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TWO NEW SPECIES OF THE PACIFIC COMPONENT OF THE *PROVENZANOI* GROUP OF *PAGURUS* (DECAPODA; ANOMURA; PAGURIDAE) AND A KEY TO THE REGIONAL SPECIES

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ABSTRACT

During studies of Pacific representatives of the *provenzanoi* group of *Pagurus,* two new species have been recognized. These species, *P. spighti* n. sp. and *P. annexus* n. sp. are described and illustrated. The assignment of two additional, poorly described species; *P. villosus* Nicolet and *P. benedicti* (Bouvier) is confirmed and these are redescribed and illustrated. *Pagurus galapagensis* (Boone) has been found to be a junior subjective synonym of *P. benedicti.* A fifth species, *P. redondoensis* Wicksten, is compared with other Pacific members of the group and its range is extended to include the west coast of Baja California, Mexico. A key to the Pacific species of the group is provided. *P. benedicti* differs appreciably in several characters previously used in the diagnosis of the *provenzanoi* group; however, the validity of its placement in this group has been substantiated by the intermediate condition of certain characters exhibited by one of the new species described herein. A continuum in certain morphological characters is demonstrated for representatives of the group.

In a preliminary attempt to subdivide the heterogeneous hermit crab genus *Pagurus,* Forest and De Saint Laurent (1968) proposed four informal species groupings, among these the *miamensis* group for a number of species endemic to the "New World's" continental shelf. In a subsequent review of two Atlantic species assigned to this group, *P. miamensis* Provenzano and *P. brevidactylus* (Stimpson), McLaughlin (1975) placed Provenzano's taxon in synonymy with Stimpson's, and renamed the group *provenzanoi* after *Pagurus provenzanoi* Forest and De Saint Laurent. In that same review, McLaughlin redefined the group and included, as Forest and De Saint Laurent (1968) had, the *Pagurus lepidus* (Bouvier) species complex and, tentatively, *P. benedicti* (Bouvier) from the eastern Pacific. McLaughlin (1975) did not concur with Haig et al.'s (1970) placement of another Pacific species, *P. galapagensis* (Boone), in this group; however, this conclusion was based only on Boone's (1932) generalized description and diagrammatic illustration. From the limited information then available, McLaughlin (1975) was unable to evaluate Ball and Haig's (1974) assignment of the Chilean species, *P. villosus* Nicolet, to the *provenzanoi* group.

Lemaitre et al. (1982) reviewed the western Atlantic species of the group, emended the group diagnosis, and provided a key to the twelve species that range from the southern part of the United States to Brazil and Argentina. Following the redescription of *P. lepidus* by Haig and McLaughlin (1991), several new Pacific species, heretofore confounded with *P. lepidus* or simply identified as species of the *P. lepidus* complex, were described (Haig and McLaughlin, 1991; Harvey and McLaughlin, 1991; Haig and Harvey, 1991). The remaining species potentially belonging to the *provenzanoi* group, i.e., *P. galapaganus, P. benedicti, P. villosus* and *P. redondoensis* Wicksten, have now been reexamined. The placement of *P. benedicti* and *P. villosus* in the group has been confirmed. *Pagurus galapagensis* has proved to be a junior subjective synonym of *P. benedicti.* The range of *P. redondoensis* has been extended to the west coast of Baja California, Mexico. A distributional pattern similar to the Atlantic species is seen in the Pacific species

of the *provenzanoi* group. They occur most abundantly in the shallow-waters of subtropical regions, but are distributed from southern California to Chile.

The *provenzanoi* group is set apart from other groups of *Pagurus* by a suite of characters that include: the usually obsolete or weakly developed rostrum; ocular acicles that vary in shape from subcircular and armed with a single spine to subrectangular and armed with several small spines; sternite of the third maxillipeds that is produced into a blunt or subtriangular, sometimes even spinose, median projection; left chela that is subtriangular in cross-section; anterolateral angles of the sternite of the fifth pereopods that are developed into distinct subovate lobes. The telson in *provenzanoi* group species has terminal margins that vary from oblique to straight and are armed with a series of small spines and often one or two more prominent spines; the lateral margin of each posterior lobe is delineated by a corneous or calcified plate that may vary from solid to divided into a series of small spines or denticles. In some species this plate may be marked anteriorly by an acute spine. Among Pacific representatives of the group, *P. benedicti* and *P. lepidus* are at opposite ends of a morphological continuum. One of the two new species described herein particularly exemplifies the clinal development of characters within the group.

MATERIALS

Materials for this study have come from the Crustacea collections of the Allan Hancock Foundation (AHF) [now part of the Crustacea collection of the Natural History Museum of Los Angeles County (LACM)], American Museum of Natural History (AMNH), National Museum of Natural History, Smithsonian Institution (USNM), Naturhistoriska Riksmuseet, Stockholm (NHRM), and from individual collectors. Specimens will be returned to their repositories of origin and/or deposited in these and the following institutions: Muséum National d'Histoire Naturelle, Paris (MNHN) and Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden (RMNH). With the exception of the Santa Catalina Island Biological Station (SCIBS), institutional abbreviations are those recommended by Leviton et al. (1985) for institutional resource collections. One measurement, shield length (SL), measured from the midpoint or tip of the rostrum to the midpoint of the posterior margin of the shield, provides an indication of size ranges of the specimens examined.

KEY TO THE PACIFIC SPECIES OF THE *PROVENZANOI* GROUP

1a. Ocular acicles with 2 or more spines, at least on one acicle 2
1b. Ocular acicles with single terminal spine 9
2a. Posterior telson plates delimited anteriorly by spine, at least on one side 3
2b. Posterior telson plates not delimited anteriorly by spine 7
3a. Articles of antennal flagellum each with evenly paired, very long setae at least in proximal half; dorsomesial face of left chela level ..... *P. annexus* n. sp. [Gulf of California and Outer Baja California, Mexico to Guatemala].
3b. Articles of antennal flagellum without evenly paired, very long setae 4
4a. Dorsomesial surface of left chela level; dorsal surfaces of carpi of 2nd pereopods each with protuberances and 1 or more spines on posterior half ..... *P. rhabdotus* Haig and Harvey [outer coast of Baja California peninsula, Mexico].
4b. Dorsomesial surface of left chela moderately to strongly sloping 5
5a. Articles of antennal flagellum with only short setae; terminal margins of telson with few small spines and large spine at each outer angle ..... *P. vetaultae* Harvey and McLaughlin [San Carlos and Guaymas area of Gulf of California, Mexico to Bay of Panama].
5b. Articles of antennal flagellum with long and short setae 6
6a. Meri of 2nd pereopods with 1 or 2 spines on ventrodistal margin, at least on one side; dactyls of ambulatory legs with 4–7 corneous spines on ventral margins ..... *P. nanodes* Haig and Harvey [Costa Rica to Ecuador].
6b. Meri of 2nd pereopods without spines on ventrodistal margin; dactyls of ambulatory legs with 5–9 corneous spines on ventral margins ..... *P. redondoensis* Wicksten [Redondo Beach, California to Baja California Sur, Mexico].
7a. Left chela with dorsomesial margin level; dorsal surfaces of carpi of 2nd pereopods each

with protuberances and 1 or more spines in posterior half ..... *P. lepidus* (Bouvier) [west Pacific coast of Baja California, Baja California Sur, and Gulf of California, Mexico to Peru].

7b. Left chela with dorsomesial margin sloping 8

8a. Dorsomesial margin of carpus of right cheliped with 4 or 5 spines; dorsolateral face of left chela unarmed or with few spinules; dactyls of ambulatory legs with 5–8 corneous spines on ventral margins ..... *P. virgulatus* Haig and Harvey [Acapulco, Mexico to Ecuador; Cocos Island].

8b. Dorsomesial margin of carpus of right cheliped with irregular double row of spines; dorsolateral face of left chela with row of spines or spinules in ventral half; dactyls of ambulatory legs with 7–13 spines on ventral margins ..... *P. arenisaxatilis* Harvey and McLaughlin [northern Gulf of California, Mexico].

9a. Antennal flagellum with long, evenly paired setae 10

9b. Antennal flagellum with long or short, but not evenly paired setae 11

10a. Carpus of left cheliped with row of spines on both dorsomesial and dorsolateral margins; posterolateral telsonal plates composed of individual spinules or denticles ..... *P. villosus* Nicolet [Peru to Chile].

10b. Carpus of left cheliped with row of spines on dorsolateral margin only; posterolateral telsonal plates entire ..... *P. spighti* n. sp. [Panama Bay, Panama].

11a. Carpi of 2nd pereopods each with single dorsodistal spine; posterolateral telsonal plates entire ..... *P. nesiotes* Haig and McLaughlin [Clipperton Island, Malpelo Island, and Galapagos Archipelago].

11b. Carpi of 2nd pereopods with 2–6 spines on dorsal surface; posterolateral telsonal plates composed of spines or spinules ..... *P. benedicti* (Bouvier) [Gulf of California and west Baja California, Mexico to Ecuador, Galapagos Archipelago].

Pagurus annexus new species
Figure 1A–K

Pagurus undescribed species (1): Haig et al., 1970: 19.
Pagurus lepidus: Haig et al., 1970: 19 (in part, see remarks).

Holotype.—♂ (SL = 1.8 mm) AHF 3832; Type locality: Bahía Chacahua, Mexico, VELERO III station 765-38.

Paratypes.—Gulf of California, Mexico: Bahía San Ignacio, Sinaloa, 1 ♂ (SL = 1.1 mm), VELERO III station 740-37, 6–10 m, March 31, 1937, AHF 3714; near Punta Piaxtla, Sinaloa, 5 ♂ (SL = 1.6–1.8 mm), VELERO III station 744-37, 12–16 m, April 1, 1937, AHF 3715; West Baja California, Mexico: Bajío Knepper, Punta Abreojos, 7 ♂, 3 ♀, 3 ovigerous ♀, 1 juvenile (SL = 0.7–2.6 mm), Magbay Expedition, 17–20 m, February 9, 1964, collectors T. Hopkins and T. Scanland, AHF 6415, MNHN; Bahía San Juanico, 2 ♂, 1 ♀ (SL = 1.4–1.6 mm), VELERO III station 616-37, 32 m, March 2, 1937, AHF 3713; off Boca de Las Animas, Bahía Santa Maria, 1 ♂, 1 ♀ (SL = 1.2, 1.4 mm), Magbay Expedition, 40 m, January 23, 1964, collectors T. Hopkins and T. Scanland, AHF 6413; same locality, 1 ♂, 3 ♀, 1 ovigerous ♀ (SL = 1.1–1.6 mm), Magbay Expedition, 20 m, January 27, 1964, collectors T. Hopkins and T. Scanland, AHF 6414. Southern Mexico: Off Black Rock, Cabo Corrientes, 1 ♂ (SL = 1.5 mm), VELERO III station 763-38, 10–20 m, January 7, 1938, AHF 3833; Bahía Tenacatita, 1 ♂ (SL = 0.9 mm), VELERO III station 964-39, 4–16 m, May 8, 1939, AHF 3935; same locality, 4 ♂, 3 ♀, 3 ovigerous ♀ (SL = 0.8–1.6 mm), VELERO III station 965-39, 16–30 m, May 8, 1939, AHF 3936; Bahía Chacahua, 29 ♂, 5 ♀ (SL = 1.3–2.0 mm), VELERO III station 765-38, 10–20 m, January 9, 1938, AHF 3834, USNM 244077, NHRM 4176, RMNH D 38107; same locality, 1 ♂ (SL = 1.3 mm), VELERO III station 927-39, 20–30 m, March 20, 1939, AHF 3934; Guatemala, off Punta San José, 1 ♂ (SL = 1.8 mm), VELERO III station 770-38, 15–25 m, January 11, 1938, AHF 3835.

Description.—Shield longer than broad, anterior margin between rostrum and lateral projections concave, anterolateral margins sloping, posterior margin truncate. Rostrum obsolete, unarmed. Lateral projections broadly rounded, unarmed or with terminal spine. Dorsal surface of shield usually with scattered tufts of setae.

