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REVISION OF *PYLOPAGURUS* AND *TOMOPAGURUS* (CRUSTACEA: DECAPODA: PAGURIDAE), WITH THE DESCRIPTIONS OF NEW GENERA AND SPECIES. PART V. *ANISOPAGURUS* McLAUGHLIN, *MANUCOMPLANUS* McLAUGHLIN, AND *PROTONIOPAGURUS* NEW GENUS

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ABSTRACT

In this fifth part of a six part series, the genera *Anisopagurus* McLaughlin and *Manucomplanus* McLaughlin, together with their respective species, are diagnosed in detail and illustrated. *Protoniopagurus bioperculatus* n. gen., n. sp., and three new species of *Anisopagurus, A. actinophorus, A. vossi* and *A. hopkinsi*, are described. Morphological variations in some of the most common or abundant species are discussed. The assignment of *Pylopagurus ungulatus* (Studer, 1883) to *Manucomplanus* is confirmed: it has proved to be the senior synonym of *Manucomplanus corallinus* (Benedict, 1892). Keys to species of *Anisopagurus* and *Manucomplanus* are presented.

In part I of this revision (McLaughlin, 1981a), *Pylopagurus* A. Milne Edwards and Bouvier, 1891, was restricted to species typified by *P. discoidalis* (A. Milne Edwards); the remainder of species assigned to *Pylopagurus* by A. Milne Edwards and Bouvier (1893) were transferred to new genera. In parts II (McLaughlin, 1981b) and III (McLaughlin, 1982), four of the remaining originally assigned species were redescribed. Part IV (McLaughlin and Gunn, 1992) dealt with several species more recently placed in *Pylopagurus* sensu lato. In part V, the last of the original taxa, i.e., *P. bartletti* (A. Milne Edwards) and *P. ungulatus* (Studer) are rediagnosed, the former as the type species of *Anisopagurus* McLaughlin, and the latter as the senior subjective synonym of *Manucomplanus corallinus* (Benedict). A new and singularly distinctive, monotypic genus, *Protoniopagurus,* is included in the pylopagurid group of genera.

On the basis of our present knowledge, *Anisopagurus* and *Protoniopagurus* are endemic tropical western Atlantic genera; *Manucomplanus* is a cosmopolitan temperate-tropic, amphi-Atlantic–Pacific genus. When first proposed (McLaughlin, 1981a), only two species, *Pylopagurus bartletti* and *P. pygmaeus* (Bouvier) were assigned to *Anisopagurus.* Although sharing essential generic characters, these two species, at first glance, are quite dissimilar. The chelae of *A. bartletti* are armed with flattened or spinulose tubercles; the ocular acicles are simple. Contrarily, the chelae of *A. pygmaeus* are provided with prominent spines; the ocular acicles are multispinose. Of the three new species described herein, both morphological chela types are represented, although all three species have simple ocular acicles. Telson morphology among the five species, however, clearly demonstrates a clinal relationship. In contrast, the five species assigned to *Manucomplanus* exhibit such basic homogeneity in chelae morphology and predictable sexual dimorphism that specific identifications can be exceedingly difficult. *Protoniopagurus* differs from all other pylopagurid-like genera in the absence of all male pleopods and reduction in the number of unpaired female pleopods from four to three. Rediagnoses of the described species and descriptions of new species are presented, together with illustrations and keys to the species of *Anisopagurus* and *Manucomplanus.*

MATERIALS

Specimens included in part V have come from the collections of the Allan Hancock Foundation, University of Southern California (AHF), now part of the collections of the Natural History Museum of Los Angeles County, California, U.S.A. (LACM); Dauphin Island Sea Lab, University of Alabama, U.S.A. (DISL); Museum of Comparative Zoology, Harvard University, Massachusetts, U.S.A. (MCZ); National Marine Fisheries Service (NMFS); P.A. McLaughlin personal collections (PMcL); National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (USNM); Forschungsinstitut Natur Museum Senckenberg, Frankfurt, Germany (SMF), Rosenstiel School of Marine and Atmospheric Science, University of Miami, Florida, U.S.A. (UMML or RSMAS); Texas A&M University, College Station, Texas, U.S.A. (TAM); and Zoologische Museum, Museum für Naturkunde der Humboldt-Universität zu Berlin, Germany (ZMB). Specimens have been returned to and/or deposited in these institutions and at the Muséum national d'Histoire naturelle, Paris, France (MNHN), Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden, Netherlands (RMNH), and Naturhistoriska Riksmuseet, Stockholm, Sweden (NHRM). Institutional abbreviations as much as possible follow the recommendations of Leviton et al. (1985). Other abbreviations used are: DU, Duke University, North Carolina, U.S.A.; JSDS, Johnson-Smithsonian Deep Sea Expedition; and USFC, United States Fish Commission. In the material examined, months are indicated by the first three letters. The symbols ♂, ♀, and ♀♀ refer to male(s), female(s), and ovigerous female(s), respectively. A single measurement in millimeters, shield length (SL), was made for each specimen examined.

