus become more slender and the propodi elongate. In specimens with shield lengths greater than 2.0 mm, the length of the dactylus varies from two-thirds to sometimes less than one-half the length of the propodus. Concurrent with changes in dactylar length and width are changes in the armature of the ventral margins. Small specimens commonly have six or seven conaceous spines on the ventral margins of the dactylus. With increasing size, the number of spines increases to seven to nine or occasionally 10. Generally the armature of the right chela consists of scattered moderately strong spines on the dorsal surface of the palm, with an inversed V of stronger spines medially. However, with increasing size, the strength of the chela armature is reduced, becoming virtually obsolete in very large specimens. Frequently the ischium of the left cheliped is armed with a row of small spines.

None of the specimens collected in the southern half of the range of *P. lepidus* had a shield length in excess of 2.0 mm, and this may be the reason that no marked changes in length–width ratios in the dactyli of the right and left 3rd pereopods were
observed. The length relationships between propodi and dactyli, however, were different in this smaller southern population. Generally the dactyli were two-thirds to three-fourths as long as the propodi. Similarly, the number of spines on the ventral margins of the dactyli varied from five to six. Few specimens exhibited strong spination on the dorsal surface of the right chela, and no spines were observed on the ventral margin of the ischium of the left chela. In the color descriptions reported for the two populations, slight variations also could be detected.

However, there are exceptions. For example, the only notable difference between the lectotype (Fig. 2A–G) and the Panamanian specimen collected by the "Eugenie" (Fig. 3A–G) is the number of dactylar spines on the ventral margins of the 2nd and 3rd pereopods. Among the northern populations a few specimens of comparable size to those found farther south, including one specimen from Puerto Peñasco, had proportionally longer dactyli and only five spines on the ventral margins. Similarly, one of the southern specimens had an appreciably more slender 3rd right dactylus with seven spines on the ventral margin. Geographically correlated differences were apparent among the 58 specimens we critically examined, but there was a sufficient number of intermediate conditions to suggest a clinal variation from north to south.

**DISCUSSION.** Bouvier's (1898) description included many of the general characteristics of most species assignable to the "Pagurus lepidus" complex, e.g., obtusely rounded rostrum, multispinose ocular acicles, spinulose chelipeds, stripped ambulatory legs. Bouvier was not aware of the number of distinct taxa in the region that could be described by these same characters.

Glassell (1937) did not provide a description of his specimens other than certain characters cited in his key to distinguish this taxon from other *Pagurus* species collected by the Templeton Crocker Expedition. None of these characters will separate *P. lepidus* from the other Pacific species of the complex. Although Glassell did describe color patterns remaining in his preserved material, these patterns fit at least three species of the complex. We have been able to reexamine these specimens now housed in the collection of the American Museum of Natural History and can confirm their identity as *P. lepidus*.

In his questioned referral of the Cliperton Island specimens to *P. lepidus*, Chace (1962) used for comparison a lot of specimens in the national collections that had previously been identified as *P. lepidus*. We have reexamined this lot from Puerto Peñasco, Mexico (USNM 99802), and found that only one of the eight specimens actually is *P. lepidus*. The remaining seven specimens represent an undescribed species (Harvey and McLaughlin, 1990). Chace (1962) recognized that his Cliperton Island specimens possessed ocular acicles with a single terminal spine, whereas the ocular acicles of Bouvier's (1898) *P. lepidus* and the Puerto Peñasco specimens had multispinose acicles. Although he was unwilling to designate a new species on the basis of one lot of comparative material, he suspected that the Cliperton Island specimens might, in fact, represent a distinct taxon. We have now been able to confirm that suspicion.

Haig et al. (1970) and Ball and Haig (1974) recognized that several species were probably confounded under the name *P. lepidus*. However, as they did not have access to Bouvier's (1898) material at that time, they were unable to accurately distinguish among these taxa. We have reexamined the materials included in both of these reports and have found that one lot of specimens from Punta Pequeña, Bahía de San Juancito, Baja California Sur, Mexico (Haig et al., 1970), and specimens from Mexico, Ecuador, and Peru (Ball and Haig, 1974) do represent *P. lepidus*.

Snyder-Conn (1980) gave a generalized description of *P. lepidus* but repeated Haig's opinion that this species had been confounded with several others represented in the Gulf of California fauna. Although one specimen that she collected has proved to be *P. lepidus*, it is probable that she included other local taxa in her report.

Moran (1984) provided notes and illustrations of the hermit crabs he identified as *Pagurus* (?) *lepidus*. However, he remarked that his identification was doubtful because this was one of several closely related species of the genus that were in need of revision. We have been able to examine two of his five specimens. These, at least, do represent *P. lepidus*.

*Pagurus lepidus* was among the decapods listed by Von Prahl (1986) as inhabiting a coral rubble community in Utría Sound, Colombia. *Pagurus lepidus* is known from this type of habitat, and the locality is within its distributional range. However, Von Prahl's report can only questionably be included in the synonymy of *P. lepidus* as other provenzani group species have similar habitats and ranges. Von Prahl was unfortunately killed in a plane crash in 1989, thus his material has not been available for verification.

More recently five other references to "*Pagurus lepidus*" have come to our attention, i.e., Westervelt (1967), Romero (1982), Rodriguez de la Cruz (1987), Romero and Carvacho (1988), and Villalobos Hiriart et al. (1989). None have been cited in the synonymy of this species as it is impossible to know which, or how many, of the species herebefore confounded under the name *P. lepidus* may be represented by these reports.

**Pagurus nesiotes new species**

Figures 4A–G, 5A–F


*Pagurus* sp.: Birkeland et al., 1975:67.
Figure 4. Pagurus nesiotes new species, paratype [USNM 22194, Clipperton Island]: A, shield and cephalic appendages; B, chela and carpus of right cheliped (dorsal view); C, chela and carpus of left cheliped (dorsal view); D, right 2nd percopod (lateral view); E, left 3rd percopod (lateral view); F, anterior lobe of sternite of 3rd percopods; G, telson. Scale = 1 mm (A–E) and 0.5 mm (F, G).

HOLOTYPE. Ovigerous ♀ (SL = 2.0 mm). Type locality. Clipperton Island, NE side, 15 m, August 28, 1958, collectors [Limbaugh, Chess, Hambly], USNM 110975.