Ocular peduncles one-half to two-thirds shield length, broadest basally, corneae slightly dilated. Ocular acicles subovate to subtriangular, usually with 2 or 3 submarginal spines, occasionally with 1 or 2 accessory spines on median margin;

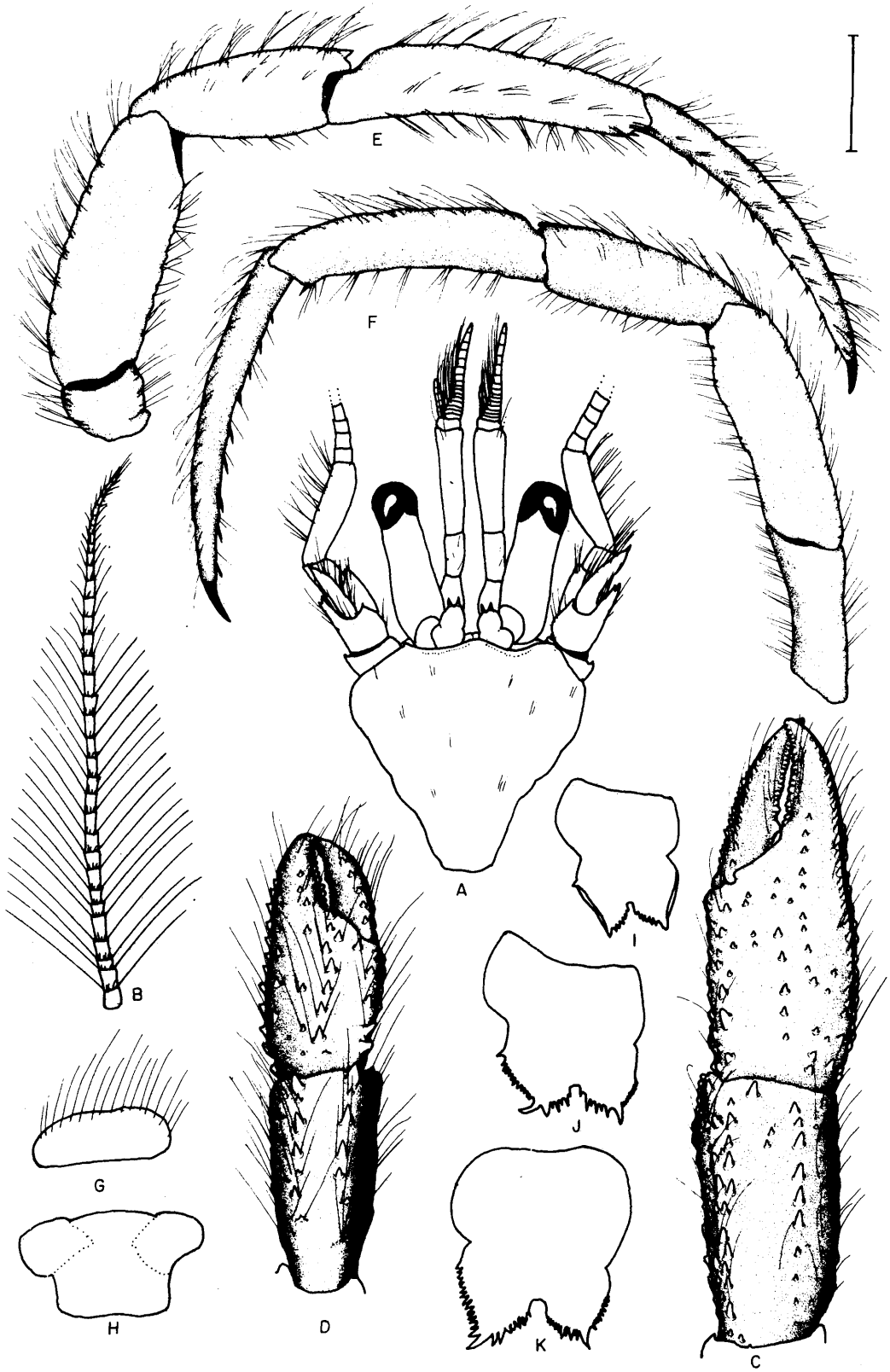

Figure 1. *Pagurus annexus* n. sp., AHF 3834. A, shield and cephalic appendages; B, antennal flagellum; C, right chela and carpus (dorsal view); D, left chela and carpus (dorsal view); E, right second pereopod (lateral view); F, left third pereopod (lateral view); G, sternite of third pereopods; H, sternite of fifth pereopods; I–K, telsons. Scales equal 1 mm (A, C–F) and 0.5 mm (B, G–K).

separated basally by slightly less to slightly more than one-half basal width of 1 acicle. Interocular lobes weakly developed.

Antennular peduncles overreaching ocular peduncles by approximately two-thirds length of ultimate segment. Ultimate segment with 1 or 2 long setae near dorsodistal margin. Penultimate segment with 1 or 2 setae dorsally. Basal segment with 1 acute spine on lateral surface dorsally.

Antennal peduncle overreaching cornea by one-third to one-half length of ultimate segment. Fifth segment with row of tufts of long setae on dorsal surface. Fourth segment with few scattered setae ventrally. Third segment with tuft of setae at ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in simple or bifid spine, lateral and/or mesial margins often with accessory spine distally, both margins also with moderately long setae, dorsomesial distal angle with small spine, mesial face with few short setae. First segment with small spine on lateral face distally, ventral margin produced and armed with 1 small spine laterally. Antennal acicle somewhat arcuate, terminating in small spine, mesial margin with tufts of moderately long setae. Antennal flagellum short, rarely overreaching left cheliped, each article in proximal half with pair of long setae (>4 articles in length) on ventral margin, paired but shorter setae in distal half; each article also with 1 to several very short setae dorsally.

Right cheliped with dactyl slightly to considerably shorter than palm, overlapped by fixed finger and with slight hiatus; in large specimens dactyl and fixed finger tend to be upturned. Cutting edge of dactyl with row of small calcareous teeth and 1 strong tooth proximally, terminating in small corneous claw; cutting edge of fixed finger with small calcareous teeth, terminating in calcareous tip. Dorsomesial margin of dactyl with row of small spines, dorsal surface level or slightly sloping to cutting edge and with few tufts of long setae, mesial face with row of small spines, ventromesial margin with row of low protuberances and tufts of long setae. Palm lengthened in larger males but remaining slightly shorter than carpus; dorsomesial margin weakly delimited by row of small spines, dorsal surface strongly convex and armed with 4 or 5 widely-spaced, longitudinal rows of acute spinules, largest medially, 1 row sometimes extending onto fixed finger, dorsolateral margin with row of small spines, mesial and lateral faces each with 1 to several longitudinal rows of spinules, ventral surface with faint rows of low, sometimes spinulose protuberances. Carpus longer than merus; dorsomesial margin with row of small spines, 1 or 2 spines on or near distal margin, dorsal surface with 1 to several small spines and longitudinal row of spines laterad of midline, dorsolateral margin not delimited, lateral and mesial faces each with 1 or more rows of small spines or spinulose protuberances and tufts of long setae, 1 or 2 acute spines on ventrolateral margin distally. Merus subtriangular; dorsal surface with long setae and usually 1 spine at distal margin, ventromesial margin unarmed or with single or double row of spinulose protuberances, ventrolateral margin with 1 spine distally and often with spinulose protuberances extending onto lateral and/or ventral surfaces.

Left cheliped with dactyl and fixed finger somewhat spoon-shaped; cutting edge of dactyl with row of corneous teeth, terminating in corneous claw. Dactyl equaling or slightly longer than palm; dorsomesial margin with row of spines, mesial face and ventromesial margin each with row of low, sometimes spinulose protuberances and tufts of long setae. Palm one-half to two-thirds length of carpus; slightly elevated in midline and usually armed with double row of spines, outer row smaller and usually extending onto fixed finger, dorsolateral face strongly sloping ventrally, with row of low protuberances or small spines in ventral half and single or double

row of spines or spinulose tubercles marginally, dorsomesial face horizontal, dorsomesial margin with row of strong spines, all surfaces with tufts of long setae. Carpus equaling or slightly longer than merus; dorsomesial and dorsolateral margins each with row of strong spines and tufts of long setae, mesial and lateral faces, and to lesser extent ventral surface, with short, transverse, sometimes spinulose, ridges and long setae. Merus triangular; dorsal surface with transverse ridges and long setae, ventrolateral margin with row of low, often spinulose protuberances and 1 or 2 acute spines distally, ventromesial margin with row of small spines in proximal half, ventral surface with long setae. Ischium with row of small, usually blunt spines on ventromesial margin.

Second and 3rd pereopods similar. Dactyls usually longer than propodi, slender, strongly curved ventrally and terminating in corneous claws; dorsal, mesial and lateral surfaces all with tufts of long setae, ventral margins each with row of 6–9 rather widely-spaced corneous spines and stiff setae. Propodi exceeding length of carpi by at least one-third own length; dorsal surfaces with tufts of long setae, ventral surfaces each with 1 corneous spine at distal margin. Carpi equaling or slightly shorter than meri; dorsodistal margins each with 1 small spine, dorsal surfaces with low protuberances and tufts of long setae, mesial and lateral faces and ventral surfaces with scattered setae. Meri with tufts of long setae on dorsal margins, ventral margins with low, sometimes spinulose protuberances and tufts of long setae. Ischia with long setae on dorsal and ventral surfaces.

Anterior lobe of sternite of 3rd pereopods subrectangular. Sternite of 5th pereopods with anterior lateral angles subovate to subquadrate. Fourth pereopods with long dactyls, very small preungual process at base of claw; propodal rasp with 3 or 4 rows of corneous scales; dorsal margins of dactyls, propodi, carpi and meri (distally) with very long setae.

Exopod of left uropod with row of thick setae on inner margin. Telson with posterior lobes subtriangular, terminal margins slightly oblique, each armed with row of spines, outermost usually strongest and often corneous-tipped, lateral margins with plate delimited anteriorly by weak to strong spine at least on one side when plate composed of fused or closely-set spinules; when plate composed of distinct individual tooth-like spines, prominent anterior spine present or absent.

Distribution.—Gulf of California, Mexico, and Outer Baja California coast to Guatemala; 3 to 40 m.

Etymology.—The specific name is from the Latin *annecto,* meaning to join and reflects the intermediate position of this species in the morphological character cline exhibited by eastern Pacific species of the *provenzanoi* group.

Affinities.—Although a quite distinctive species, *P. annexus,* appears most closely allied to *P. spighti* n. sp. and *P. villosus.* All three species have paired long setae on each article of the antennal flagellum (at least in the proximal half); however, where the latter two species have a simple ocular acicle armed with a single submarginal spine, the ocular acicles of *P. annexus* usually are armed with two or three submarginal spines. *Pagurus annexus* is distinguished from the other eastern Pacific species with multifid ocular acicles by the distinctive form of the acicles, the paired long setae of the antennal flagellum and the development of lateral marginal telsonal plates.

Remarks.—During our re-examination of the AHF collections, we found that the specimens from Bajío Knepper, Punta Abreojos, west Baja California, Mexico, cited by Haig et al. (1970) as *P. lepidus* were instead *P. annexus.*

Pagurus spighti new species
Figure 2A–G

Holotype.—♂ (SL = 1.3 mm) AHF 8114; Type locality: sample 75, Panama Bay, Panama.

Paratypes.—Panama Bay, Panama, 1 ovigerous ♀ (SL = 1.2 mm), sample 75, rock and cobble areas, December 12, 1981, collector T. Spight, AHF 8115; same locality, 1 ♂ (SL = 1.2 mm), sample 78, March 26, 1982, collector T. Spight, USNM 244076.

Description.—Shield as broad or broader than long, anterior margin between rostrum and lateral projections concave, anterolateral margins sloping, posterior margin truncate. Rostrum obsolete, unarmed. Lateral projections obtusely triangular or broadly rounded, unarmed or with marginal spinule. Dorsal surface of shield with few scattered setae.

Ocular peduncles approximately two-thirds shield length, broadest basally, corneae slightly dilated. Ocular acicles subovate to subtriangular, with single submarginal spine; separated basally by slightly less than one-half to complete basal width of 1 acicle. Interocular lobes weakly delineated.

Antennular peduncles overreaching ocular peduncles by approximately three-fourths length of ultimate segment. Ultimate segment with 1 or 2 long setae near dorsodistal margin, few setae on dorsal surface and row of long setae on ventral margin. Penultimate segment with few setae ventrally. Basal segment with 1 acute spine on lateral surface dorsally.

Antennal peduncle overreaching cornea by one-third to one-half length of ultimate segment. Fifth segment with row of widely-spaced, long setae on dorsal surface. Fourth segment with few scattered setae. Third segment unarmed or with small spinule at ventrodistal angle. Second segment with dorsolateral distal angle produced, terminating in acute simple or bifid spine, lateral and mesial margins with moderately long setae, dorsomesial distal angle with small spine, mesial face with few setae. First segment with ventral margin produced and armed with 1 spine laterally. Antennal acicle somewhat arcuate, terminating in small spine, mesial margin with tufts of long setae. Antennal flagella short, rarely overreaching left cheliped, each article with pair of long setae (>3 articles in length) on ventral margin and 1 or 2 short setae on dorsal surface, setae decreasing in length distally.