Anisopagurus McLaughlin, 1981

Pylopagurus: A. Milne Edwards and Bouvier, 1893: 74 (in part).—Forest and De Saint Laurent, 1968: 145 (in part). Not *Pylopagurus* A. Milne Edwards and Bouvier, 1891.

Anisopagurus McLaughlin, 1981a: 5. Type species, by original designation, *Pylopagurus bartletti* (A. Milne Edwards, 1880). Gender: masculine.

Diagnosis.—Eleven pairs of phyllobranch gills. Ocular acicles triangular, with 1 to several strong marginal or submarginal spines; separated basally by slightly less to more than basal width of 1 acicle. Maxillule (Fig. 1a) with external lobe of endopod weakly developed, not recurved, internal lobe with 1 terminal bristle. Maxilla (Fig. 1b) with proximal lobe of scaphognathite moderately broad. First maxilliped (Fig. 1c) with exopod broadened basally. Third maxilliped with well developed crista dentata and 1 accessory tooth. Sternite of 3rd maxillipeds with small to strong spine on either side of midline.

Right cheliped with chela usually suboperculate; propodal-carpal articulation varying from 0° to approximately 15° from perpendicular. Left cheliped with chela generally triangular in cross-section, occasionally with lateral margin expanded; propodal-carpal articulation varying from 0° to approximately 45° from perpendicular. Sternite of 3rd pereopods with anterior lobe subrectangular, subquadrate, subtriangular or subovate. Fourth pereopods with moderately long dactyls; usually with moderately well developed preungual process at base of claw; propodal rasp consisting of 3 or 4 rows of corneous scales. Sternites of pereopods 3–5 sometimes with capsulate setae.

Abdomen typically flexed. Uropods asymmetrical. Telson with transverse suture; posterior lobes equal or subequal, terminal margins rounded, somewhat oblique, or excavated, unarmed or with few to numerous small spines. Males with 3 unpaired biramous pleopods with endopods reduced. Females with paired 1st pleopods modified as gonopods, with four unpaired biramous pleopods, 2nd–4th with both rami well developed, 5th with endopod reduced.

Distribution.—Western Atlantic: from southeastern coast of United States, Gulf of Mexico, Caribbean Sea to northern Brazil. Depth range: subtidal to 1,016 m.

Etymology.—From the Greek *anisos* meaning unequal, and *pagouros*, a crab, referring to the unequal, uropods that distinguishes this genus from the morphologically rather similar *Agaricochirus* McLaughlin.