PARATYPES. 1 ♂, 1 ovigerous ♀ (SL = 1.8, 1.4 mm). Clipperton Island, NE side, 15 m, August 28, 1958, collectors [Limbaugh, Chess, Hambly], USNM 221940. Malledo Island, Colombia, 3 ♂ (SL = 1.6–1.8 mm), subtidal, February 29–March 3, 1972, collector C. Birkeland, AHF 728 (LACM 72-345.1). Galapagos Islands: Charles Island, 1 ♀ (SL = 1.5 mm), "Eugenie" Expedition, 15–22 m, May 15–17, 1852, NHRM 7167; Post Office Bay, Charles Island, 1 ♂ (SL = 1.3 mm), "Velerio III" station 167–34, 30 m, January 19, 1934, AHF 3424 (LACM 34-40.4); Post Office Bay, Charles Island, 3 ♂ (SL = 1.2–1.6 mm), "Velerio III" station 193–34, 15–18 m, January 27, 1934, AHF 3426 (LACM 34-67.4); off James Bay, James Island, 1 ♂ (SL = 1.4 mm), "Velerio III" station 182–34, 60 m, January 24, 1934, AHF 3425 (LACM 34-56.2); west side Academy Bay, Santa Cruz Island, 3 ♂, 1 ♀, 1 ovigerous ♀ (SL = 1.3–2.4 mm), 3–8.5 m, August 25–27, 1976, collector P. Abrams, formerly AHF 762, now divided between MNHN, RMNH D 38105; 00°54'11"S, 90°18'15"W, 12 m, 3 ovigerous ♀, 5 juveniles (SL = 0.6–2.2 mm), "Anton Bruun" station 16/66112, 8–10 m, May 19, 1966, collector S. Earle, SOSC; south end of Darwin (Culpepper) Island, 2 ♂, 2 ♀ (SL = 1.2–2.2 mm), approximately 11 m, May 13, 1984, LACM 84-29.4; south side of Darwin (Culpepper) Island, 2 ♂ (SL = 1.3, 2.3 mm), 9–13 m, May 13, 1984, LACM 84-29.5; northwest side of Pinta (Abingdon) Island, 1 ♂, 1 ovigerous ♀ (SL = 1.8, 2.0 mm), 10–13 m, May 17, 1984, LACM 84-37.1; off Punta Espéjo, east end Marchena (Bindloe) Island, 1 ovigerous ♀ (SL = 1.9 mm), 12 m, May 11, 1984, LACM 84-26.1.

DIAGNOSIS. Shield as long or longer than broad. Ocular acicles terminating in single spine. Antennal flagellum naked or with 1–4 very short setae every 1–4 articles. Carpus of right cheliped with irregular double row of spines on dorsomesial margin. Left cheliped with dorsomesial surface of palm strongly sloping, margin usually spinulose or spinose. Dactyli of ambulatory legs with 6–10 corneous spines on ventral margins; carpi each usually with spine at dorsodistal margin. Posterior lobes of telson with terminal margins oblique to rounded, lateral margins with narrow plate undifferentiated or with individual denticles clearly distinguishable, no delimiting spine anteriorly. In preservative, chelipeds with finger tips white, carpal and merial segment solidly.

Haig and McLaughlin: Redescription of Pagurus lepidus

8 ■ Contributions in Science, Number 425
colored. Ambulatory legs each with longitudinal stripes and additional broad distal band on merus.

**DESCRIPTION.** Shield equal to or longer than broad, anterior margin between rostrum and lateral projections concave, anterolateral margins sloping or slightly terraced, posterior margin rounded truncate. Rostrum obsolete or obtusely triangular, sometimes weakly produced; lateral projections broadly rounded or obtusely triangular, unarmed. Dorsal surface of shield with scattered setae.

Ocular peduncles one-half to four-fifths shield length, broad basally, and usually tapering to very slightly dilated corneae. Ocular acicles subtriangular to subovate, terminating in 1 marginal or submarginal spine, rarely with 2nd spine in close proximity; separated basally by two-thirds basal to slightly more than basal width of 1 acicle; interocular lobes weakly developed.

Antennular peduncles equaling or exceeding ocular peduncles by up to one-half length of ultimate segment. Ultimate segment with few setae on dorsal surface. Penultimate segment with few scattered setae. Basal segment with 1 acute spine on dorsolateral margin.

Antennal peduncles overreaching corneae by less than one-fourth to more than one-third length of ultimate segment. Fifth and 4th segments with few tufts of setae. Third segment with acute spine at ventrodorsal margin, partially obscured by tuft of setae. Second segment with dorsolateral distal angle produced, terminating in 1 or 2 spines, lateral margin sometimes with small spine distally and with long setae; dorsomesial distal angle unarmed or with small spine, mesial face with scattered setae. First segment with small spine on lateral face distally, ventral margin produced and armed with 1 spine laterally. Antennal acicle somewhat arcuate, terminating in usually acute spine, mesial margin with moderately long setae. Antennal flagellum naked or with 1-4 very short setae every 1-4 articles.

Right cheliped with dactylus one-fourth to one-half again as long as palm. Slight hiatus between dactylus and fixed finger. Cutting edge of dactylus with 1 strong and several small calcareous teeth in

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**Figure 5.** *Pagurus nesiotes* new species, paratype [formerly AHF 762; now RMNH D 38105; Galapagos Islands]: A, shield and cephalic appendages; B, chela and carpus of right cheliped (dorsal view); C, chela and carpus of left cheliped (dorsal view); D, left 3rd pereopod (lateral view); E, anterior lobe of sternite of 3rd pereopods; F, telson. Scale = 1 mm (A-E) and 0.5 mm (F).
proximal half and row of very small calcareous teeth distally, terminating in small corneous claw. Cutting edge of fixed finger with 1 very prominent broad tooth proximally and small calcareous teeth distally, terminating in corneous tip. Dactylus equaling or exceeding length of propodus by approximately one-fourth own length with single or double row of small acute spines on dorsomesial margin proximally but sloping ventrally to tip, dorsal surface somewhat elevated in midline and armed with row of strong spines and long setae, mesial and ventral surfaces with scattered long setae. Palm equaling or two-thirds the length of carpus; dorsomesial margin with irregular row of acute strong spines and often 2nd adjacent row, dorsal surface with scattered small spines, 2 rows of strong spines occasionally forming inverted V in midline and extending onto fixed finger as row of smaller spines, dorsolateral margin with row of moderately weak to strong spines, decreasing in size on fixed finger, surfaces with scattered long setae. Carpus equaling or slightly longer than merus; dorsomesial margin with double, sometimes irregular, row of spines, 1 or 2 spines on or near distal margin, dorsal surface with row of smaller spines lateral of midline, tending to become obsolete in large individuals, dorsolateral margin not delimited or with row of small spines, lateral face with tufts of long setae, laterodistal margin often with 1 or 2 spines dorsally, ventrolateral margin usually with 1 or 2 spines distally, mesial face with scattered setae. Merus subtriangular; dorsal margin with tufts of setae, distal margin with 1 or 2 spines, ventromesial and ventrolateral margins each with row of spines, strongest laterally. Ischiium unarmed or with row of small spines or low tubercles on ventromesial margin.