Right cheliped with dactyl slightly shorter than palm and with slight hiatus between dactyl and fixed finger. Dactyl very slightly overlapped by fixed finger; cutting edge with row of small calcareous teeth and 1 strong tooth proximally, terminating in calcareous or corneous tooth. Cutting edge of fixed finger with 1 large and several small calcareous teeth, terminating in calcareous or corneous tip. Dorsomesial margin of dactyl with double or triple row of small spines or tubercles, dorsal surface slightly elevated in midline and armed with row of small spines, at least in proximal half; surfaces with tufts of long setae. Palm slightly longer than carpus; dorsomesial margin with double row of small spines, dorsal surface strongly convex and armed with 2–4 widely-spaced, longitudinal rows of small spines or tubercles, largest medially, 1 row sometimes extending onto fixed finger, dorsolateral margin with row of small spines or tubercles, stronger in female; all surfaces with tufts of long setae, partially obscuring armature. Carpus equaling or slightly longer than merus; dorsomesial margin with short, double row of spines and tufts of long setae, 1 or 2 spines on or near distal margin, dorsal surface with 1 to several small spines, dorsolateral margin not delimited, lateral face with tufts of long setae, mesial face with tufts of long setae and 2 or 3 strong spines on distal margin. Merus subtriangular; dorsal surface with long setae and 1 or 2 spines at distal margin, ventromesial and ventrolateral margins each with 1 to several acute

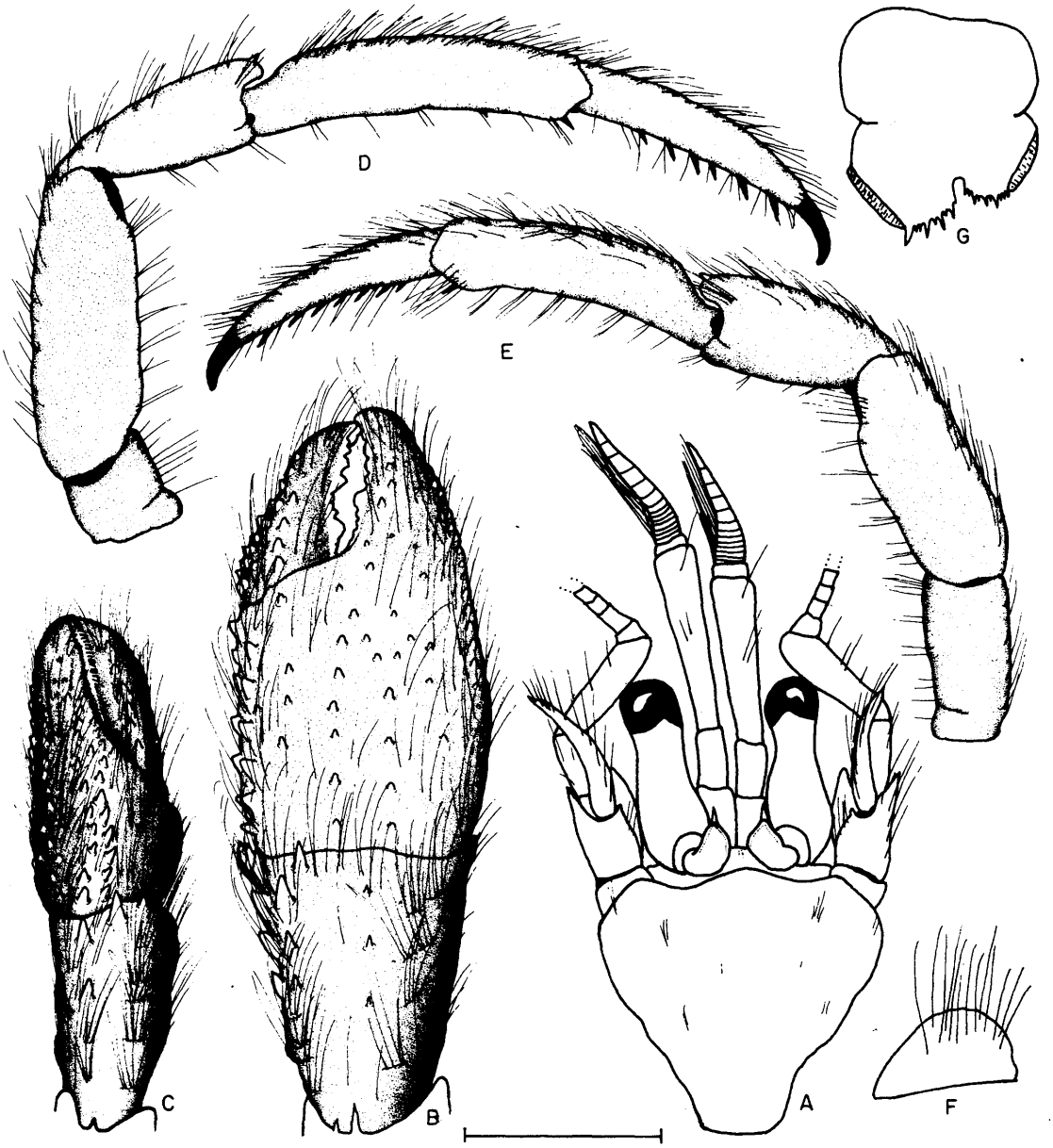

Figure 2. *Pagurus spighti* n. sp., USNM 244076. A, shield and cephalic appendages; B, right chela and carpus (dorsal view); C, left chela and carpus (dorsal view); D, right second pereopod (lateral view); E, left third pereopod (lateral view); F, sternite of third pereopods; G, telson. Scales equal 1.0 mm (A–E) and 0.5 mm (F, G).

spines distally and numerous long setae. Ischium with acute spine on ventrolateral margin.

Left cheliped with dactyl and fixed finger somewhat spoon-shaped. Dactyl considerably longer than palm; cutting edge with row of corneous teeth, terminating in corneous claw. Dorsal surface of dactyl with row of small spines, dorsomesial margin with row of low protuberances, ventromesial margin with row of low, sometimes spinulose protuberances; all surfaces with tufts of long setae. Palm two-thirds to three-fourths length of carpus; strongly elevated in midline and armed with double row of spines, extending onto fixed finger as irregular single

row, dorsolateral face strongly sloping ventrally, with irregular row of small spines in ventral half and single or double row of spines or spinulose tubercles marginally, dorsomesial face strongly sloping and with few low protuberances or small spines, dorsomesial margin not delimited; all surfaces with tufts of long setae. Carpus equaling or slightly longer than merus; dorsolateral margin with 2 or 3 strong spines, distal margin with 1 prominent and 1 smaller spine, dorsomesial margin unarmed but often with low, transverse ridges and tufts of long setae, mesial and lateral faces, and to lesser extent, ventral surface also with short transverse ridges and tufts of long setae, laterodistal margin with small spine, ventrolateral margin with acute spine distally. Merus triangular; dorsal surface with transverse ridges and long setae, ventrolateral margin with row of acute spines at least distally, ventromesial margin with 1 to several small spines, ventral surface with long setae. Ischium unarmed or with row of small spinulose protuberances and long setae on ventromesial margin.

Second and 3rd pereopods similar. Dactyls slightly shorter than propodi, terminating in strong corneous claws, dorsal, mesial and lateral surfaces all with tufts of long setae, ventral margins each with row of 6–8 corneous spines and long stiff setae. Propodi slightly to considerably longer than carpi; dorsal surfaces with tufts of long setae, ventral surfaces each with 1 corneous spine at distal margin and additional 1 or 2 corneous spinules (2nd). Carpi slightly shorter than meri; dorsodistal margins each with 1 small spine, dorsal surfaces with tufts of long setae, mesial and lateral faces and ventral surfaces with few scattered setae. Meri with tufts of long setae on dorsal surface, ventral margins with tufts of long setae and occasionally 1 or 2 small spines on 2nd left. Ischia with long setae on ventral surfaces.

Anterior lobe of sternite of 3rd pereopods semisubcircular, slightly skewed, unarmed but with long setae anteriorly. Fourth pereopods with very small preungual process at base of claw; propodal rasp with 4–6 rows of corneous scales.

Exopod of left uropod with 2–4 thick setae on inner margin. Telson with terminal margins slightly oblique or rounded, each armed with row of spines; lateral margins with narrow plate; no anterior spine.

Color.—Ocular peduncles "clear"; corneae black. Antennules "clear." Antennae brown, with white, clear bands. Ambulatory legs "white, one row brown streaks per segment" (T. Spight, field notes).

Distribution.—Known only from Panama Bay, Panama, intertidal.

Etymology.—This species is named for the collector, Tom Spight.

Affinities.—In having simple ocular acicles, *P. spighti* appears most similar to *P. nesiotes* Haig and McLaughlin and *P. villosus*. Both *P. spighti* and *P. villosus* are easily distinguished from *P. nesiotes* by the presence of long, paired setae on the ventral margins of the articles of the antennal flagella. The flagella in *P. nesiotes* are either naked or provided with 1–4 very short setae every 1–4 articles. *Pagurus villosus* is distinguished from *P. spighti* by the row of strong spines on the dorsomesial margin of the carpus of the left cheliped. The dorsomesial margin of the carpus of *P. spighti* is unarmed.

Pagurus villosus Nicolet
Figure 3A–G

Pagurus villosus Nicolet, 1849: 188; 1854, Crust. pl. 1, figs. 5, 5a–b.—Rathbun, 1910: 598.—Porter, 1935: 137; 1936a: 153; 1936b: 339.—Haig, 1955: 25.—Gordan, 1956: 337.—Haig, 1968: 21.—

Del Solar et al., 1970: 24.—Retamal and Yañez, 1973: 7, 22 [in key], 1 fig.—Ball and Haig, 1974: 102.—Haig, 1974: 130 [in key].

Eupagurus villosus: Stimpson, 1858: 237.

?*Pagurus villosus*: Alcock, 1905: 170.

?*Pagurus benedicti*: Rathbun, 1910: 557, 597 (in part), not pl. 48, fig. 1; not *Pagurus benedicti* (Bouvier) (see remarks).

Holotype.—Not seen; Type locality: Chile.

Material Examined.—Peru: Talara, 3 ♂, 3 ovigerous ♀ (SL = 1.4–2.5 mm), TE VEGA station 18-2, 5 m, April 9, 1968, collector E. Ball, AHF 2602-01; Ancon, near Playa Hermosa, 2 ovigerous ♀ (SL = 1.8, 2.1 mm), Peruvian Coastal Island Investigations station PH28-11, 0–2 m, January 26, 1974, AHF 111-03; Paita Harbor, 1 ♀ (SL = 1.7 mm), TE VEGA station 18-3, 3.5 m, April 13, 1968, collector E. Ball, AHF 2603-04; Paita, off pier, 2 ♀ (SL = 1.7, 2.0 mm), TE VEGA station 18-3, 13 m, April 10, 1968, collector E. Ball, AHF 2809-01; Paita, off Telegraph Pt, 5 ♂, 10 ovigerous ♀ (SL = 2.0–2.6 mm), TE VEGA station 18-3, April 12, 1968, 4.5 m, collector E. Ball, AHF 2810-01; near SE side San Lorenzo I., 1 ovigerous ♀ (SL = 1.7 mm), 5 m, February 5 (?1907), collector R. E. Coker, USNM 40479; off Isla Lorenzo near Callao, 4 ♂, 1 ♀ (SL = 1.9–3.0 mm), VELERO III station 365-35, 18 m, January 10, 1935, AHF 2799-01; Bahía de la Independencia, 12 ♂, 5 ♀, 5 ovigerous ♀ (SL = 1.2–3.4 mm), VELERO III station 829-38, 18 m, February 9, 1938, AHF 2797-01; Bahía Sechura, 16 ♂, 2 ♀, 7 ovigerous ♀, 2 juveniles (SL = 1.0–3.0 mm), VELERO III station 845-38, 17 m, February 15, 1938, AHF 2798-01; Bahía San Nicolas, 1 ♂, 1 ovigerous ♀ (SL = 1.9, 2.7 mm), VELERO III station 821-38, shore, February 6, 1938, AHF 2796-01. Chile: San Vincente, 2 ♂, 3 ovigerous ♀ (SL = 1.5–2.5 mm), October 20, 1959, collector Jeldes, AHF 2856-01; Caleta Leandro, Bahía Concepción, 1 ♂, 2 ovigerous ♀ (SL = 1.8–3.5 mm), April 22, 1971, donated by Museum of Zoology, University of Concepción, AHF 932-01; Bahía de la Herradura, 3 ♂, 1 ovigerous ♀ (SL = 1.7–2.5 mm), 16 m, October 7, 1974, collector R. Dubois, AHF 185-02.

Redescription.—Shield as long or longer than broad, anterior margin concave between rostrum and lateral projections, posterior margin truncate. Rostrum broadly rounded or obsolete, unarmed. Lateral projections obtusely triangular or broadly rounded, unarmed, or with tiny terminal spinule. Dorsal surface of shield with few scattered setae.

Ocular peduncles approximately two-thirds shield length, with row of tufts of setae on dorsal surface mesially, corneae slightly dilated. Ocular acicles subovate to subtriangular, with single submarginal spine; separated basally by approximately two-thirds basal width of 1 acicle.

Antennular peduncles overreaching ocular peduncles by two-thirds to three-fourths length of ultimate segment. Ultimate segment with 1 or 2 long setae near dorsodistal margin and row of setae on ventral surface. Basal segment usually unarmed.