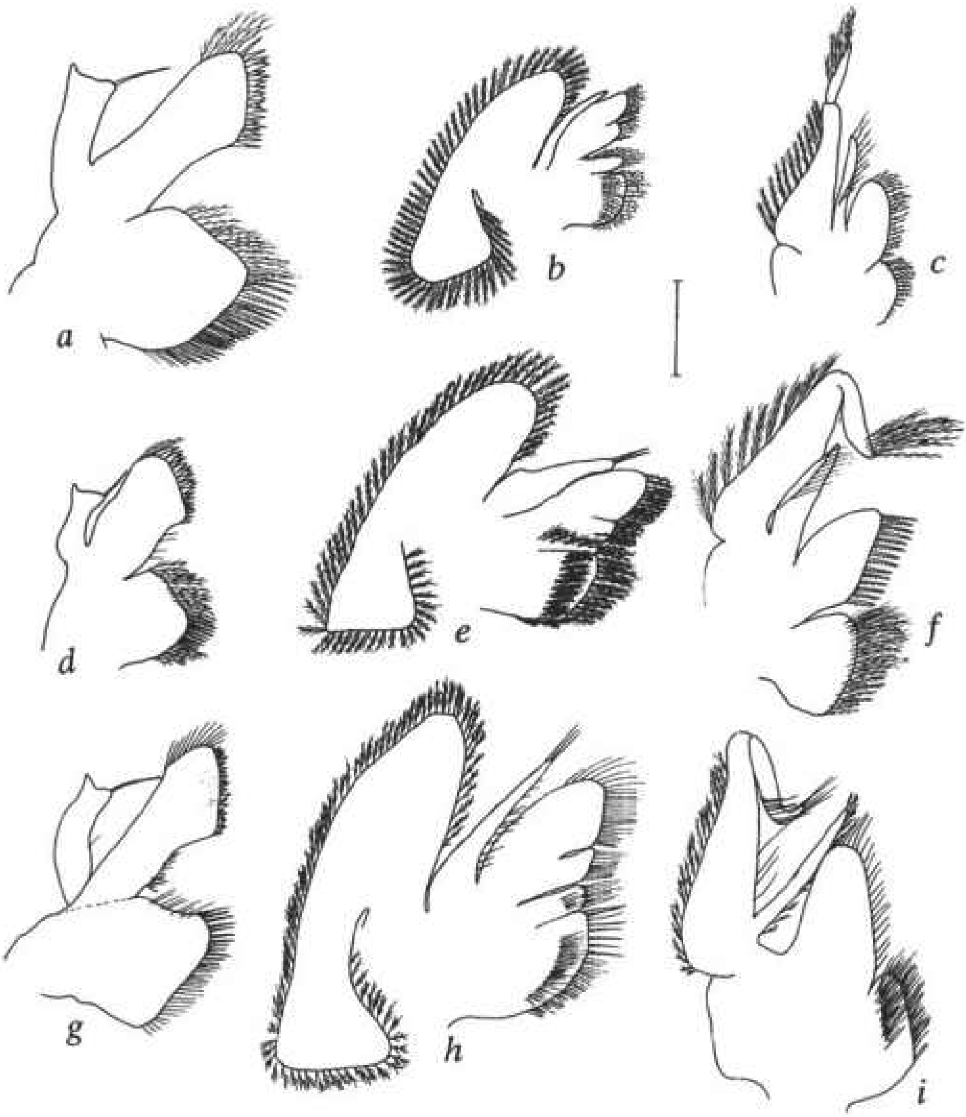

Figure 1. Mouthparts, internal view. a–c, *Anisopagurus bartletti* (A. Milne Edwards); d–f, *Manucomplanus ungulatus* (Studer); g–i, *Protoniopagurus bioperculatus* n. gen., n. sp. a, d, g, maxillule; b, e, h, maxilla; c, f, i, 1st maxilliped. Scale equals 0.5 mm (a, d–f), and 1 mm (b, c, g–i).

Key to the Species of *Anisopagurus*

1a. Ocular acicles simple 2
1b. Ocular acicles multispinose . . . . *A. pygmaeus*
2a. Mesial face of palm of right chela without vertical ridges 3
2b. Mesial face of palm of right chela with vertical ridges (Fig. 10c) . . . . *A. vossi* n. sp.
3a. Chela of left cheliped narrow and elongate, more than 2 times as long as broad . . . . *A. actinophorus* n. sp.
3b. Chela of left cheliped moderately short and broad, at most 2 times as long as broad 4
4a. Carpus of left cheliped with 2 obliquely divergent rows of spines on distal half of dorsal surface; ocular peduncles short, distinctly less than SL, and broadened distally . . . *A. bartletti*