Left cheliped with dactylus and fixed finger somewhat spoon-shaped. Dactylus one and one-fourth to twice length of palm; cutting edge with row of corneous teeth, terminating in corneous claw. Cutting edge of fixed finger with small calcareous teeth that may be replaced distally with corneous teeth. Dorsal surface of dactylus with row of small spines in proximal half near cutting edge and row of spines or spinulose tubercles on dorsomesial margin, surfaces with scattered long setae. Palm one-third to one-half length of carpus; dorsal surface with midline elevated and armed with irregular double row of strong spines, extending onto fixed finger as single row, dorsomesial face strongly sloping ventrally, armed with irregular row of very small spines or spinules in ventral half and single or double row of spines marginally, dorsomesial face strongly sloping, surface and margin each sometimes with row of moderate to strong spines or only with few small spinules, all surfaces with scattered long setae. Carpus equaling or slightly shorter than merus; dorsolateral margin with row of strong spines and tufts of long setae, dorsomesial margin with few spines or more frequently with few spinulose tubercles, distal margin usually with strong spine, lateral face sometimes spinulose, laterodistal margin usually with 2 or 3 spines, ventrolateral margin with row of strong acute spines, mesial face with scattered setae and occasionally 1 or 2 small spinules or tubercles on ventromesial margin distally. Merus triangular; dorsal margin with tufts of setae, ventromesial margin with 2 to several spines, ventrolateral margin with row of acute spines and long setae. Ischiium with acute spine at ventrolateral distal angle and usually with row of small spines on ventromesial margin.

Second and 3rd pereopods similar. Dactyli one-half to two-thirds length of propodi (shortest on left 3rd and generally shorter in larger individuals), one-third to one-sixth as broad proximally as long, terminating in strong curved corneous claws, dorsal, mesial, and lateral faces all with scattered moderate to long setae, ventral margins each with row of 6–10 corneous spines and few short to moderately long setae. Propodi exceeding length of carpi by one-fourth to one-third own length; dorsal surfaces with tufts of long setae; ventral surfaces each with corneous spine at distal margin (2nd) and often 1 or 2 additional spines in distal third or occasionally row of spinules (3rd). Carpi one-half to three-fourths length of meri; dorsodistal margins each usually with 1 small spine, occasionally lacking on left 3rd, dorsal surfaces with low protuberances and tufts of long setae, mesial and lateral faces and ventral surface with scattered setae. Meri each with low protuberances on dorsal and ventral surfaces, lateral face of 2nd with strong acute spine at ventrodistal angle and sometimes with 1 or 2 spines on ventral margin (left). Ischia with few setae on dorsal and ventral margins.

Anterior lobe of sternite of 3rd pereopods varying from subrectangular to subsemiovate, unarmed. Fourth pereopods apparently without preungual processes at base of claw; propodal rasp of 4 or 5 rows of corneous scales; dorsal margins of segments with long setae.

Exopod of left uropod with row of 3–6 thick setae and frequently 1 or 2 thinner setae on inner margin. Telson with posterior lobes subtriangular; terminal margins oblique or rounded, each armed with row of spines, largest at external angle; lateral margin with narrow plate delimited, sometimes with individual denticles clearly developed; no anterior spine.

COLOR (in formalin for 2 months). Shield and ocular acicles pale orange. Antennular peduncles purple, penultimate segment with distal orange ring; flagellum orange. Antennal peduncles orange, distal segment with longitudinal red stripe; acicle orange with white tip. Ocular peduncles pale with random purple blotches. Chelipeds orange with purple tubercles; chelae paler, with white fingers; medial and carpal segments red. Meri of 2nd and 3rd pereopods purple with broad distal orange band; carpi purple with little orange distally; proximal halves of propodi purple, distal halves white with patch of orange distally; dactyls white with purple proximally. All areas appearing purple overlaid with nar-
row longitudinal stripes. Fourth and 5th pereopods pale orange (JH, unpublished data, lab notes).

**DISTRIBUTION.** Cliperton Island, Malpelo Island, and Galapagos Archipelago; subtidal to 60 m.

**ETYMOLOGY.** The specific name is from the Greek *nestiotes*, an island dweller; a noun in apposition.

**AFFINITIES.** Of species within the *P. lepidus* complex, *P. nestiotes* appears most closely related to *Pagurus villosus* Nicolet, 1849, with which it shares the less common character, simple ocular acicles. *Pagurus nestiotes* can immediately be distinguished from *P. villosus* by the setation of the antennal flagella. In the former species one to four short setae are present on every one to four articles. In the latter species a pair of long setae is present on each article, at least in the proximal half. *Pagurus nestiotes* is distinguishable from *P. lepidus* not only by its simpler ocular acicles but by the marked slope of the dorsomesial face of its left chela.

**DISCUSSION.** As previously indicated, Chace (1962) believed that his Cliperton Island specimens agreed in most general respects with Bouvier's (1898) description of *P. lepidus* and with specimens from Puerto Peñasco, Sonora, Mexico, previously identified as *P. lepidus*. However, he noted one striking difference, i.e., the lack of multispinose ocular acicles, which were described for *P. lepidus* and which were present in the Mexican specimens. Although Chace (1962) felt that it was quite possible this character might prove to be of specific importance, he was reluctant to assign a new specific name to the Cliperton Island material until more information was available from other localities.

We have been able to examine the specimen discussed in Birkeland et al. (1976) and cited in that report only as *Pagurus* sp. It too is *P. nestiotes*. As far as is presently known, this is truly an insular species.

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**LITERATURE CITED.**


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TWO NEW HERMIT CRABS OF THE GENUS PAGURUS (PROVENZANOI GROUP) (CRUSTACEA, ANOMURA, PAGURIDAE) FROM THE EASTERN PACIFIC, WITH NOTES ON THEIR ECOLOGY

ALAN W. HARVEY AND PATSY A. McLINH

ABSTRACT. During ecological studies of the shallow-water hermit crab fauna of the northwestern Gulf of California, Mexico, two new species of the provenzanoi group of Pagurus were recognized. Additional material has shown that one of these species, P. vetaultae n. sp., has been found as far south as Panama, whereas the second, P. arenisaxatilis n. sp., appears not only to be endemic to the northern Gulf of California, Mexico, but to be one of the most abundant hermit crabs in the region. It is the only species in the northern Gulf that commonly inhabits both rocky and sandy shores. Despite the broader distribution of P. vetaultae through shallow subtidal regions of Mexico and Central America, this species appears to be restricted to coarse gravel substrates. Both species are described and illustrated.