Antennal peduncle overreaching ocular peduncles by one-fourth to one-third length of ultimate segment. Fifth and fourth segments each with several tufts of setae. Third segment unarmed or with small spinule at ventrodistal angle. Second segment with dorsolateral distal angle produced, terminating in acute, simple or bifid spine, lateral and mesial margins with moderately long setae, dorsomesial distal angle unarmed or with small spine. First segment with ventral margin produced and armed with 1 small spine laterally. Antennal acicle somewhat arcuate, terminating in small spine, mesial margin with tufts of long setae. Antennal flagella short, rarely overreaching left cheliped; each article with pair of long setae (>3 article length) on ventral margin, at least in proximal half and with 2 or 3 short to moderately long setae on each article dorsolaterally.

Right cheliped with dactyl equaling or slightly shorter than palm, slightly overlapped by fixed finger and with slight hiatus. Cutting edge of dactyl with row of small corneous teeth and 1 strong calcareous tooth proximally; terminating in corneous claw. Cutting edge of fixed finger with 1 broad multidenticulate tooth and several small calcareous teeth, interspersed with corneous teeth; terminating in corneous claw. Dorsomesial margin of dactyl with double row of small spines

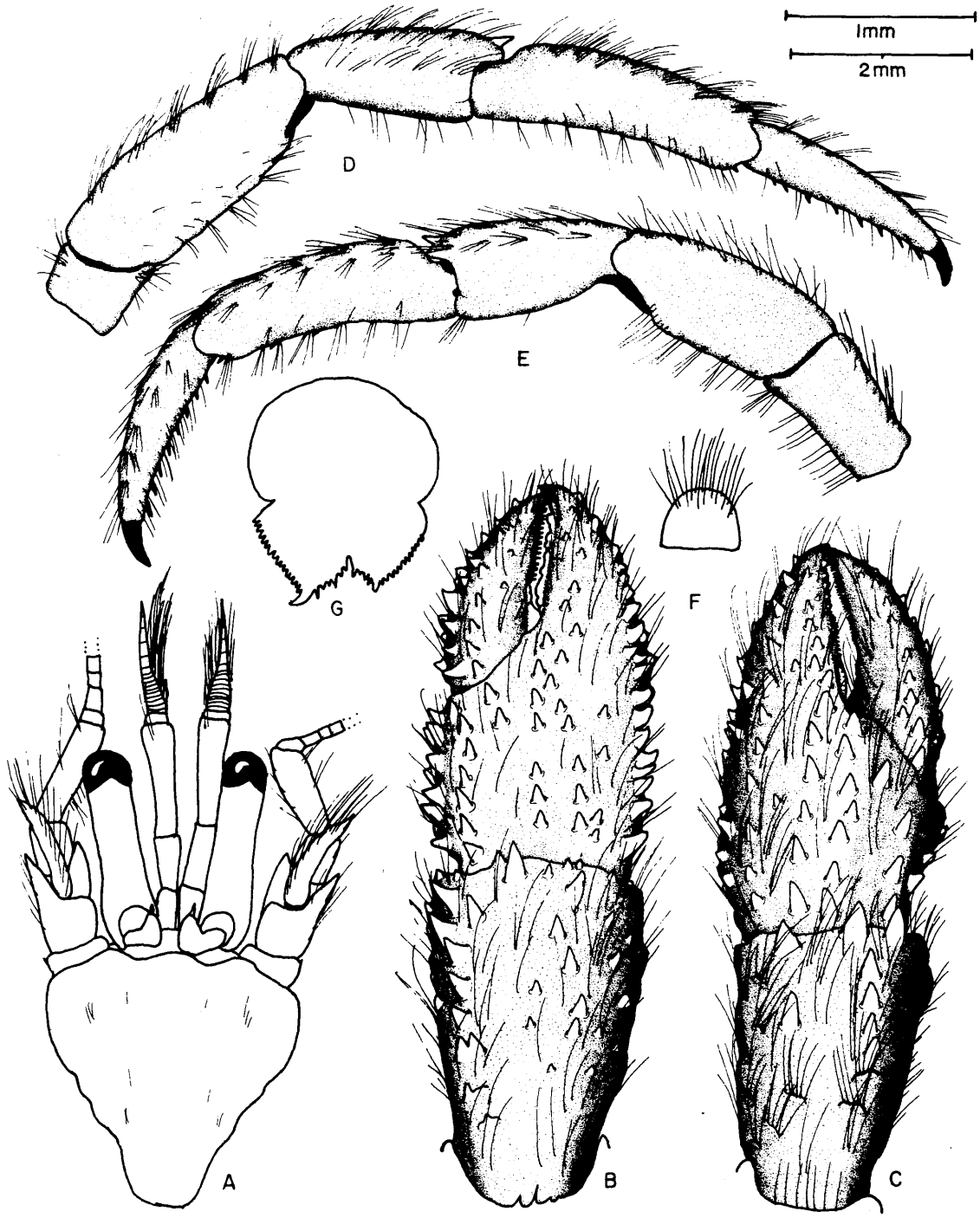

Figure 3. *Pagurus villosus* Nicolet, AHF 2810-01. A, shield and cephalic appendages; B, right chela and carpus (dorsal view); C, left chela and carpus (dorsal view); D, right second pereopod (lateral view); E, left third pereopod (lateral view); F, sternite of third pereopods; G, telson. Scales equal 2.0 mm (A–E) and 1 mm (F, G).

or tubercles becoming single row in distal third, dorsal surface elevated in midline and armed with row of small spines; all surfaces with tufts of long setae. Palm approximately three-fourths length of carpus; dorsomesial margin with single or double row of weak to strong spines, often strongest at proximal angle, dorsal surface convex and armed with 3 longitudinal rows of spines, strongest medially,

1 or 2 rows extending onto fixed finger, dorsolateral margin with row of weak to strong spines, lateral face with row of smaller spines near dorsal margin; all surfaces with tufts of long setae partially obscuring armature. Carpus slightly shorter than merus, mesial face increasing in depth (in cross-section) with increasing specimen size; dorsomesial margin with irregular row of spines and tufts of long setae, 2 or 3 spines on or near distal margin, dorsal surface with scattered spines and irregular row laterad of midline in small specimens, decreasing in size and number with increasing specimen size, dorsolateral margin not delimited, lateral face with several spines or spinulose tubercles dorsally, ventrolateral margin with 2 or 3 blunt to acute spines or tubercles distally, mesial face with scattered long setae and 2 or 3 spines or tubercles on distal margin, ventromesial margin with 1 or 2 tubercles distally. Merus subtriangular, dorsal surface with few long setae and 2 or 3 spines at distal margin, ventromesial and ventrolateral margins each with several spines or spinulose tubercles and numerous long setae. Ischium unarmed.

Left cheliped with dactyl and fixed finger somewhat spoon-shaped. Dactyl considerably longer than palm; cutting edge with row of corneous teeth, terminating in corneous claw. Dorsal surface of dactyl with row of small spines, dorsomesial margin with row of spines or tubercles, all surfaces with tufts of long setae. Palm approximately one-half to two-thirds length of carpus; dorsal surface strongly elevated in midline to form prominent crest armed with row of strong spines, 1 adjacent row of slightly smaller spines extending onto finger fixed as irregular row, dorsolateral face strongly sloping ventrally, with 1 to several irregular rows of spines in ventral half and single or double row of spines or spinulose tubercles marginally, dorsomesial face in small specimens appearing nearly horizontal as result of row of prominent spines on dorsomesial margin, dorsomesial surface in large specimens strongly sloping and with dorsomesial margin unarmed or only with small tubercles, ventromesial margin usually with 3 spines or spinulose tubercles, surfaces all with tufts of long setae. Carpus equaling or slightly longer than merus; dorsolateral margin with 2 usually strong spines, dorsomesial margin with row of moderately strong to strong spines, mesial and lateral faces and margins with transverse ridges and tufts of long setae. Merus triangular; dorsal surface with transverse ridges and long setae, ventrolateral margin with 2 widely-spaced spines proximally, ventromesial margin with row of acute spines, ventral surface with long setae. Ischium with row of small, sometimes widely-spaced spinulose protuberances or small spines and long setae on ventromesial margin.

Second and 3rd pereopods similar. Dactyls equal to or slightly shorter than propodi, terminating in corneous claws; dorsal, mesial and lateral surfaces all with tufts of long setae, ventral margins each with row of 6–8 corneous spines and long, stiff setae. Propodi one-fourth to one-third longer than carpi; dorsal surfaces with tufts of long setae, ventral surfaces each with 1 or 2 corneous spines at distal margin and often 1–5 additional spinules on ventral margin. Carpi slightly shorter than meri; dorsodistal margins each with 1 small spine or very rarely with 2 distal spines, dorsal surfaces with tufts of long setae, mesial and lateral surfaces and ventral faces with scattered setae. Meri with tufts of long setae on dorsal and ventral margins. Ischia with long setae on dorsal and ventral margins.

Anterior lobe of sternite of 3rd pereopods semisubcircular. Fourth pereopods with no preungual process apparent at base of claw; propodal rasp with 4–6 rows of corneous scales.

Exopod of left uropod with several thick setae on inner margin. Telson with terminal margins oblique, each armed with row of spines, strongest at outer angles; lateral margins each with narrow plate of individual spinules or denticles, no anterior spine.

Color.—Carapace mottled light tan and white. Ocular peduncles mottled olive green on white with deep white pigment spots, ocular acicles olive drab, corneae brown and gold. Antennule with ultimate segment light green, penultimate segment with brown bands distally; flagellum very light green. Antennal flagellum irregularly banded brown and white, almost transparent near base. Chelipeds tan with white tubercles and white at tip of fixed finger. Ambulatory legs brown and white splotched. Distal third of propodus and dactyl white (E. Ball, field notes).

Distribution.—Peru to Chile; intertidal to 40 m (Haig, 1955).

Affinities.—As may be seen from the redescription, *P. villosus* is a highly variable species, particularly with regard to the armature of the chelae. *Pagurus villosus* is closely allied to *P. spighti,* sharing such diagnostic characters as long, paired setae on the articles of the antennal flagellum and simple ocular acicles. Small specimens of *P. villosus,* in which the spines of the dorsomesial margin of the left chela are strong, giving the dorsomesial surface an almost horizontal appearance, are easily distinguished from *P. spighti* by this character alone. However, with increasing specimen size these spines, as most others of the palms and carpi of both chelipeds, usually decrease in size; the dorsomesial surface of the left chela becomes more obviously sloped. In these specimens, the most reliable character for separating the two species is the row of spines on the dorsomesial margin of the carpus of the left cheliped of *P. villosus.* This margin is unarmed in *P. spighti.*

Remarks.—Haig (1955) included, without comment, Rathbun's (1910) report and figure of ?*P. benedicti* in the synonymy of *P. villosus.* In a subsequent report, Haig (1968) again included Rathbun's (1910) description of ?*P. benedicti,* but not her figure (pl. 48, fig. 1) in the synonymy of *P. villosus.* We have now reexamined Rathbun's specimen (USNM 40479) and confirmed its identity as *P. villosus.* This specimen is an ovigerous female, whereas the specimen figured by Rathbun is neither *P. villosus* nor an ovigerous female. Rathbun gave no indication that a specimen other than the one included in her description had been photographed; however, plate 48, figure 1 is clearly a specimen of *P. benedicti* sensu stricto.

Pagurus benedicti (Bouvier)
Figures 4A–I, 5A–J

Eupagurus minutus Benedict, 1892: 14 (not *Pagurus minutus* Hess, 1865: 160).
Eupagurus benedicti Bouvier, 1898: 381.—Alcock, 1905: 180.
Pagurus benedicti: Schmitt, 1924: 382.—Boone, 1931: 143, fig. 2; 1932: 5, fig. 1.—Steinbeck and Ricketts, 1941: 455.—Gordan, 1956: 326.—Parker, 1964: 168, 170.—Forest and De Saint Laurent, 1968: 116.—Ball and Haig, 1974: 102.—McLaughlin, 1975: 373.
?*Pagurus benedicti*: Rathbun, 1910 (in part), pl. 48, fig. 1; not pp. 557, 597 (=*P. villosus* Nicolet).
Nympagurus galapagensis Boone, 1932: 17, fig. 5.—Gordan, 1956: 320.
? *Clibanarius panamensis*: Schmitt, 1939: 11 (not *Clibanarius panamensis* Stimpson, 1859); see remarks.
Pagurus galapagensis: Haig et al., 1970: 20.—McLaughlin, 1975: 373.—Snyder-Conn, 1980: 284.
Not *Pagurus minutus* (Benedict): Makarov, 1938: 320, misspelling of *Pagurus munitus* [=*Elassochirus gilli* (Benedict), see remarks].

Holotype.—[*Pagurus minutus* (Benedict)] ♂ (SL = 2.1 mm) USNM 16712. Type locality: ALBATROSS station 3022, off Georges Island, Gulf of California, Mexico.