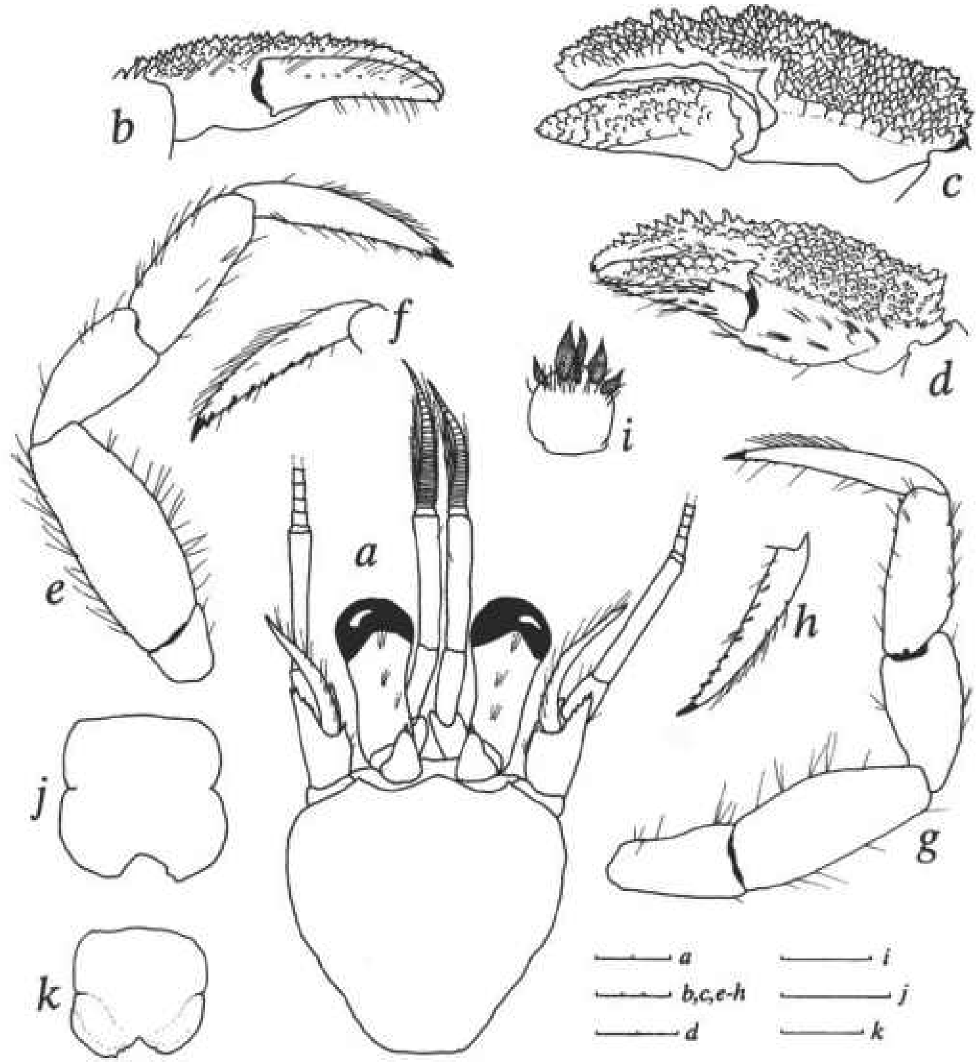

Figure 2. *Anisopagurus bartletti* (A. Milne Edwards): a, shield and cephalic appendages; b, left chela, mesial view; c, d, right cheliped, dorsomesial view (dactyl shown on c detached); e, right 2nd pereopod, lateral view; f, dactyl of same, mesial view; g, left 3rd pereopod, lateral view; h, dactyl of same, mesial view; i, anterior lobe of sternite of 3rd pereopods; j, k, telson. Scales equal 2 mm (a, d), 3 mm (b, c, e–h), 0.5 mm (i), and 1 mm (j, k). (a–c, e–h, j, holotype male, MCZ 3975; d, female, GERDA 462, USNM; i, female, PILLSBURY 984, USNM; k, female, BLAKE 300, MCZ 4017).

4b. Carpus of left cheliped with 1 slightly oblique row of spines on dorsal surface; ocular peduncles moderately long, as long as SL, slender, not broadened distally .... *A. hopkinsi* n. sp.

Anisopagurus bartletti (A. Milne Edwards, 1880)
Figures 1–4

Eupagurus Bartletti A. Milne Edwards, 1880: 41 (type locality: BLAKE station 223, St. Vincent, restricted by subsequent lectotype selection by A. Milne Edwards and Bouvier, 1893).
Pylopagurus Bartletti A. Milne Edwards and Bouvier, 1893: 91, pl. 7, figs. 1–9.

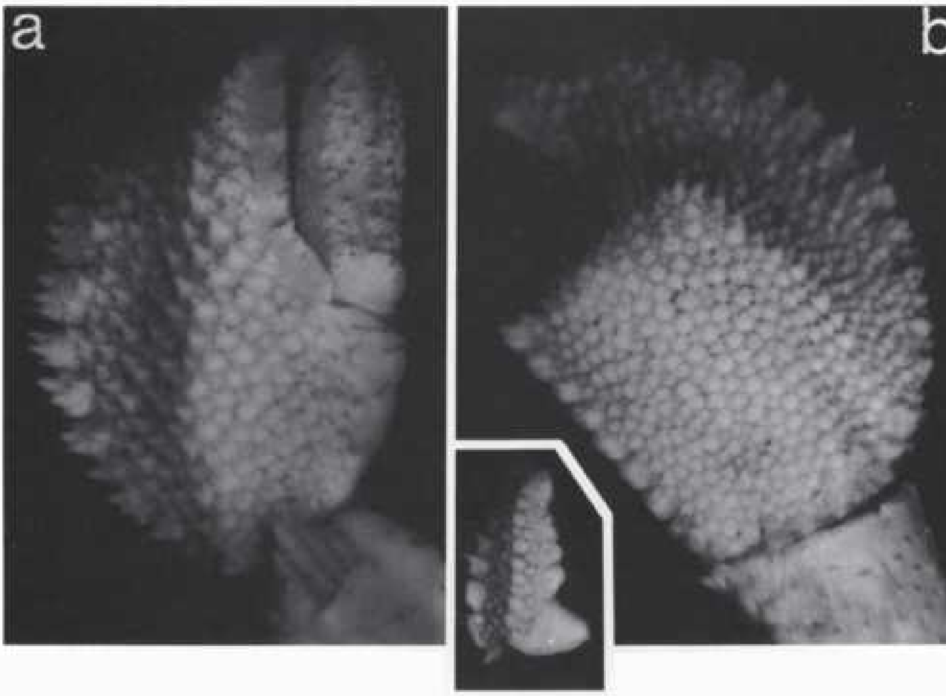

Figure 3. Chelae of *Anisopagurus bartletti* (A. Milne Edwards): a, left (3.8×); b, right, detached dactyl shown in inset (3.9×). (Holotype male, MCZ 3975).

Pylopagurus bartletti: Alcock, 1905: 189 (list).—Gordan, 1956: 340 (lit.).—McLaughlin, 1981a.
Anisopagurus bartletti: McLaughlin, 1981a: 6 (by implication).—Abele and Kim, 1986: 31, 361 (key), 369 unnumbered fig. b.

Type Material.—Lectotype: by subsequent selection by A. Milne Edwards and Bouvier (1893), ♂ (SL 7.1 mm), MCZ 3975.

Material Examined.—See Table 1.

Diagnosis.—Shield approximately as broad as long; rostrum rounded, unarmed; lateral projections obtusely triangular or broadly rounded, usually with terminal, submarginal spine or spinule. Ocular peduncles short (0.6 to 0.8 length of shield), moderately slender basally, broadened distally and with corneae slightly dilated; ocular acicles triangular, moderately broad basally, with strong submarginal spine; separated basally by approximately basal width of 1 acicle.