INTRODUCTION

Following the description of Pagurus lepidus (Bouvier, 1898) virtually all small intertidal pagurids from the Gulf of California, Mexico, and/or the west coast of Baja California, Mexico, were routinely assigned to this taxon or to a complex of species confounded under this name (e.g., Glassell, 1937; Haig et al., 1970; Ball and Haig, 1974; McLoughlin, 1975; Snyder-Conn, 1980). Haig and McLoughlin (1990) recently reexamined the syntypes of Bouvier's (1898) species and provided a detailed description and illustrations of this taxon. For the first time it is now possible to accurately report on some of the other taxa in this species complex.

Field and laboratory studies by one of us (AWH) on the intertidal hermit crabs of the northern Gulf of California included three species previously assigned to the Pagurus lepidus complex. One has proved to be P. lepidus s.s.; the other two are new species described herein, together with brief summaries of their ecology. One of these species, P. vetaultae n. sp., was first found in the Bay of Panama by Carl Bovallius during a trip to the Pacific coast of Central America in 1882–83 but was never described. The other, although quite abundant on a variety of substrates in the intertidal region, appears restricted in its distribution to the Gulf of California.

As with Atlantic species of the provenzanoi group (see McLoughlin, 1975; Lemaître et al., 1982), Pacific representatives are morphologically difficult to distinguish from one another. One extensively used diagnostic character is the dorsomesial surface of the left chela. It is described either as horizontal (Fig. 1A) or sloping (Fig. 1B, C) and usually is not influenced by animal size. However, in P. vetaultae n. sp., the slope of the dorsomesial face varies from slight to substantial. The armament of this surface may be so strong that it gives the slightly sloping surface the visual impression of being horizontal.

MATERIALS

Materials for this study have come from the Crustacea collections formerly of the Allan Hancock Foundation (AHF) (now part of the Crustacea collection of the Natural History Museum of Los Angeles County), National Museum of Natural History, Smithsonian Institution (USNM), Naturhistoriska Riksmuseet, Stockholm (NHRM), and from individual collectors. Specimens will be re-
turned to their repositories of origin and/or deposited in these and the following museums: Rijksmuseum van Natuurlijke Historie, Leiden (RMNH), Natural History Museum of Los Angeles County (LACM), Museum National d’Histoire Naturelle (MNHN). Material formerly belonging to the Allan Hancock Foundation is indicated by an original AHF catalog number in addition to its current LACM number, which follows the AHF number in parentheses. One measurement, shield length (SL), provides an indication of size ranges of the specimens examined.

**DESCRIPTIONS**

_Pagurus arenisaxatilis_ new species

Figure 2A–H

_Pagurus lepidus_: Chace, 1962:623, in part (by implication) (see remarks).

**HOLOTYPE.** Ovigerous ♀ (SL = 2.1 mm), USNM 243896. **Type locality.** Between Pelican Point and Choya Bay, Sonora, Mexico, February 3, 1988, collector A. Harvey.

**PARATYPES.** Baja California, Mexico: San Felipe Bay, 6 ♀, 2 ♂, 1 ovigerous ♀ (SL = 1.2, 2.4 mm), intertidal, January 1, 1976, collectors R. Brusca, B. Wallerstein, AHF 7615 (LACM 76-595.1); San Felipe Bay, 1 ♀ (SL = 1.9 mm), “Velero III” station 1071-40, 5 m, February 2, 1940, AHF 4015 (LACM 40-43.1); off Diggis Point, San Felipe Bay, 1 ♀, 1 ovigerous ♀ (SL = 1.5, 1.7 mm), 30 m, June 3, 1934, collector S. Glassell, USNM; off Willard Point, Bahía San Luis Gonzaga, 1 ♀ (SL = 2.1 mm), “Velero III” station 716-37, 3.5–5.5 m, March 23, 1937, AHF 3711 (LACM 37-119.6); Sonora, Mexico: Adair Bay, 1 ♂ (SL = 2.2 mm), Choya Bay Survey station 67041, 6 m, March 18, 1967, collectors Burch and Kawchak, AHF 673 (LACM 67-242.1); same locality, 1 ♀ (SL = 2.5 mm), Choya Bay Survey station 67042, 10 m, March 18, 1967, collectors Burch and Kawchak, AHF 678 (LACM 67-242.1); same locality, 4 ♀, 2 ♂ (SL = 0.9–2.1 mm), Choya Bay Survey station 70106, shore, July 18, 1970, collectors Burch and Seivings, AHF 709, 7010 (LACM 70-283.1); Pelican Point, 2 ♀ (SL = 1.8, 2.3 mm), Choya Bay Survey station 68043, shore, April 13, 1968, collectors Burch and Avery, AHF 6819 (LACM 68-384.1); between Pelican Point and Choya Bay, 6 ovigerous ♀ (SL = 1.5–2.1 mm), intertidal, February 3, 1988, collector A. Harvey, NHRM, RMNH; same locality, 4 ovigerous ♀ (SL = 1.7–2.7 mm), intertidal, January 19, 1988, collector A. Harvey, LACM 88-291.1; same locality, 5 ♀, 3 ♂, 1 ovigerous ♀ (SL = 0.9–2.6 mm), intertidal, July 26, 1988, collector A. Harvey, USNM; same locality, 2 ovigerous ♀ (SL = 1.7, 1.8 mm), intertidal, February 22, 1989, collector A. Harvey, MNHN; off Choya, 1 ♀ (SL = 2.0 mm), Choya Bay Survey station 67164, 17.5 m, November 4, 1967, collectors Burch, Hanson, and Skoglund, AHF 679 (LACM 67-243.1); sandy beach, Choya, 4 ♀, 1 ovigerous ♀ (SL = 1.7–2.1 mm), Choya Bay Survey station 66033, shore, August 15, 1966, collectors T. and B. Burch, AHF 6612 (LACM 66-355.1); same locality, 1 ♀ (SL = 1.7 mm), Choya Bay Survey station 66046, shore, October 14, 1966, collectors Burch, Avery, and Scott, AHF 6613 (LACM 66-356.1); Choya Bay, 16 mile reef, 1 ♀ (SL = 1.3 m), station GA-72, March 1968, collectors G. and M. Avery, AHF 6818 (LACM 68-385.1); Puerto Peñasco, 1 ♀, 1♀, 5 juveniles (SL = 0.8–1.4 mm), November 23–26, 1955, collector E.P. Chace, USNM 211423; same locality, 2♀, 3♂, 2 ovigerous ♀ (SL = 2.0–2.9 mm), 1967, collector A. Havens, RMNH; same locality, 1 ♀, 3♂, 1 ovigerous ♀ (SL = 2.0–2.9 mm), intertidal, December 3, 1967, collector A. Havens (NHRM Cat. No. 4175); same locality, 1 ♀ (SL = 2.1 mm), Choya Bay Survey station 69030, shore, February 15, 1969, collectors Burch, Hanson, Bennett, and Schroder, AHF 6913 (LACM 69-229.1); off Rocky Point, 2 ♀ (SL = 1.8, 1.9 mm), “Velero III” station 1072-40, 20 m, February 2, 1940, AHF 4016 (LACM 40-44.6); inside Georges Island (just south of Bahia San Jorge), 1 ♀ (SL = 1.5 mm), “Velero III” station 1075-40, 21–23 m, February 3, 1940, AHF 4017 (LACM 40-47.1); south of Isla Tiburon, 1 ♀ (SL = 1.8 mm), “Velero III” station 731-37, 122.5 m, March 28, 1937, AHF 3712 (LACM 37-134); south side Isla Tiburon, 1 ♀ (SL = 3.2 mm), “Curry-Orcal” Cruise station 194, 13 m, March 27, 1960, collector R.H. Parker, AHF 6055 (LACM 60-181.1).