Holotype.—[*Pagurus galapagensis* (Boone)]: ♀ (ovigerous) (SL = 4.2 mm) AMNH 12238. Type locality: *Arcturus* station 54, Gardner Bay, off Hood Island, Galapagos Islands.

Other Material Examined.—Gulf of California, Mexico: Punta Peñasco, Sonora, 1 ♂, 1 ♀ (SL = 2.1, 2.5 mm), VELERO III station 721-37, 15–22 m, March 24, 1937, AHF 2811-01; Off Isla San Jorge, Sonora, 2 ♂, 2 ♀ (SL = 2.4–4.0 mm), VELERO III station 722-37, 18 m, March 25, 1937, AHF 2812-01; Bahía Tepoca, Sonora, 19 ♂, 13 ♀, 1 ovigerous ♀ (SL = 1.1–3.0 mm), VELERO III station 1078-40,

20–24 m, February 4, 1940, AHF 2813-01; North of Punta Lobos, Sonora, 1 ♂ (SL = 2.4 mm), VELERO III station 725-37, 18 m, March 26, 1937, AHF 2814-01; Off Puerto Libertad, Sonora, 1 ♂ (SL = 2.1 mm), station P-208-60, Curray Orca Cruise, 13 m, March 30, 1960, collector R. H. Parker, AHF 2805-01; South of Isla Tiburón, 3 ♂ (SL = 2.4–3.8 mm), VELERO III station 1044-40, 4–30 m, January 25, 1940, AHF 2807-01; Off Punta Baja, Sonora, 1 ♂ (SL = 2.8 mm), station P-184-60, Curray-Orca Cruise, 15 m, March 25, 2960, collector R. H. Parker, AHF 2815-01; Ensenada de San Francisco, Sonora, 1 ♂ (SL = 2.2 mm), VELERO III station 1087-40, 27–33 m, February 7, 1940, AHF 2816-01; Outside Bahía Guaymas, Sonora, 3 ♂, 1 ♀ (SL = 2.0–2.6 mm), VELERO III station 1039-40, 11–18 m, January 23, 1940, AHF 2817-01; Between islas Angel de la Guarda and Mejía, Baja California, 1 ♀ (SL = 2.7 mm), VELERO III station 1056-40, 12–22 m, January 28, 1940, AHF 2806-01; Puerto Refugio, Isla Angel de la Guarda, 1 ♂ (SL = 2.4 mm), VELERO III station 542-36, 27–55 m, March 4, 1936, AHF 2818-01; Puerto Refugio, 5 ♂ (SL = 1.3–3.5 mm), VELERO III station 1048-40, 20–40 m, January 26, 1940, AHF 2819-01; same locality, 2 ♂, 1 ♀ (SL = 1.5–2.3 mm), VELERO III station 1052-40, 11 m, January 27, 1940, AHF 2820-01; Bahía de Los Angeles, Baja California, 3 ♂ (SL = 1.9–2.4 mm), VELERO III station 539-36, 2 m, March 3, 1936, AHF 2821-02; Vicinity of Puerto San Carlos, Baja California, 3 ♂, 1 ♀ (SL = 2.3–3.2 mm), VELERO IV station 1765-49, 2–18 m, March 24, 1949, AHF 2822-01; South of Isla Tortuga, Baja California Sur, 1 ♀ (SL = 1.8 mm), VELERO III station 576-36, 38 m, March 13, 1936, AHF 2823-01; Puerto Escondido, Baja California Sur, 1 ♂ (SL = 1.7 mm), VELERO IV station 1747-49, 13 m, March 18, 1949, AHF 2824-01. West Baja California Peninsula, Mexico: Bahía Magdalena, Baja California Sur, 1 ♀ (SL = 3.4 mm), TE VEGA station 18-23, 3–5 m, April 2, 1968, collector E. Ball, AHF 2630-08; Punta Entrada, Bahía Magdalena, 1 ♂, 1 ♀ (SL = 2.0, 2.3 mm), Magbay Expedition, 6 m, February 1, 1964, collectors T. Hopkins and T. Scanland, AHF 2804-01. Southern Mexico: Bahía Tenacatita, Jalisco, 3 ♂ (SL = 1.5–2.0 mm), VELERO III station 965-39, 15–27 m, May 8, 1939, AHF 2825-01; Off Bahía Braithwaite, Isla Socorro, Islas Revillagigedos, 1 ♂ (SL = 1.6 mm), VELERO III station 924-39, 31–84 m, March 18, 1939, AHF 2826-01; Just south of Cabo Henslow, Isla Socorro, 1 ♂ (SL = 2.5 mm), SEARCHER station 53, 9–15 m, February 15, 1972, AHF 2827-01. Central America: 1 ♂ (SL = 2.0 mm), April 4, 1882, collector C. Bovallius, NHRM 7191; 2 ♂, 1 ♀ (SL = 1.5–3.2 mm), April 27, 1882, collector C. Bovallius, NHRM 7183, 7185; Sennora, 1 ovigerous ♀ (SL = 2.4 mm), 6 m, April 20, 1882, collector C. Bovallius, NHRM 7186; Magicienne Bay, 1 ♂ (SL = 2.5 mm), 12 m, April 22, 1882, collector C. Bovallius, NHRM 7187. Costa Rica: Puerto Parker, 2 ♂ (SL = 1.3, 2.6 mm), VELERO III station 934-39, 6–15 m, March 24, 1939, AHF 2828-01; Bahía Potrero, 1 ovigerous ♀ (SL = 2.5 mm), SEARCHER station 414, 11 m, February 17, 1972, AHF 2829-01; Bahía Cocos south of Puerto Culebra, 1 ovigerous ♀ (SL = 1.5 mm), VELERO III station 116-33, 4 m, March 13, 1933, AHF 2830-01; Bahía Brasilito, 2 ♀ (SL = 2.1, 2.5 mm), TE VEGA station 18-18, 11 m, May 13, 1968, collector E. Ball, AHF 2622-08. Panama: Bahía Honda, 1 ♂, 2 ♀, 3 ovigerous ♀ (SL = 1.3–3.1 mm), VELERO III station 249-34, 27–37 m, February 22, 1934, AHF 2831-01; Golfo de Panama, 6 ♂, 1 ♀, 5 ovigerous ♀ (SL = 1.8–2.6 mm), 14–20 m, April 22–25, 1882, collector C. Bovallius, NHRM 7175; Pacific Panama, 2 ♂ (SL = 2.7, 3.0 mm), collector P. Abrams, AHF 164-08. Colombia: Punta Cotudo, 1 ♂ (SL = 3.8 mm), TE VEGA station 18-12b, 6 m, April 30, 1968, collector E. Ball, AHF 2612-05; Off Isla Gorgona, 1 ♂, 2 ovigerous ♀ (SL = 2.2–3.0 mm), VELERO III station 224-34, 18 m, February 12, 1934, AHF 2832-01. Ecuador: Manta, 1 ♀ (SL = 2.3 mm), TE VEGA station 18-5, 6.5 m, April 19, 1968, collectors E. Ball and P. Smith, AHF 2605-05; Off Isla La Plata, 1 ovigerous ♀ (SL = 2.7 mm), VELERO III station 212-34, 82–101 m, February 10, 1934, AHF 2833-01. Galapagos Islands: Tagus Cove, Isla Isabela [Albemarle Island], 1 ♂, 2 ovigerous ♀ (SL = 1.7–2.7 mm), VELERO III station 66-33, 18–37 m, February 9, 1933, AHF 2834-01; same locality, 1 ♂ (SL = 2.9 mm), VELERO III station 148-34, 22–46 m, January 13, 1934, AHF 2835-01; same locality, 1 ♂ (SL = 2.9 mm), VELERO III station 326-35, 27 m, December 10, 1935, AHF 2836-01; Cartago Bay, Isla Isabela [Albemarle Island], 3 ♂ (SL = 2.2–3.0 mm), VELERO III station 799-38, 27–33 m, January 22, 1938, AHF 2837-01; Sulivan Bay, Isla San Salvador [James Island], 5 ♂, 1 ♀, 1 ovigerous ♀ (SL = 2.0–2.6 mm), VELERO III station 177-34, 10–37 m, January 23, 1934, AHF 2839-01; Off Isla Seymour [North Seymour Island], 4 ♂, 2 ovigerous ♀ (SL = 1.7–2.9 mm), VELERO III station 348-35, 27 m, December 13, 1934, AHF 2840-01; Isla Santa Maria [Charles Island], 2 ♀, 2 ovigerous ♀ (SL = 1.9–2.4 mm), "Eugenie Expedition," 26–24 m, May 15–17, 1852, NHRM 7167; Black Beach, Isla Santa Maria [Charles Island], 1 ♂ (SL = 2.0 mm), VELERO III station 166-34, shore, January 19, 1934, AHF 2838-01; Gardner Bay, Isla Española [Hood Island], 1 ♂ (SL = 4.6 mm), VELERO III station 25-33, 4 m, January 24, 1933, AHF 2808-01.

Redescription.—Shield slightly to considerably longer than broad, surface usually with few scattered setae, anterior margin between rostrum and lateral projections concave, posterior margin truncate. Rostrum obsolete. Lateral projections usually with small terminal spinule.

Ocular peduncles two-thirds to slightly exceeding shield length, dorsomesial

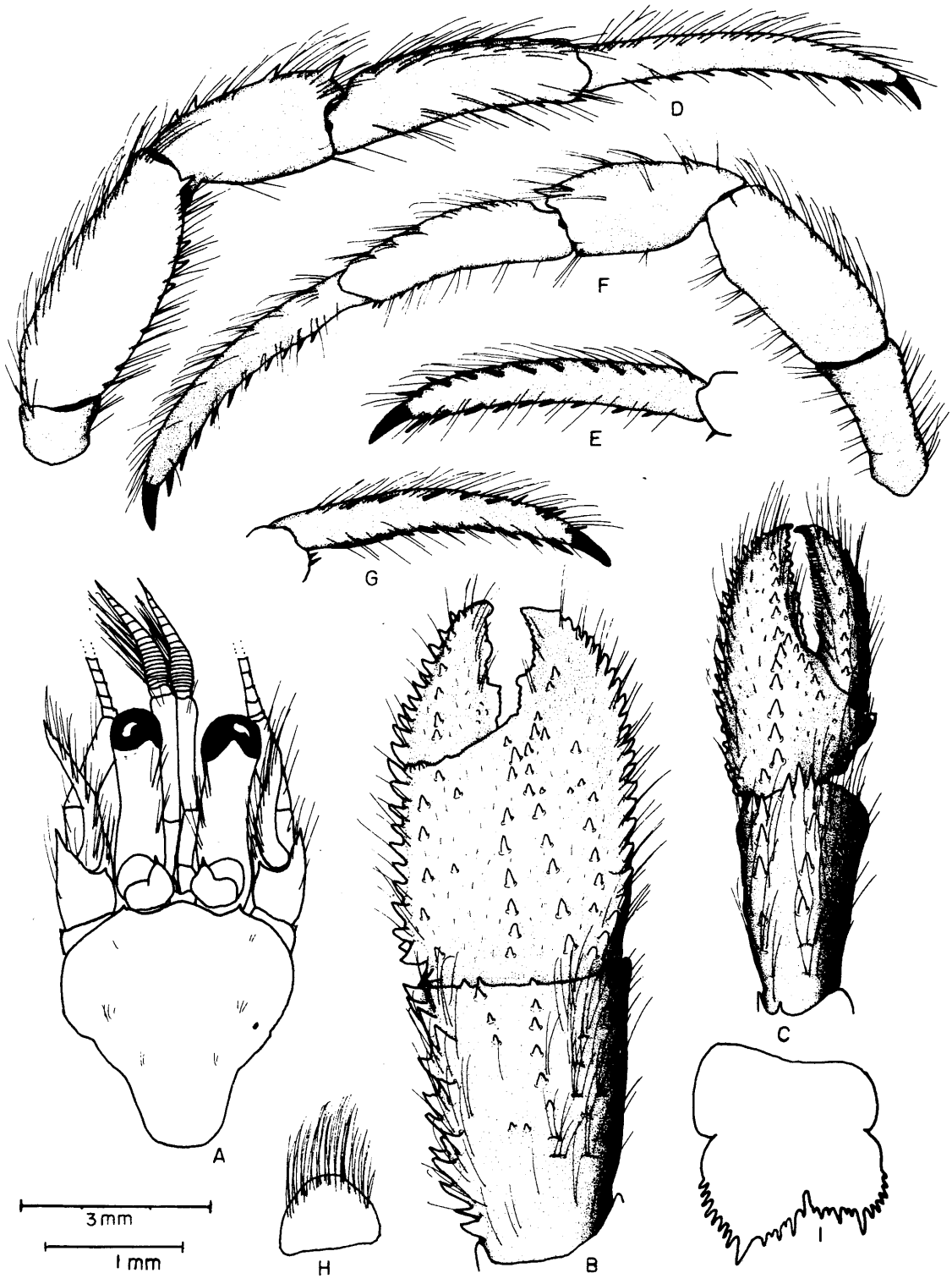

Figure 4. *Pagurus benedicti* (Bouvier), AHF 2807-01. A, shield and cephalic appendages; B, right chela and carpus (dorsal view); C, left chela and carpus (dorsal view); D, right second pereopod (lateral view); E, dactyl of second right pereopod (mesial view); F, left third pereopod (lateral view); G, dactyl of third left pereopod (mesial view); H, sternite of third pereopods; I, telson. Scales equal 3.0 mm (A–G) and 1 mm (H, I).