Right cheliped with dorsal surface of palm roundly or triangularly convex; dorsal surfaces of dactyl (mesially), fixed finger, and palm all armed with closely-spaced, flattened or spinulose tubercles (see variations); dorsomesial and dorsolateral margins each with row of strong, usually multidenticulate spines, dorsomesial distal angle not prominently produced, proximal margin of palm often with 3 or 4 prominent spines. Carpus with row of strong spines on dorsomesial margin, dorsal and ventral surfaces usually with low, sometimes spinulose or spinose protuberances; ventromesial and ventrolateral margins with small tubercles or blunt spines, at least in large specimens. Ventromesial and ventrolateral margins of merus each usually with row of small to moderately strong spines, ventral surface often with scattered small spines or spinules.

Left cheliped with single or double row of small spines or tubercles on dor-

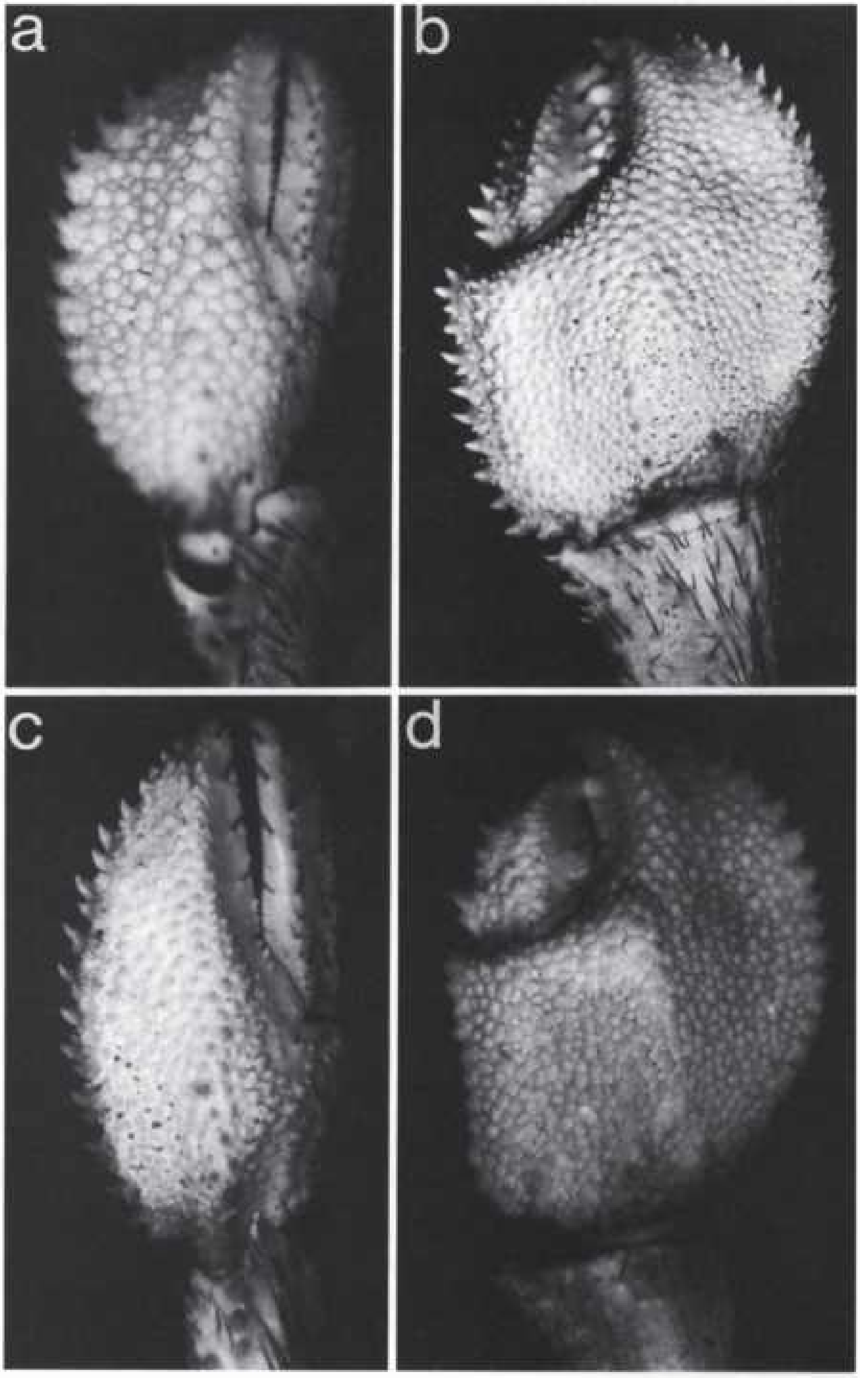

Figure 4. Chelae of *Anisopagurus bartletti* (A. Milne Edwards), showing variations. a, left (9.1×); b, right (7.6×); c, left (13.8×); d, right (8.4×). (a, b, male, SILVER BAY 2428, USNM; c, d, male, NR-4, USNM).

somesial margin of dactyl frequently becoming corneous-tipped in large specimens, dorsal midline with single or double row of small, often corneous or corneous-tipped, spines or spinules. Chela at most twice as long as broad (see variations). Palm and fixed finger with closely-spaced, flattened or spinulose tubercles on dorsal surface, at least laterally. Carpus with 2 short, obliquely diverging rows of strong spines on distal half of dorsal surface, dorsolateral and/or dorsomesial margins often with few small spines; ventrolateral margin with row of small spines. Ventrolateral and ventromesial margins of merus each with row of spines, strongest laterally.