**DIAGNOSIS.** Shield slightly longer than broad. Ocular peduncles one-half to two-thirds shield length. Articles of antennal flagella with irregularly alternated long and short setae. Carpus of right cheliped with irregular double row of spines on dorsomesial margin and 1 or 2 additional spines near distal margin. Left cheliped with dorsomesial face of palm strongly sloping; ischium with ventromesial margin unarmored or with few spines.
Dactyli of ambulatory legs each with 8–13 corneous spines on ventral margin. Anterior lobe of sternite of 3rd pereopods subsemicircular. Posterior lobes of telson with simple to spinous lateral margins, without delimiting spine anteriorly. In life, chelipeds with distal halves of dactyli and fixed fingers white, palms and carpi tan to olive.

**DESCRIPTION.** Shield (Fig. 2A) slightly longer than broad, anterior margin between rostrum and lateral projections concave, anterolateral margins sloping; posterior margin subtruncate. Rostrum obsolete, unarmed. Lateral projections broadly rounded, with very small terminal spine. Dorsal surface of shield with scattered tufts of setae (not illustrated).

Ocular peduncles (Fig. 2A) one-half to two-thirds shield length, broad basally and moderately stout, corneae slightly dilated. Ocular acicles subrectangular, multispinose (2–5 marginal or submarginal spines), separated basally by slightly more than one-half basal width of 1 acicle. Interocular lobes weakly developed.

Antennular peduncles (Fig. 2A) overreaching ocular peduncles by one-half to two-thirds length of ultimate segment. Ultimate segment with few setae on dorsodistal margin and scattered on dorsal and ventral margins (setae not shown). Penultimate segment with few setae ventrally. Basal segment with 1 acute spine on dorsolateral face.

Antennal peduncles (Fig. 2A) overreaching corneae by approximately one-half length of ultimate segment. Fifth and 4th segments with few tufts of setae. Third segment with small spinelet at ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in acute spine, lateral and mesial margins with long or moderately long setae and occasionally small accessory spine; dorsomesial distal angle with small spine, mesial face with long setae. First segment with small spine on lateral face distally, ventral margin produced and armed with 1 spine laterally. Antennal acicle somewhat arcuate, terminating in small spine, mesial margin with moderately long setae. Antennal flagellum usually with 2 or 3 moderately long (2–3 articles length) and usually 2–4 short setae or bristles per article, at least in proximal half.

Mouthparts typical for species of the provenzanoi group as described by McLaughlin (1975) and Lemaître et al. (1982).

Right cheliped (Fig. 2B) with dactylus approximately as long as palm, slightly overlapped by fixed finger. Cutting edge of dactylus with 1 or 2 strong and several small calcareous teeth in proximal half and row of small corneous teeth in distal half, terminating in small corneous claw. Cutting edge of fixed finger with 1 strong calcareous tooth in proximal half and small calcareous teeth interspersed with corneous teeth distally, terminating in corneous tip. Dorsomesial margin of dactylus with row of small acute spines, dorsal surface slightly elevated in midline and also armed with row of small spines and tufts of long stiff setae, dorsomesial margin with tufts of long stiff setae, ventral surface with few scattered setae. Palm slightly shorter than carpus; dorsomesial margin with irregular double row of spines and dense tufts of setae, dorsal surface with irregular rows of spines and tufts of long setae proximally and usually scattered small spines on fixed finger, dorsolateral margin with row of spines extending to tip of fixed finger and with tufts of long setae. Carpus approximately as long as merus; dorsomesial margin with irregular double row of spines, 1 or 2 spines on or near distal margin, dorsal surface with row of small spines laterad of midline and 2nd row near weakly delimited dorsolateral margin, ventrolateral margin with 1 or 2 small spines distally, dorsal surface with numerous long setae, lateral and mesial faces with scattered setae. Merus subtriangular; dorsal margin with few tufts of setae, distal margin with 1 small spine, ventromesial margin unarmed, ventrolateral margin with short row of small spines. Ischium unarmed.

Left cheliped (Fig. 2C) with dactylus and fixed finger somewhat spoon-shaped. Dactylus one-third to one-half times longer than palm; cutting edge with row of corneous teeth, terminating in corneous claw, dorsal midline and dorsomesial margin each with row of spines in proximal half, dorsal surface also with row of stiff setae near cutting edge and second row of longer setae in midline, mesial margin and ventral surface also with tufts of long setae. Palm one-half to two-thirds length of carpus; elevated in midline and armed with irregular double row of spines, extending nearly to tip of fixed finger, dorsolateral face strongly sloping ventrally, with row of small spines or spinules in ventral half and second row of protuberances or spines and tufts of long setae marginally, dorsomesial face strongly sloping, with few scattered spines or low protuberances and tufts of setae; dorsomesial margin not delimitated. Carpus slightly shorter than merus; dorsomesial margin with row of numerous small spines, dorsolateral margin with row of few widely spaced strong spines, and both with tufts of long setae, distal margin with 1 strong spine, dorsal surface and mesial and lateral faces with scattered setae, laterodistal and ventrolateral margins each with acute spine. Merus subtriangular; dorsal margin with tufts of setae, ventrolateral margin with row of acute spines in distal half, ventromesial margin with short row of spines only on proximal half and with tufts of setae. Ischium unarmed or with few spinules on ventromesial margin.