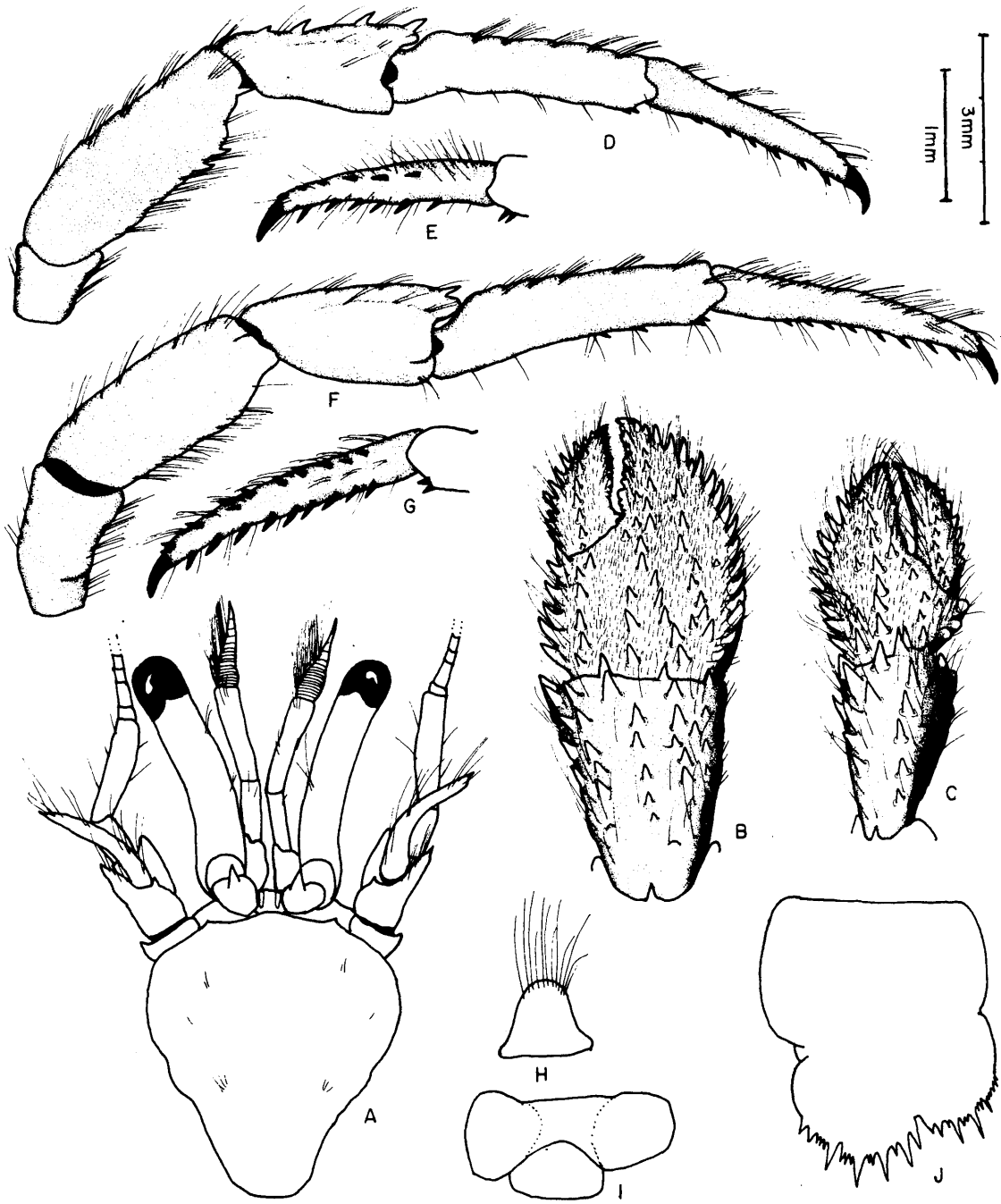

Figure 5. *Pagurus galapagensis* (Boone), holotype AMNH 12238. A, shield and cephalic appendages; B, right chela and carpus (dorsal view); C, left chela and carpus (dorsal view); D, right second pereopod (lateral view); E, dactyl of second right pereopod (mesial view); F, left third pereopod (lateral view); G, dactyl of third left pereopod (mesial view); H, sternite of third pereopods; I, sternite of fifth pereopods; J, telson. Scales equal 3.0 mm (B–G) and 1 mm (A, H, I).

surface with row of tufts of setae; corneae slightly dilated. Ocular acicles ovate to subtriangular, with subterminal single spine; separated basally by one-half to entire basal width of 1 acicle. Interocular lobes weakly delineated, sometimes weakly calcified.

Antennular peduncles, when extended, equaling or overreaching corneae by

one-third to one-half length of ultimate segment. Ultimate and penultimate segments with few tufts of setae. Basal segment with acute spine on lateral surface.

Antennal peduncles slightly shorter to slightly longer than ocular peduncles. Fifth segment with row of tufts of setae on dorsal surface. Fourth segment with few scattered setae. Third segment unarmed or with acute spine at ventrodistal angle. Second segment with dorsolateral distal angle produced, terminating in simple or bifid spine and with row of setae on mesial margin, dorsomesial distal angle with small spine. First segment usually with spine at laterodistal angle, one acute spine distoventrally. Antennal acicle sometimes reaching nearly to tip of corneae, terminating in simple acute spine, mesial margin with row of tufts of setae. Antennal flagellum usually as long or longer than length of ambulatory legs; each article frequently with 1 or 2 long, but not paired, setae and 2–4 shorter setae, at least in proximal third to half.

Right cheliped with palm and fingers moderately broad, dactyl equaling or exceeding length of palm. Cutting edge of dactyl with broad, multidenticulate tooth proximally and several smaller calcareous teeth interspersed with corneous teeth distally; terminating in corneous or calcareous claw. Dorsal surface of dactyl with numerous short setae sometimes giving mat-like appearance and scattered longer setae, particularly near cutting edge, row of moderately strong to strong spines on slightly elevated midline and row of very strong spines on distally depressed dorsomesial margin, ventral surface with few tufts of setae. Palm slightly shorter or equal to length of carpus; dorsomesial and dorsolateral margins each with row of strong spines, latter extending almost to tip of fixed finger, dorsal surface with 2 rows of prominent spines usually forming inverted V medially and 1 or 2 rows of small to moderately strong spines near each margin of palm, few spines or spinules proximally on fixed finger, dorsomesial and dorsolateral margins and mesial, lateral and ventral surfaces all with long setae, dorsal surface of palm and fixed finger with numerous, very short setae, sometimes giving mat-like appearance. Carpus slightly shorter or equaling length of merus; dorsomesial margin with double row of strong, acute spines, dorsal surface with median row of spines or spinules, at least in distal half and second similar or stronger row laterad of midline, dorsolateral margin not delimited, distal margin with 1 or 2 spines, lateral and mesial faces sometimes slightly spinulose and with tufts of setae. Merus with 1 or 2 spines at dorsodistal margin, dorsal surface with low, transverse ridges and tufts of setae. Ventrolateral margin with row of small to large spines or tubercles, ventromesial margin with 1 or 2 spines proximally. Ischium with row of spines or spinules on ventromesial margin and 1 acute spine at ventrolateral distal angle.

Left cheliped with chela narrowly to broadly triangular, dactyl and fixed finger somewhat spoon-shaped and with slight hiatus. Dactyl approximately two and one-half to three times length of palm; cutting edge with row of corneous teeth, terminating in corneous claw. Dorsal surface of dactyl with row of small spines in midline, dorsomesial margin with row of small spinules or spinulose tubercles, surfaces and margin with numerous long setae. Palm approximately one-third length of carpus; dorsal surface with numerous very short setae, often giving mat-like appearance, elevated in midline and with row of spines extending almost entire length of fixed finger, dorsolateral margin with row of strong, acute spines and tufts of long setae, dorsomesial surface sloping, and with 3 blunt spines and tufts of long setae marginally, dorsolateral and dorsomesial surfaces sometimes with few spines or tubercles. Cutting edge of fixed finger with row of small calcareous teeth interspersed with corneous teeth, terminating in small calcareous claw. Carpus slightly shorter to approximately equaling length of merus; dorsomesial and dorsolateral margins each with row of spines, dorsodistal margin

with 2 or 3 acute spines, mesial face with transverse ridges and tufts of setae, distal margin sometimes with 1 or 2 spines, ventromesial margin with few low protuberances, lateral face with 1 spine on distal margin and row of acute or blunt spines on ventral margin. Merus with spine at dorsodistal margin and tufts of setae on dorsal surface, ventrolateral margin with row of strong, acute spines, ventromesial margin with row of strong spines in proximal half. Ischium with row of spinules on ventromesial margin, 1 acute spine on laterodistal margin ventrally.

Ambulatory legs exhibiting some degree of sexual dimorphism. Dactyls at least one-third longer than propodi (males), or usually shorter than or equal to length of propodi (females); ventral margins each with row of 6–11 corneous spines (fewest in females), mesial faces each with row of 4–10 corneous spines dorsally (fewest in females), dorsal surfaces with numerous tufts of setae. Propodi one-fourth to one-third longer than carpi; 1 corneous spinule at ventrodistal margin and 2–5 additional spinules on ventral surface, dorsal surfaces with transverse rows of long setae. Carpi two-thirds to four-fifths length of meri; dorsal surfaces of 2nd each with row of 3 or 4 widely spaced spines, rarely as few as 2 or as many as 6, dorsal surfaces of 3rd with 1 spine at distal margin (females) and 1 small additional spine near posterior margin (males). Meri with tufts of setae on dorsal margins, ventrolateral distal angle with acute spine (2nd) or unarmed (3rd), ventral margin with 1 to several acute spines (2nd) or unarmed (3rd). Ischia unarmed.

Anterior lobe of sternite of 3rd pereopods subsemicircular to roundly triangular. Sternite of 5th pereopods with lateral lobes subovate to subrectangular, widely separated. Fourth pereopod with 5 or 6 rows of corneous scales in propodal rasp; no preungual process at base of claw.

Exopod of left uropod with row of thick setae on ventral margin. Telson with posterior lobes slightly asymmetrical, terminal margins level, slightly rounded or slightly oblique, armed with several large calcareous spines interspersed with smaller calcareous spines, lateral margins similarly armed.

Color.—Shield mottled olive to brown and white with brown patches and pink or red anteriorly. Ocular peduncles varying from mottled green to opaque with interrupted longitudinal tan or brown stripes; corneae silver or black with flecks of gold. Ocular acicles mottled tan or olive and white. Antennular peduncles varying from uniform green to faint olive base color and with interrupted light tan longitudinal stripes. Antennal peduncles mottled olive or brown and white, or orange-tan forming longitudinal interrupted stripes on ultimate segment. Flagellum transparent but with tint of red-brown every 2–8 articles interrupted by white or clear article with white chromatophore. Right cheliped with red-orange band on white base color distally on dactyl and fixed finger; palm and proximal portions of dactyl and fixed finger faint olive and white with orange-tipped spines dorsally, mottled olive or tan and white on other surfaces. Carpus usually with longitudinal reddish stripes on white background, occasionally mottled olive and white, merus mottled olive, brown or tan and white. Left cheliped similar but sometimes with white-tipped protuberances on mesial margin of dactyl and orange patch on dorsal surface of carpus. Dactyls of ambulatory legs with reddish coloration near tips, faint longitudinal red, olive or brown stripes centrally and overlaying reddish-tan proximal band. Propodi with red, olive-tan or brown longitudinal stripes and red or reddish-orange band centrally. Carpi and meri with opaque base color, central and proximal faint bands of reddish-tan overlaid with red, olive-tan or brown longitudinal stripes (E. Ball, field notes; P. McLaughlin, lab notes).

Distribution.—Gulf of California and West Baja California, Mexico to Ecuador, Galapagos Islands; 2–84 m.

Affinities.—*Pagurus benedicti* is distinct among Pacific species of the *provenzanoi* group, being set apart from all other species by the armature of the telson. As previously discussed, *P. annexus* appears to be the most closely related species, exhibiting character states intermediate between those found in *P. benedicti* and some of the other *provenzanoi* group species.