Ambulatory legs generally similar in armature; propodus of left 3rd usually longer than propodi of right and of left 2nd. Dactyls longer than propodi; each with row of 6–9 strong corneous spines on ventral margin; dorsal surfaces each with numerous tufts of long stiff setae. Propodi and carpi each with row of low protuberances and tufts of stiff setae on dorsal surfaces; carpi usually also with small spine at dorsodistal margin, smaller or absent on 3rd.

Sternite of 3rd pereopods with anterior lobe generally subquadrate, often with 3 to 5 capsulate setae. Telson with posterior lobes concave medially, separated by small, shallow median cleft; margins with few to several small, often blunt spines.

Distribution.—Gulf of Mexico, Straits of Florida and Florida Keys, Caribbean (Yucatán Peninsula, Mexico; Lesser Antilles; Colombia) to off mouth of Amazon River, Brazil; 49–555 m.

Affinities.—In the general shape and armature of the right cheliped, *A. bartletti* closely resembles *A. actinophorus* n. sp. and *A. hopkinsi* n. sp.; however, in *A. bartletti* the tubercles frequently are spinulose rather than completely flattened as they are in the other two species. The relatively shortness of the fixed finger and dactyl of the left cheliped of *A. bartletti* immediately distinguish this species from *A. actinophorus. Anisopagurus bartletti* is distinguished from *A. hopkinsi* by the armature of the dorsal surface of the carpus of the left cheliped, which has two obliquely divergent rows of spines; only one slightly oblique row is present in the latter. The ocular peduncles of *A. bartletti* are distally broadened and distinctly shorter than the SL, whereas in *A. hopkinsi* they are moderately slender and at least as long as the SL.

Variations.—This species exhibits considerable variations in the shape and armature of the chelae. The dorsal surface of the right palm can be rounded, or frequently elevated in the midline. The spiniform tubercles on the dorsal surface of the right palm can be large, acute (Figs. 2c, 3b); or less frequently small, flattened, and with small blunt to sharp spines (Figs. 2d, 4b, d). On the left chela, the length/width ratio varies from 1.5 to 2 (Figs. 3a, 4a, c); the lateral margin varies from nearly subcircular to broadly rounded in outline, and is armed with strong simple to trifid spines (Figs. 3a, 4a, c).

Remarks.—*Anisopagurus bartletti* is frequently found living in association with an actinian that covers entirely its gastropod shell. No evidence of a chitinous carcinoecium was found in any of the material examined. One other species in the genus, *A. actinophorus* n. sp., is also found living in association with an actinian (see also remarks under that species).

Anisopagurus actinophorus new species

Figures 5, 6a, b

Holotype.—♂ (SL 3.7 mm), USNM 267676; type locality: GERDA station 893, off Yucatán Peninsula, Mexico, 21°10'N, 86°21'W.

Table 1. *Anisopagurus bartletti* (A. Milne Edwards) material examined

Locality	Depth (m)	Station deposition	Date	Sex			SL (mm)	Collector
				♂	♀	♀♀		
Gulf of Mexico								
27°08′N 84°53′W	320	Oregon 954 USNM 97467	3 Apr 1954	1			3.9	NMFS
26°31′N 85°53′W	218	Blake 50 MCZ 4091	—	1			4.3	A. Agassiz
25°08′N 84°19′W	298	Oregon 1026 USNM 97468	19 Apr 1954		1		4.5	NMFS
Straits of Florida and Florida Keys								
25°10′N 80°06′W	183	Gerda 763 USNM	15 Sep 1965		1		3.5	RSMAS
25°02′N 80°12′W	185	Gerda 452 UMML 32:4694	22 Jan 1965	1			3.2	RSMAS
24°59′N 80°14′W	183	Silver Bay 3519 USNM	9 Nov 1961	1			4.7	NMFS
24°40′N 80°48′W	150	Gerda 589 USNM	14 Apr 1965	1			2.1	RSMAS
24°34′42″N 80°58′36″W	139–85	Gerda 1035 PMcL	26 Feb 1969	1			3.9	RSMAS
Western Dry Rocks, Key West, Florida	165	— USNM	—			1	4.9	Henderson
24°20′N 82°44′W	174	Silver Bay 2428 USNM	29 Oct 1960	1			5.1	NMFS
24°19′N 82°43′W	174–201	Gerda 462 USNM	25 Jan 1965		1		3.3	RSMAS
24°29′N 82°29′W	188–189	Gerda 432 USNM	28 Nov 1964	1			4.0	RSMAS
24°08′N 80°59′W	525–555	Gerda 368 USNM	15 Sep 1964	1			2.8	RSMAS
Caribbean								
18°26′24″N 63°12′36″W	421–439	Pillsbury 984 USNM	22 Jul 1969		1		5.4	RSMAS
14°21′N 81°55′W	192–263	Pillsbury 1354 PMcL	31 Jan 1971		2		2.0, 2.8	RSMAS
14°05.2′N 60°50.3′W	274–567	Pillsbury 891 PMcL	7 Jul 1969	2	1		3.1–3.7	RSMAS
St. Vincent	267	Blake 223 MCZ 3975	18 Feb 1879	2			4.3, 7.1	A. Agassiz
13°13.9′N 61°04.7′W	241–262	Pillsbury 876 PMcL	6 Jul 1969	1			1.5	RSMAS
Barbados	366	Blake 291 MCZ 2766, 4090, 4092, 13020	9 Mar 1879	6	3	2	2.4–5.2	A. Agassiz
Barbados	150	Blake 300 MCZ 4017	10 Mar 1879			1	4.8	A. Agassiz
Barbados	382	Blake 274 MCZ 2684, 4093, 4113	5 Mar 1879	1	2		3.7–4.2	A. Agassiz
Barbados	—	NR-12-4 USNM	—	5			1.6–2.6	J. Lewis
Barbados	—	NR-18-1-4 USNM	—	2			2.7, 2.9	J. Lewis