Second and 3rd pereopods (Fig. 3D, E) similar. Dactyli one-half to two-thirds length of propodi, slightly less to slightly more than one-fifth as broad as long; terminating in strong curved corneous claw; dorsal, mesial, and lateral surfaces all with tufts of moderate to long setae, ventral margins each with row of 8–13 corneous spines and long setae. Propodi exceeding length of carpi by one-fourth to one-third own length; dorsal surfaces with tufts of long setae, ventral surfaces each with single or pair of corneous spines at distal margin and 1 or 2 ad-
Figure 2. *Pagurus arenisaxatilis* new species, paratype USNM 243893: A, shield and cephalic appendages; B, chela and carpus of right cheliped (dorsal view); C, chela and carpus of left cheliped (dorsal view); D, right 2nd pereopod (lateral view); E, left 3rd pereopod (lateral view); F, anterior lobe of sternite of 3rd pereopods; G, telson with simple lateral margins of posterior lobes. Paratype RMNH: H, telson with spinous lateral margin on right posterior lobe. Scale = 1 mm (A–E) or 0.5 mm (F–H).
dential spines in distal third. Carpi approximately equaling length of meri; dorsodistal margins each with 1 small spine, dorsal surfaces with low, occasionally spinose, protuberances and tufts of long setae, mesial and lateral faces and ventral surfaces with scattered setae. Meri with tufts of long setae on dorsal and ventral margins, ventrolateral margins each with acute spine distally and frequently also 1-3 spines on ventral margin (2nd) or unarmed (3rd). Ischia with row of long setae on ventral margins.

Anterior lobe of sternite of 3rd pereopods (Fig. 2F) subsemicircular, unarmed. Fourth pereopods with small preungual process at base of claw; propodal rapt with 3–5 rows of conormous scales, dorsal margins of dactyli, propodi, carpi, and meri (distally) with long dense setae.

Exopod of left uropod with row of thick setae on inner margin. Telson (Fig. 2G, H) with posterior lobes subtriangular to subquadrate, terminal margins usually oblique, each armed with 3 or 4 strong spines, interspersed with smaller spines, lateral margins with narrow plate simple (Fig. 2G), or less frequently with row of spines (Fig. 2H); no anterior spine on lateral plate.

COLOR (in life). Antennal flagellum olive drab to brown with white in patterns of 2 dark–1 white, 3 dark–1 white, 4 dark–1 white, progressing distally. Shield with tan to brown splotches. Ocular peduncles, antennules, and antennae mottled or spotted with tan to olive. Right cheliped with distal half of dactylus and tip of fixed finger white, palm, carpus, and merus tan to olive. Left cheliped with tips of dactylus and fixed finger white, palm tan to olive with spines often white-tipped; carpus tan to olive; merus tan to olive with white band distally on mesial and lateral faces and dorsally separated from distal margin by dark patch. Ambulatory dactyli with 3 short olive to tan stripes proximally on white background; propodi with median band consisting of short tan to olive stripes; carpi with longitudinal tan to olive stripes on white background covering most of segment; meri with central band composed of tan to olive stripes (PAMcL, lab notes).

DISTRIBUTION. At present known only from the northern Gulf of California, Mexico, intertidal to 30 m.

ETYMOLOGY. The specific name is derived from the Latin arena, sand, and saxatilis, dwelling among stones, reflecting the mixed habitat of this species.

AFFINITIES. Pagurus arenisaxatilis is similar in general morphology to the other Pagurus lepidus complex species occurring in the Gulf of California. Like these other species, in life it is characterized by longitudinal stripes on the ambulatory legs. However, the irregular long and short setae on the articles of the antennal flagella immediately distinguish this species from the others. In the absence of the antennal flagella, P. arenisaxatilis is best distinguished by a combination of characters, i.e., sloping dorsomesial face of left chela, long pereopodal dactyli with 8–13 ventral spines, and no de-limiting spine on the anterior margin of the lateral telson plates. This species exhibits considerable variation in the development of the lateral plates of the posterior lobes of the telson. Although no anterior telsonal spine has been observed in any of the specimens examined, the plate may be undifferentiated, composed of partially to completely fused denticles (Fig. 2G) or differentiated into distinct small teeth (Fig. 2H). In the development of the multifid ocular acicles, this species also exhibits differences from the other Gulf species. The acicle tends to be ovate in shape with a single large spine usually prominent medi ally, and with one to four smaller spines developed mesiad of it. In most other species the multifid acicles are subrectangular in shape and consist of three to five equally strong spines.

REMARKS. One lot of specimens in the national collections from Puerto Peñasco, Mexico, identified as P. lepidus was used by Chace (1962) for comparison with specimens from Clipperton Island. Haig and McLaughlin (1990) reexamined this lot (USNM 99802) and found that only one of the eight specimens was referable to P. lepidus. The remainder are identifiable as P. arenisaxatilis.

ECOLOGY. Pagurus arenisaxatilis is one of the most abundant hermit crabs in the northern Gulf of California. Of the intertidal pagurid hermit crabs in the area, it has the broadest vertical range, extending from the upper midintertidal to the shallow subtidal, and is the only species commonly found on both rocky and sandy shores.

This small species uses a variety of shells, usually less than 20 mm in length, such as Morula ferruginosa (Reeve), Anachis coronata (Sowerby), A. varia (Sowerby), small specimens of Cerithium stercusmuscarum (Valenciennes), and Olivella dama (Wood). Local patterns of shell use may vary widely, however, depending on which shell species are locally common and perhaps also on the presence of other hermit crab species. Shells used by P. arenisaxatilis tend to be in poor condition; in a sample of 118 specimens collected during the winter of 1985, 74% of shells used were damaged, and 89% were at least partially encrusted by coralline algae. Other common encrusters included several bryozan species (36.4%) and spirorbid (29.7%) and serpulid (15.2%) polychaetes. Several non-encrusting epi bionts are also commonly associated with P. arenisaxatilis-occupied shells. Most notably, the polychaete Polydora sp. (33.1%) is typically found in the apex of the shell, the slipper limpet Crepidula (20.3%), believed to be a new species, is found just inside the shell aperture, and a gammariid amphipod (seasonally variable, sometimes near 100%) is found deep inside the shell. Like most hermit crabs in the northern Gulf, P. arenisaxatilis is relatively free of the external parasites that infect hermit crabs in other regions. An abdominal byprid isopod, Stegophryxus n. sp. (J. Markham, personal communication), is rare (<1%); a single specimen, subsequently lost, carried an unidentified rhizocephalan.
Pagurus vetulatae new species

Figures 1B, C; 3A–H

HOLOTYPE. δ (SL = 2.1 mm), USNM 243894. Type locality. Venecia Cove (near San Carlos and Guaymas, Sonora, Mexico), March 20, 1989, collector S. Vetaut.