Remarks.—Benedict (1892) described a specimen from the Gulf of California, Mexico, as *Eupagurus (=Pagurus) minutus.* It was an unfortunate choice of names, first because the name was preoccupied by *P. minutus* Hess presumably from Australia, and second because of its similarity to another species described in the same report as *P. munitus* Benedict (as *Eupagurus*). In his report on Anomura of the Far Eastern Seas, Makarov (1938, 1962) included the eastern North Pacific species *P. munitus* (=*Elassochirus gilli,* cf. McLaughlin, 1974) in his synonymy of *P. cavimanus* (Miers). In the English summary of his original Russian paper, Makarov (1938: 320) cited the North Pacific species as *P. minutus.* This confusion of the specific names *munitus* and *minutus* is probably why he included "California," which he mistakenly confounded with the Gulf of California, Mexico, in his distribution of *P. cavimanus.*

Bouvier (1898), as the 'first revisor,' renamed Benedict's species *P. benedicti.* Bouvier noted one difference between Benedict's (1892) description and his own specimen from La Paz, i.e., two rows of spines on the carpus of the left cheliped rather than the single row described by Benedict. We have now examined Benedict's specimen (USNM 16712) and found that while the spines are quite small, there is a second row of spines on the carpus of the left cheliped. Therefore, we are confident that Bouvier (1898) was accurate in his assumption that he was dealing with Benedict's (1892) species. If an author proposes a new name expressly as a replacement, both names have the same name-bearing type (International Code of Zoological Nomenclature, 1985, Art. 72e), thus Benedict's (1892) specimen remains the type of *P. benedicti.* This specimen has not been figured here as most calcification is lacking, the right cheliped is now damaged and the abdomen is missing. However, the specimen has been carefully compared and agrees with the figured specimen from south of Tiburón Island, Gulf of California, Mexico.

As previously indicated, Rathbun's (1910) identification of a specimen from Isla de San Lorenzo, Peru, as ?*P. benedicti* is incorrect. The specimen is actually *P. villosus*; however, Rathbun's figure (pl. 48, fig. 1) is of *P. benedicti.*

In a report on the Crustacea of the Bay of Panama, Boone (1931) noted, rather curiously, that Benedict's type was "a very young adult." She also stated, correctly, that Rathbun's specimen from Peru was also in the U.S. National Museum. However, it would appear that she did not examine either specimen. The type of *P. benedicti,* although small, is a mature male; Rathbun's (1910) specimen is not *P. benedicti.* Boone (1931: 143, fig. 2) described and illustrated a specimen from Saboga Island Harbor, Pearl Islands, Bay of Panama. The same illustration and essentially the same description were used in her subsequent Galapagos paper (Boone, 1932: 5, fig. 1) when she reported *P. benedicti* from ARCTURUS station 54, Gardner Bay, Hood Island. In this latter report, Boone also described *Nympagurus galapagensis,* a new genus and species based on a single ovigerous female from the same ARCTURUS station. *N. galapagensis* was not reported again, other than in literature citations (Gordan, 1956) until Haig et al. (1970) cited its wide distribution throughout the Panamic faunal province. After reexamining Boone's (1932) type, Haig et al. concluded that *Nympagurus galapagensis* fell within the definition of *Pagurus* and placed the species in *Pagurus.* Although Ball and Haig

(1974) referred to both *P. benedicti* and *P. galapagensis* in their report on hermit crabs from the tropical eastern Pacific, these authors were not entirely convinced of the distinctness of the two species. We have now re-examined the types of both taxa, numerous lots from the Allan Hancock Foundation collections and several lots from the early Central American exploratory expeditions housed in the Naturhistoriska Rijksmuseet, Stockholm. Diagnoses based on the two type specimens are sufficiently distinct to suggest two separate taxa. However, the type of *P. benedicti* is a male; the type of *P. galapagensis* is a female. When collections from individual localities contain both males and females we have found sexual dimorphism, not specific distinctness, to be responsible for observed differences. Therefore, we believe that *P. galapagensis* is a junior subjective synonym of *P. benedicti.*

Waldo L. Schmitt identified and labeled a specimen (USNM 78254) that he collected during the 1938 Presidential Cruise at Socorro Island, Revillagigedo Islands, Mexico, as *Clibanarius panamensis*?; however, in his publication of the Crustacea collected during that cruise (Schmitt, 1939), the question mark was not included. We have examined Schmitt's specimen (♂, SL = 4.4 mm) which, at least now, is missing both chelipeds and the left second pereopod; the dactyl of the left third pereopod is a regenerated stub. This specimen is clearly not *Clibanarius panamensis,* but agrees well with *P. benedicti* in the shape and armature of the telson, armature of the dactyl and carpus of the right second pereopod, and the shape of the sternites of the third and fifth pereopods. Although the rostrum is obsolete in *P. benedicti,* the anterior margin of the shield is usually slightly convex. In Schmitt's specimen this margin is straight between the lateral projections; the antennal flagellum lacks setae. The ocular acicles, although having the single spine characteristic of *P. benedicti,* are more poorly developed anteriorly, but are basally broader than in typical *P. benedicti.* Because of these differences and the absence of chelipeds, we can only questionably assign this specimen to *P. benedicti.*

Pagurus redondoensis Wicksten
Figure 6A–H

Pagurus redondoensis Wicksten, 1982: 605, figs. 1–3.—Harvey and McLaughlin, 1991: 20.
Pagurus lepidus: Haig et al., 1970: 19 (in part, see remarks).

Holotype.—♂ (SL = 2.1 mm) AHF 783; Type locality: station RA7803#3, King Harbor Project, Redondo Beach, California.

Other Material Examined.—California: Off Redondo Beach, 3 ♂, 1 ovigerous ♀ (SL = 1.3–2.3 mm), VELERO III station 1139-40, 20–36 m, May 6, 1940, AHF 2841-01; off Redondo Beach, 2 ♂, 1 ♀ (SL = 1.6–3.0 mm), 46 m, May 1941, collectors J. and T. Burch, AHF 2842-01; Sportfishing landing, Redondo Beach, 29 ♂, 9 ♀, 2 ovigerous ♀ (SL = 0.8–2.6 mm), 4.5 m, December 6, 1987, collector A. Howe, AHF 2843-01, USNM, NHRM, RMNH, MNHN; Anaheim Landing, 1 ovigerous ♀ (SL = 2.2 mm), station 1445-42, shore, February 12, 1942, collector AHF field party, AHF 2844-01; Catalina Harbor, Santa Catalina Island, 1 ♂ (SL = 0.8 mm), mid-intertidal, 14 December, 1970, collector C. Swift, AHF 2845-01; Little Harbor, Santa Catalina Island, 1 ♂, 1 ♀ (SL = 2.0, 2.1 mm), SCIBS station 35:67, to 12.2 m, June 5, 1967, collectors R. Given and D. Lees, AHF 2846-01; same locality, 4 ♂, 3 ovigerous ♀ (SL = 1.8–2.8 mm), SCIBS station 43:67, 4.5–7.6 m, August 9, 1967, collector D. Lees, AHF 2847-01; San Clemente, 2 ovigerous ♀ (SL = 1.6, 1.8 mm), 9.4 m, 1975, collector J. Boaz, AHF 2848-01; Alligator Head, 1 ♂, 1 ♀ (SL = 2.7, 3.0 mm), 3 m, June 10, 1964, collector T. Scanland, AHF 2849-01. West coast of Baja California, Mexico: Ensenada, 5 ♂ (SL = 1.7–2.2 mm), November 28, 1936, collector S. Glassell, AHF 2850-01; 3.75 miles NNW of Punta Eugenia, 1 ♂ (SL = 1.8 mm), VELERO IV station 1702-49, 36.4 m, March 5, 1949, AHF 2851-01; Dewey Channel opposite San Eugenio Point, 3 ♂ (SL = 1.5–1.7 mm), VELERO III station 1260-41, February 27, 1941, AHF 2852-01; Vicinity of Punta Abreojos, 7 ♂, 5 ♀, 1 ovigerous ♀ (SL = 1.2–2.3 mm), RV SEARCHER station 1, shore, January 27, 1971, AHF 2853-01; 2.6 miles W of Punta Pequeña, 1 ♂ (SL = 1.6 mm), BLACK DOUGLAS station B6411-26, AHF 2854-01; Punta Redonda, 1 ♂ (SL = 2.7 mm), Magbay Bay Expedition, 15 m, February 5, 1964, collectors T. Hopkins and T. Scanland, AHF 2855-01.

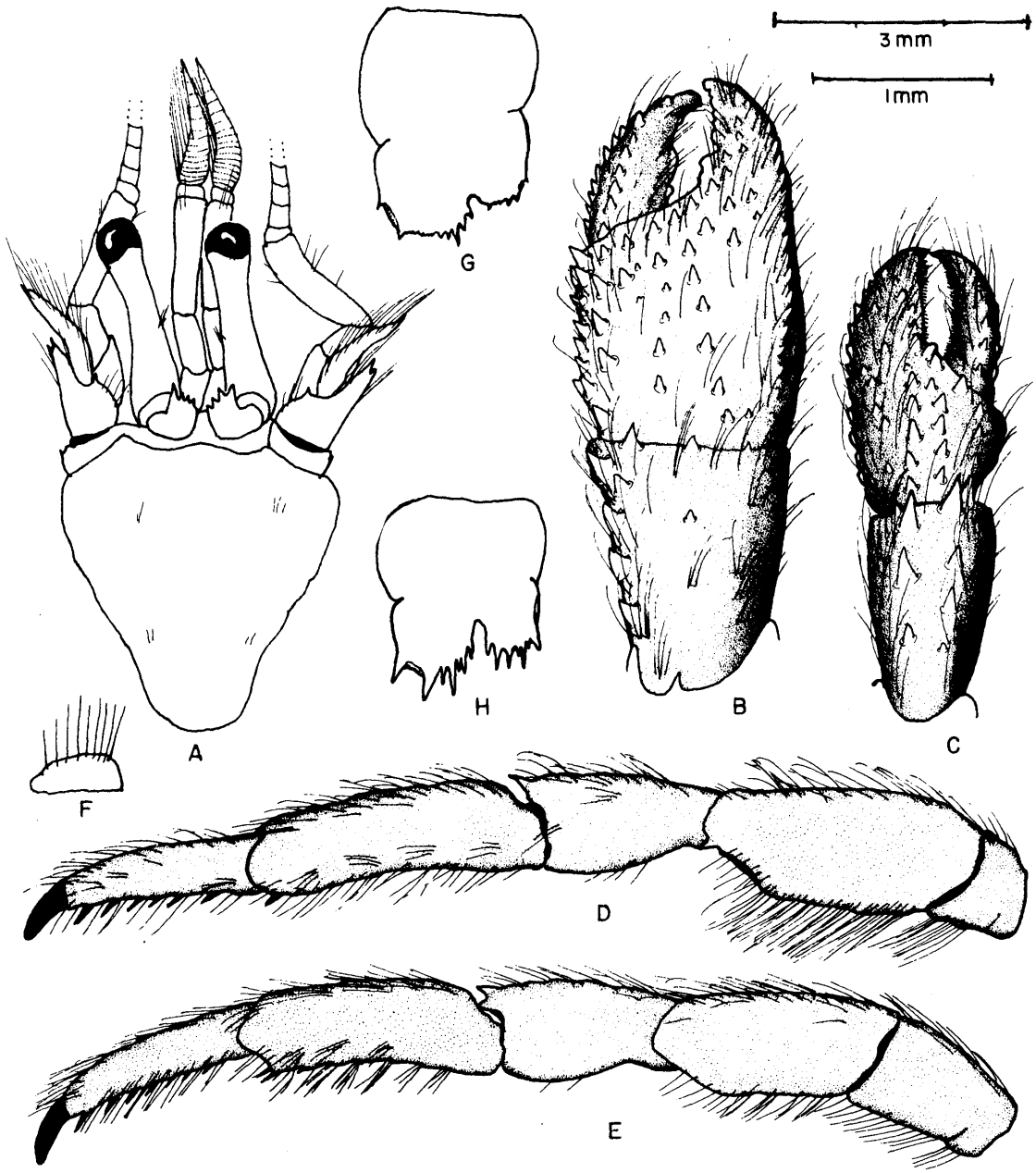

Figure 6. *Pagurus redondoensis* Wicksten, AHF 2849-01. A, shield and cephalic appendages; B, right chela and carpus (dorsal view); C, left chela and carpus (dorsal view); D, left second pereopod (lateral view); E, left third pereopod (lateral view); F, sternite of third pereopods; G, H, telsons. Scales equal 3.0 mm (A–E) and 1 mm (F–H).

Description (amending Wicksten, 1982).—Shield usually considerably longer than broad. Rostrum usually obsolete.

Ocular peduncles two-thirds to four-fifths shield length. Ocular acicles with 3–6 marginal spines; separated basally by one-half to entire basal width of 1 acicle.

Antennal peduncles without spine at ventrodistal margin of 3rd segment; 2nd segment with dorsolateral distal angle produced and terminating in simple or bifid spine, occasionally with additional spine on lateral margin distally. Antennal

flagellum short, not overreaching right cheliped; each article with 2 or 3 short (<1 article length) and 2 or 3 longer setae, at least in proximal half.