Table 1. Continued

Locality	Depth (m)	Station deposition	Date	Sex ♂	Sex ♀	Sex ♀♀	SL (mm)	Collector
Barbados	—	N-4 PMcL	—	4	1		1.8–3.7	J. Lewis
13°01'30"N 59°34'W	320	OREGON 5018 USNM	29 Sep 1964	1			5.4	NMFS
09°41'N 75°57'W	49	OREGON 5719 USNM	16 Oct 1965			2	5.1, 6.4	NMFS
Northeastern South America								
02°04'N 47°00'W	229	OREGON 2080 USNM 101663	17 Nov 1957	1			4.8	NMFS

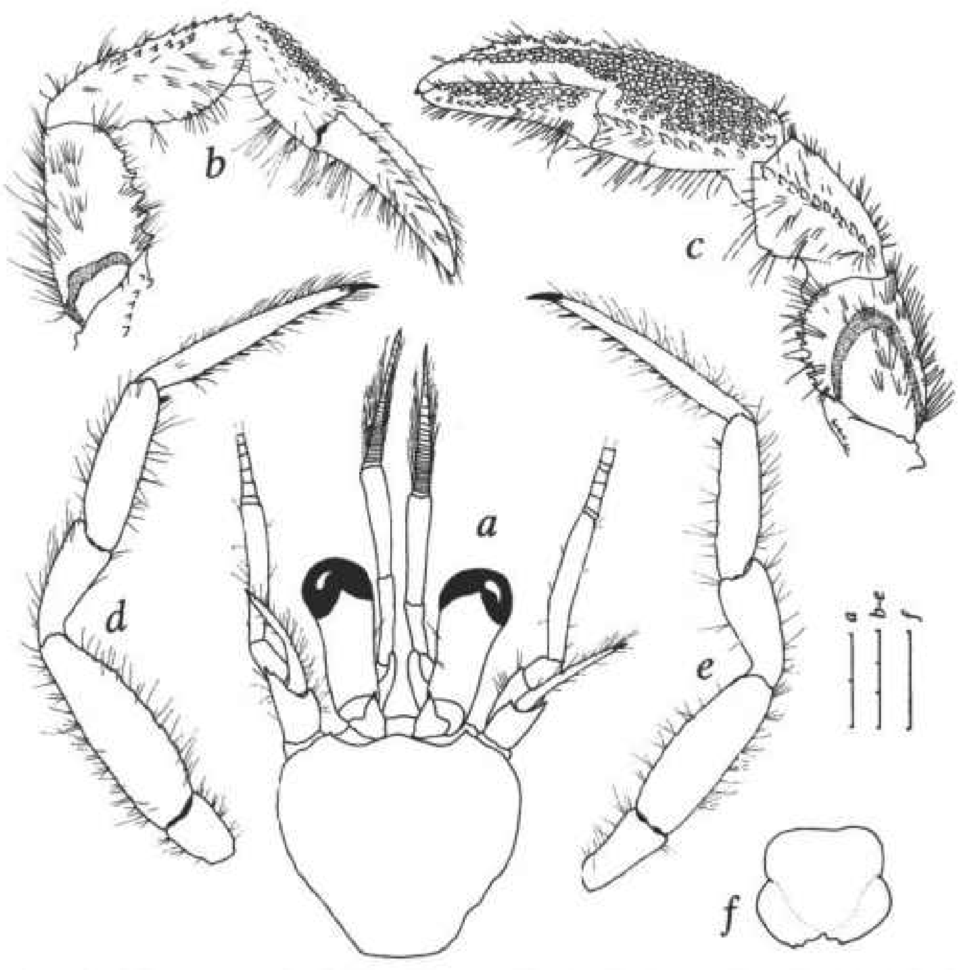

Figure 5. *Anisopagurus actinophorus* n. sp.: a, shield and cephalic appendages; b, left cheliped, mesial view; c, right cheliped, mesial view; d, right 2nd pereopod, lateral view; e, left 3rd pereopod, lateral view; f, telson. Scales equal 2 mm (a), 3 mm (b–e), and 1 mm (f). (Male, GERDA 893, USNM 267677).