PARATYPES. Venecia Cove, Sonora, Mexico, 1 δ, 2 ovigerous τ (SL = 1.7–1.8 mm), March 20, 1989, 3–7 m, collector S. Vetaut, USNM 243895. Hymalaya Bay, Sonora, Mexico, 1 τ (SL = 1.4 mm), −1 m, November 24–26, 1988, collectors S. Vetaut and A. Harvey, AHF 882 (LACM 88-292.1). Northeast of Bahia Santa Elena, Costa Rica, 1 δ (SL = 2.0 mm), “Searcher” station 384, 18 m, February 13, 1972, AHF 729 (LACM 72-8.1); Las Perlas, Pedro Gonzalez, Gulf of Panama, 5 δ, 2 τ (SL = 1.3–2.3 mm), April 22–25, 1882, collector C. Boivillius, NHRM 7175, 7180.

OTHER MATERIAL. 8 δ (SL = 1.1–1.8 mm), “Searcher” station 471, north side Isla del Cano, Costa Rica, 9 m, March 14, 1972, AHF 2794-01 (LACM 72-63.1).

DIAGNOSIS. Shield as long or slightly longer than broad. Ocular peduncles three-fourths to four-fifths shield length. Articles of antennal flagella with very short setae. Carpus of right cheliped with 3 or 4 widely spaced spines on dorsomesial margin, distal margin with 2 or 3 strong spines. Left cheliped with dorsomesial surface of palm slightly to strongly sloping; ischiium with acute spine at ventrolateral distal angle. Dactyli of ambulatory legs each with 6–9 corneous spines on ventral margin, dactylus of left 3rd pereopod four-fifths to nine-tenths length of propodus. Anterior lobe of sternite of 3rd pereopods subrectangular to subsemicircular. Posterior lobes of telson with lateral margins simple but delimited by spine anteriorly, at least on 1 side. In life, chelipeds each with 2 or 3 broad dark brown stripes on palms, dactyli and fixed fingers each with 1 stripe dorsally on cream base color; carpi with 2 dark brown stripes dorsally.

DESCRIPTION. Shield (Fig. 3A) as long as to slightly longer than broad, anterior margin between rostrum and lateral projections concave, anterolateral margins sloping, posterior margin truncate. Lateral projections broadly rounded, unarmed, overreaching obsolete unarmed rostrum. Dorsal surface of shield with scattered setae (not shown in illustration).

Ocular peduncles (Fig. 3A) three-fourths to four-fifths shield length, moderately slender, with corneae only slightly dilated. Ocular acicles subrectangular, multispinose (3–5 marginal or submarginal spines); separated basally by approximately one-half basal width of 1 acicle. Interocular lobes weakly developed.

Antennular peduncles (Fig. 3A) overreach ocular peduncles by one-third to one-half length of ultimate segment. Ultimate and penultimate segments with few scattered setae (not shown in illustration). Basal segment with 1 acute spine on lateral face.

Antennal peduncles (Fig. 3A) overreaching cornea by one-fourth to one-third length of ultimate segment. Fifth and 4th segments with scattered setae. Third segment unarmed or with very small spine at ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in acute spine, lateral margin with accessory spine and few long setae; dorsomesial distal angle unarmed or with small spine, mesial face with long setae (not illustrated). First segment with small spine on lateral face distally, ventral margin produced and armed with 1 spine laterally. Antennal acicle somewhat arcuate, terminating in small spine, mesial margin with moderately long setae. Antennal flagellum reaching to or beyond tip of right cheliped, with 2 or 3 very short (<1 article length) setae every article.

Mouthparts typical for provenzanoi group species (cf. Lemaitre et al., 1982).

Right cheliped (Fig. 3B) with dactylus approximately as long as palm, overlapped by fixed finger. Slight hiatus between dactylus and fixed finger. Cutting edge of dactylus with 1 or 2 strong and few smaller calcareous teeth in proximal half and row of small corneous teeth in distal half, terminating in small corneous claw. Cutting edge of fixed finger with 1–4 strong calcareous teeth in proximal half, smaller calcareous teeth interspersed with small corneous teeth in distal half, terminating in corneous tip. Dorsomesial margin of dactylus with row of small acute spines, dorsal surface slightly elevated in midline and also armed with row of more widely spaced spines and tufts of long setae, dorsomesial margin and ventral surface with tufts of long stiff setae. Palm slightly shorter than carpus; dorsomesial margin with irregular double row of spines, strongest proximally, dorsal surface with two widely separated rows of spines and long setae and numerous tufts of long stiff setae, few additional spines distally and on fixed finger, dorsolateral margin with low protuberances or small spines proximally increasing in size distally and on fixed finger. Carpus slightly shorter than or equal to length of merus; dorsomesial margin with row of 3 or 4 spines, dorsodistal margin with 1–3 acute spines, dorsal surface with row of small spines or tubercles lateral of midline and also numerous tufts of long setae, dorsolateral margin not delimited, distolateral margin with 0–3 small spines, lateral and mesial faces with scattered setae, ventrolateral distal angle with acute spine. Merus subtriangular; dorsal margin with few tufts of setae, dorsodistal margin with 1 spine, ventromesial margin unarmed or with row of low protuberances or spinules, sometimes 1 small spine distally, ventrolateral margin with 1–3 acute spines in distal half. Ischiium unarmed or with small spine at ventrolateral distal angle.

Left cheliped (Figs. 1B, C; 3C, D) with dactylus and fixed finger somewhat spoon-shaped, with prominent hiatus. Dactylus longer than palm; cutting edge with row of corneous teeth, terminating in corneous claw, dorsal surface with row of spines in midline and row of spines or protuberances on dorsomesial margin, all surfaces with tufts of long setae. Palm one-half to two-thirds length of carpus; dorsal surface slightly elevated in midline, and armed
Figure 3. *Pagurus vetaultae* new species, paratype USNM 243895: A, shield and cephalic appendages; B, chela and carpus of right chelifed (dorsal view); C, chela and carpus of left chelifed; D, chela and carpus of left chelifed (dorsal view, Bay of Panama paratype NHRM 7175); E, right 2nd pereopod (lateral view); F, left 3rd pereopod (lateral view); G, anterior lobe of sternite of 3rd pereopods; H, telson. Scale = 1 mm (A–F) or 0.5 mm (G, H).

with double row of spines, extending onto the fixed finger as single or double row, dorsolateral face strongly sloping ventrally with row of small spines in ventral half and second row of spines marginally, dorsomesial face weakly to strongly sloping with few low protuberances or scattered spinules, dorsomesial margin indicated by row of small to moderately strong spines, all surfaces with numerous tufts of long stiff setae. Carpus shorter than merus; dorsomesial and dorsolateral margins each with row of strong spines and tufts of long setae, mesial and lateral faces each with short transverse ridges and long setae, laterodistal margin with acute spine dorsally and 2nd spine at ventral angle. Merus triangular; dorsal margin with tufts of setae and acute spine at distal margin, ventromesial and ventrolateral margins each with row of spines and tufts of long setae. Ischium with acute spine at ventrolateral distal angle.