Right cheliped considerably larger than left. Dactyl with row of spines on dorsomesial margin and second row on slightly elevated dorsal midline. Palm with irregular, usually double row of spines on dorsomesial margin and with 2 or 3 irregular rows of small spines on dorsal surface, dorsolateral margin with row of spines decreasing in strength on fixed finger; dorsal surface of fixed finger with few spines or spinules; all surfaces with scattered, moderately long setae. Carpus with row of strong spines on dorsomesial margin, distal margin with 2 or 3 spines or spinules, dorsal surface usually with few spines or spinules, dorsolateral margin not delimited, ventrolateral margin with 1 or 2 small spines distally. Merus with acute spine at distal margin; ventral margins with long setae, ventrolateral margin also with 1–3 spines distally.

Left cheliped sometimes with prominent hiatus between dactyl and fixed finger; dactyl with row of spines in dorsal midline and spines or protuberances on dorsomesial margin. Palm with dorsal midline elevated and armed with double row of strong spines, extending onto fixed finger as single row; dorsolateral surface with irregular row of spines or spinules, dorsolateral margin with spines or spinulose protuberances; dorsomesial face weakly to strongly sloping and armed with few spines or spinules, dorsomesial margin with few, sometimes spinulose, protuberances. Carpus with dorsomesial and dorsolateral row of strong spines; laterodistal margin with 1 to several spines, usually strongest at ventrodistal angle. Merus with row of spines on ventromesial and ventrolateral margins.

Second and 3rd pereopods with dactyls two-thirds to three-fourths length of propodi, occasionally nearly as long as propodi; ventral margins each with row of 5–8 corneous spines and tufts of setae, dorsal margins with tufts of setae. Propodi with 1 (2nd) or 2 (3rd) corneous spines at ventrodistal margin, 3rd frequently also with additional corneous spine in distal fourth of ventral surface. Meri with acute spine at ventrolateral distal angle (2nd) or unarmed (3rd); dorsal and ventral margins with long setae.

Sternite of 3rd pereopods subrectangular, anterior margin with long setae. Telson with terminal margins straight or slightly oblique, armed with several small to strong spines, lateral margins each with entire or denticulate corneous plate, delimited at least on one side by moderate to strong spine.

Color.—Antennules: brown narrow band at distal end of antepenultimate segment of peduncle and a similar subdistal band on ultimate segment. Antennae: flagella with alternating 1 white article, 2 or 3 reddish-brown articles. Acicle and peduncle white, irregularly blotched with reddish-brown. Shield and ocular acicles grayish blue. Ocular peduncles pale yellowish-white. Right cheliped (all markings reddish-brown): merus with narrow band near distal end, on dorsal surface and extending part way down lateral and mesial faces. Carpus with oblique longitudinal stripe on lateral and mesial faces. Chela with oblique longitudinal blotch on lateral and mesial faces, and faintly striped on dorsal surface. Walking legs somewhat variable: dactyls with broad band proximally; propodi with broad band or longitudinal stripes in proximal half; carpi with one or two short to long stripes on lateral face.

Distribution.—Southern California to west coast of Baja California Sur, Mexico; intertidal to 46 m.

Affinities.—As noted by Haig and Harvey (1991) and Harvey and McLaughlin (1991), *P. redondoensis* appears most closely related to *P. nanodes* Haig and Harvey and *P. vetaultae* Harvey and McLaughlin. In living specimens, *P. redon-*

doensis may be distinguished from *P. nanodes* by its pattern of reddish-brown or brown longitudinal stripes on the carpus of the right cheliped and carpi of the pereopods. The carpus of the right cheliped of *P. nanodes* is reported as being brown laterally and white, shading to orange mesially; the carpi of the pereopods are brown (Haig and Harvey, 1991). At present, *P. nanodes* has not been found further north than the western coast of Costa Rica, whereas *P. redondoensis* is known only from southern California and the outer coast of Baja California, Mexico. *Pagurus vetaultae* has been reported from the Gulf of California, Mexico to as far south as Panama; therefore, it is most probable that confusion in specific identities might occur between *P. redondoensis* and *P. vetaultae.* Color patterns provide good means for distinguishing between the two species in the field. Although cheliped coloration appears to be similar, the dactyls, propodi, carpi and meri of ambulatory legs of *P. vetaultae* all are striped; the dactyls of *P. redondoensis* have a proximal band, but no stripes. Harvey and McLaughlin (1991) distinguished between preserved specimens of the two species by the setation of the antennal flagellum, i.e., very short setae in *P. vetaultae* in contrast to short and longer setae in *P. redondoensis.* In the absence of the antennal flagellum, the difference in length ratios of the dactyl and propodus of the left 3rd pereopod were proposed to be diagnostic, i.e., the dactyl two-thirds to three-fourths the length of the propodus in *P. redondoensis* but appreciably longer in *P. vetaultae.* In the numerous lots of *P. redondoensis* that we have now examined, this has not proved to be a dependable distinction. Rather, we have found that the armature of the telson is sufficiently different in the two taxa to provide a more reliable character. In *P. redondoensis* the terminal margin is armed with several spines varying in strength from small to quite large (Fig. 1G, H). The terminal margins of *P. vetaultae* are armed with a few small spines and a single large spine at each outer angle (cf. Harvey and McLaughlin, 1991: fig. 3H).

Remarks.—Although much of the material we have examined was also seen by Wicksten (1982), she designated a holotype and only three specimens as paratypes. Wicksten's original description of this species was detailed and generally quite adequate. However, the only comparisons that she could make at the time were with Atlantic representatives of the *provenzanoi* group. Consequently, similarities and distinctions among Pacific taxa, such as those given above, could not have been anticipated.

One specimen from Punta Redonda collected during the Magbay expedition was reported by Haig et al. (1970) as *Pagurus lepidus.* Subsequent reexamination has shown that it should correctly be assigned to *P. redondoensis.*

Discussion

Studies of both adult morphology and larval development suggest that the *provenzanoi* group of *Pagurus* is one of several monophyletic groups within the genus (McLaughlin, 1975; Lemaitre et al., 1982; McLaughlin and Gore, 1988; McLaughlin et al., 1991a, 1991b). Nevertheless, a range of variation in morphological characters is recognized in both Atlantic and Pacific representatives. In the eastern Pacific, *P. lepidus* exhibits many of the characters most typical of the *provenzanoi* group, *P. benedicti* far fewer. However, the discoveries of *P. annexus* n. sp. and *P. spighti* n. sp., together with the recent descriptions of several species previously referred to only as the *P. lepidus* complex (Haig and McLaughlin, 1991; Haig and Harvey, 1991) have shown that in many respects *P. lepidus* represents one extreme of a morphological cline within the group, *P. benedicti* represents the other. If only these two species were available for comparison, the homogeneity

of the *provenzanoi* group could be seriously doubted. However, *P. annexus* appears to bridge this gap in a number of characters. For example, Lemaitre et al. (1982) described the sternite of the third maxilliped as produced into a subtriangular, blunt or subacute median projection. In *P. lepidus* the sternite is produced into a spine-like median projection. In *P. benedicti* the sternite bears a simple, rounded projection. In *P. annexus* there is a more typical, moderately well-developed, but bluntly rounded median projection. As in Atlantic representatives of the group (cf. McLaughlin, 1975: fig. 7), the anterolateral angles of the sternite of the fifth pereopods in *P. lepidus,* are developed laterally into subovate lobes which are almost perpendicular to the anterior margin of the median portion of the sternal plate. In *P. benedicti* these lobes are more widely separated and lie nearly parallel to the anterior median margin (Fig. 5I). In *P. annexus* a somewhat intermediate condition exists (Fig. 1H).

In the original diagnosis of the group (as the *miamensis* group), Forest and De Saint Laurent (1968) described the ocular acicles as varying between uni- and multispinose, the majority of assigned species having unispinose acicles. However, they proposed that the multispinose condition arose differently among species assigned to the group. In some instances the acicular margins were entire, the several spines were developed submarginally. In contrast, other species possessed acicles in which the acicular margins were broken into a series of spinose projections. McLaughlin (1975) suggested that because the development of a multispinose condition in some *provenzanoi* group species was identical in at least one representative of another genus, armature of the ocular acicles was not of phylogenetic significance. It would now appear that while the multispinose acicular condition has arisen independently on more than one occasion in both the Paguridae and Diogenidae, a developmental continuum can be seen among Pacific *provenzanoi* group species. In *P. villosus* and *P. spighti* the ocular acicles are provided with a single submarginal spine. In *P. benedicti* and *P. nesiotes* the single spine may be marginal or submarginal, and occasionally in the later species a second spine may be present. Two or three submarginal acicular spines are common in *P. annexus*; however, as few as one and as many as four have been observed and occasionally one or two accessory, marginal spinules may be present. *Pagurus arenisaxatilis* Harvey and McLaughlin has two to five marginal or submarginal acicular spines, whereas three or four and three to five marginal or submarginal spines are reported for *P. redondoensis, P. vetaultae, P. rhabdotus* Haig and Harvey and *P. virgulatus* Haig and Harvey. Three to six marginal or submarginal spines occur in *P. nanodes* and three to six marginal spines are present in specimens of *P. lepidus.*

Setation of the antennal flagellum has frequently been considered a response to a particular mode of feeding (Boltt, 1961; Schumacher, 1977). Little is known of the feeding habits of any of the *provenzanoi* group species; however, two distinct setation patterns occur in both Atlantic and Pacific representatives, together with several intermediate conditions. Among Pacific species, *P. annexus, P. villosus* and *P. spighti* all have long, paired setae, at least on the proximal articles of the flagellum (Fig. 1B). At the opposite extreme, species such as *P. nesiotes* and *P. vetaultae* have only extremely short antennal setae. Intermediate conditions range from short and only slightly longer setae in *P. lepidus* through the irregular patterns of long and short setae seen in *P. arenisaxatilis* and *P. redondoensis* to the long, but unpaired setae of *P. benedicti.*

The most convincing evidence for a continuum is seen in the development of the posterior lobes of the telson. In all species of the group, the lateral margins of the posterior lobes are each delineated by a corneous or weakly calcified plate.

These plates may be entire or broken up into distinct denticles or spines. In none of the Atlantic species is the plate clearly delimited anteriorly by a prominent spine, although *P. gymnodactylus* Lemaitre occasionally may have one or more spinules anteriorly (Lemaitre, 1982: fig. 1c). Among the Pacific species, *P. lepidus, P. spighti, P. nesiotes* and *P. virgulatus* all have the lateral margins of the posterior telsonal lobes represented by fused chitinous plates (Fig. 2G); the anterior margins are not delimited by a spine. Similarly there is no delimiting spine in *P. arenisaxatilis*; however, the lateral margin may consist of a chitinous plate or a series of spines. In *P. rhabdotus, P. redondoensis* and *P. vetaultae* the lateral plates are again chitinous but are delimited, at least on one side, by a distinct spine. A similar delimiting spine is present in *P. nanodes,* but the lateral margin may consist of a solid chitinous plate or a series of denticles. The opposing condition, in which the lateral margins of the posterior telsonal lobes are broken up into a number of weak to strong spines, is seen in *P. villosus* (chitinous) and *P. benedicti* (calcareous) (Figs. 3G, 4I, 5J). *Pagurus annexus* again represents a transitional condition. In small individuals of this species (SL = 1.4 mm), the lateral telsonal plates are chitinous or weakly calcified, with fused elements; an anterior spine is developed only on one side (Fig. 1I). In large individuals (SL < 2.0 mm) the lateral telsonal plates are represented by distinct, individual calcareous spines; no delimiting anterior spine is present (Fig. 1K). In individuals of intermediate size (SL = 1.8 mm) the strength of the anterior delimiting spine decreases with increasing animal size; at the same time the telsonal plates begin to be represented by more and more individual spines (Fig. 1J).

The acutely triangular left chela (dorsal view) is a character that was introduced into the diagnosis of the *provenzanoi* group by McLaughlin (1975). It was the configuration of the left chela of *P. galapagensis,* as illustrated by Boone (1932: fig. 5), that led McLaughlin (1975) to doubt Haig et al.'s (1970) assignment of this species to the group. Although Boone's (1932) illustration is diagrammatic, the chela of the holotype is truly quite broad (Fig. 5C). However, males of *P. benedicti* usually have a much more narrowly triangular left chela. This broadening trend is also seen in *P. villosus* (Fig. 3C) and in *P. nesiotes* (cf. Haig and McLaughlin, 1991: fig. 3B).

Lemaitre et al. (1982) noted that species of the *provenzanoi* group were among the most abundant of the shallow-water hermit crabs of the subtropical Atlantic, Gulf of Mexico and Caribbean Sea, with a few species ranging farther north along the eastern coast of the United States to Georgia and the Carolinas, and south to Brazil and Argentina. The abundance of *provenzanoi* group species in the shallow waters of the subtropical Pacific appears comparable, with one or two species ranging as far north as southern California and as far south as Chile.

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