Second and 3rd pereopods (Fig. 3E, F) generally similar. Dactyli one-half to three-fourths length of propodi (2nd and 3rd right), or four-fifths to ninetenths length of propodus (left 3rd); terminating in strong curved corneous claws, dorsal, mesial, and lateral surfaces all with tufts of moderate to long setae, ventral margins each with row of 6–9 corneous spines and long stiff setae. Propodi exceeding length of carpi by one-fourth to one-third own length; dorsal surfaces with tufts of long stiff setae, ventral surfaces each with 1 corneous spine at distal margin and usually 1 additional spine in distal third (2nd) or pair of spines at distal margin and 1 additional spine in distal quarter (3rd). Carpi slightly less than to approximately equaling length of meri;
dorsodistal margins each with 1 spine, dorsal surfaces with low protuberances and tufts of long setae, mesial and lateral faces and ventral surface with scattered setae. Meri with tufts of long setae on dorsal margins, ventral margins with small spine on ventrolateral margin distally (2nd) or with low protuberances and tufts of long setae (3rd). Ischia with row of long setae on dorsal and ventral margins.

Anterior lobe of sternite of 3rd pereopods (Fig. 3G) subrectangular to subsemicircular, slightly skewed, unarmed. Fourth pereopods with very small preunical process at base of claw; propodal raps of 5 or 6 rows of corneous scales, dorsal and ventral margins of segments with long setae.

Exopod of left uropod with several thick setae on inner margin. Telson (Fig. 3H) with subrectangular posterior lobes; terminal margins oblique, each armed with row of spines, outermost strongest; lateral margins with narrow plate delimited anteriorly by small to moderately large spine at least on one side.

**COLOR** (in life). Carapace base color cream, with areas of light orange brown, sometimes with bluish tinge centrally, and darker brown patch on each side laterally. Ocular peduncles generally opaque with narrow white ring at base of cornea, reddish flecks and darker patch proximally and distally; cornea black with flecks of pink. Antennal peduncles transparent or with brownish tinge, each segment with proximal and subdistal white chromatophore and median black ring. Antennal peduncles transparent with longitudinal reddish-brown stripe dorsally and ventrally on 5th segment, 4th segment with white chromatophore distally and dark brown mesial and lateral patches; acicile light blue-gray with white chromatophores and brown bands; flagellum with 3 reddish-brown articles separated by 1 transparent article with white chromatophore. Chelae of cheliped with 2 broad or 3 more narrow dark brown stripes proximally on palm and 1 stripe each on dactylus and fixed finger, otherwise cream-colored; carpi with 2 dark brown stripes dorsally, dark brown or black mesially and with dark and light stripe laterally; meri dark brown with cream-colored dorsal stripe and distal band. Dactyli of ambulatory legs cream-colored distally with 3 short dark brown stripes over bluish-gray base color proximally; propodi and carpi each with broad dark stripes, meri with dark dorsal stripe and lateral patch (PAMcL, lab notes; AWH, field notes).

**ETYMOLOGY.** This species (pronounced “vet-toe-late”) is named for its collector, Sarah Vetault.

**DISTRIBUTION.** San Carlos–Guaymas area of the Gulf of California, Mexico, to Bay of Panama, 1–7 m.

**AFFINITIES.** Pagurus vetauldae morphologically is most closely allied with *P. redondoensis* Wicksten from southern California. In both species the dorsomesial margin of the left chela slopes; however, it may only be weakly sloping and be so strongly armed with spines as to give the visual impression of a level surface. Both species also have a similar number of corneous spines on the ventral margins of the dactyli of the 2nd and 3rd pereopods and similar armature of the dorsomesial margin of the carpus of the right cheliped. However, the two species may be easily separated by the length of the antennal flagella and the setation of the flagellar articles. We have reexamined the holotype of *P. redondoensis* (AHF 783) and several of Wicksten’s nonparatypic specimens and found the flagella usually shorter than the right cheliped. Wicksten (1982) described the articles of the antennal flagella as having “1 or 2 short (1 or 2 articles in length) setae on each side.” However, in addition to these short setae, one or two considerably longer setae also are present on at least every second article in the proximal half of the flagellum. Only very short (<1 article in length) setae are present on the flagellum of *P. vetauldae* over its entire length. In the absence of the antennal flagella, which Wicksten notes can be easily broken, the length ratios of the dactylus and propodus of the 3rd pereopod usually provide a reliable diagnostic character for separating the two taxa. In *P. vetauldae* the dactylus is nearly (four-fifths to nine-tenths) as long as the propodus. In *P. redondoensis* the dactylus is usually only two-thirds to three-fourths the length of the propodus, although this is not true of the holotype. In life *P. vetauldae* is easily distinguished by its distinctive coloration.

**DISCUSSION.** Although only the materials specified are paratypes, we have examined additional, but damaged, specimens from Costa Rica, whose disarticulated appendages clearly are referable to *P. vetauldae*.

**ECOLOGY.** This species was found at low densities in the shallow subtidal in the central Gulf of California primarily on coarse gravel substrates, in contrast to the sympatric *P. lepidus* and *P. galapagensis* (Boone), which prefer rocky substrates with dense patches of *Sargassum* (*P. lepidus* similarly favors *Sargassum* beds in the northern Gulf intertidal, where it co-occurs on rocky shores with the far more numerous *P. arenisaxatidis*). *Pagurus vetauldae* collected in Hymala Bay used *Morula feruginosa* and *Anachis coronata* shells, which tended to be heavily encrusted with coralline algae but otherwise lacked the significant epibiotic populations or physical damage that characterize the shells used by *P. galapagensis* and the more northern *P. arenisaxatilis*. One of the Costa Rican specimens was parasitized by an abdominal bopyrid isopod. The single female specimen was damaged and could only be identified as *Stegophyryx* (n.? sp. (J. Markham, personal communication).

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