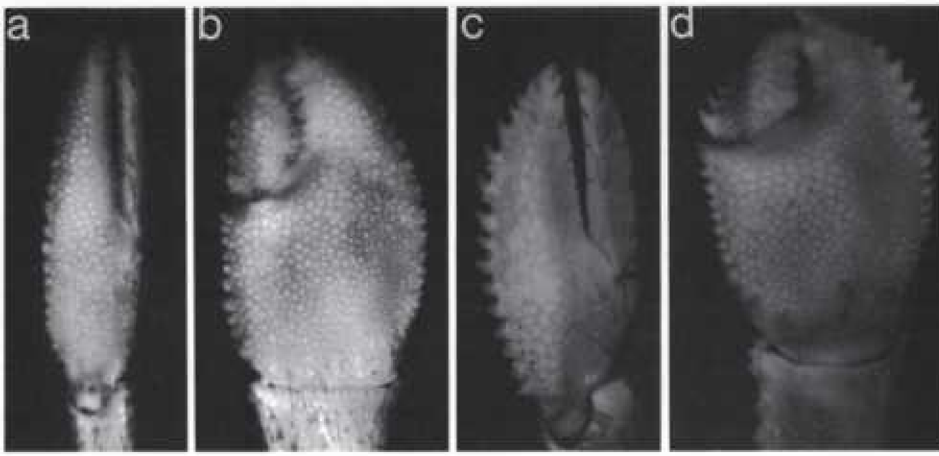

Figure 6. Chelae of *Anisopagurus actinophorus* n. sp. (a, b) and *A. hopkinsi* n. sp. (c, d): a, left (2.6×); b, right (2.1×); c, left (5.6×); d, right (3.9×). (a, b, male, GERDA 1275, PMcL; c, d, male, TAM 65-A-9-20, PMcL).

Material Examined.—See Table 2.

Description.—Shield approximately as broad as long; anterior margin between rostrum and lateral projections concave; anterolateral margins sloping; posterior margin truncate. Rostrum rounded, unarmed. Lateral projections obtusely triangular, with small terminal spinule. Shield with few scattered setae. Ocular peduncles short (slightly less than length of shield), with corneae slightly dilated, few short setae and 1 stiff seta on mesial face in distal half; ocular acicles triangular, moderately broad basally, with strong submarginal spine, dorsal surface concave; acicles separated basally by approximately basal width of 1 acicle.

Antennular peduncles overreaching ocular peduncles by approximately ⅔ length of ultimate segment. Ultimate and penultimate segments unarmed; basal segment with 1 or 2 spines on lateral face.

Antennal peduncles overreaching ocular peduncles by approximately ½ length of ultimate segment. Fifth and fourth segments with few scattered setae. Third segment with small spinule on ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in small spinule, lateral margin with scattered setae, mesial margin with few small spinules; dorsomesial distal angle with spine, mesial margin with few setae. First segment produced ventrally and with row of 4 or 5 small spinules laterally. Antennal acicle arcuate, slightly overreaching ocular peduncles, terminating in small spinule, mesial margin with a row of tufts of setae. Antennal flagella long, with 1 or 2 short setae every 3 to 6 articles.

Right cheliped elongate, but only slightly overreaching left. Dactyl slightly longer than palm, with row of small, blunted spines and tufts of setae on dorsomesial margin, dorsal surface elevated in midline and partially to fully covered with closely-spaced platelets; cutting edge with few calcareous teeth, terminating in calcareous tooth tipped with very small corneous spinule; mesial face and ventral surface with few scattered setae. Palm approximately as long as carpus; dorsomesial margin with row of broad, bi- or trifid spines, dorsolateral margin with similar row of spines, smaller in size proximally and on fixed finger; dorsal surface of palm slightly elevated in midline, surface partially to entirely covered

Table 2. *Anisopagurus actinophorus* n. sp. material examined

Locality	Depth (m)	Station deposition	Date	Sex ♂	Sex ♀	Sex ♀♀	SL (mm)	Collector
Straits of Florida								
24°50′N 80°37′W	37	GERDA 594 USNM 270142	14 Apr 1965	1			4.2	RSMAS
24°03′N 81°10′W	961–1016	GERDA 368 PMcL	15 Sep 1964	1			2.8	RSMAS
Western Caribbean								
21°13′N 86°25′W	283–247	GERDA 947 USNM 270145	27 Jan 1968	6	1	1	2.0–3.1	RSMAS
21°11′N 86°30′W	164–311	GERDA 954 USNM 270147, PMcL	28 Jan 1968	17	7	3	2.9–4.8	RSMAS
21°10′N 86°21′W	242–320	GERDA 893 USNM 267676, 267677	10 Sep 1967	13	4	10	2.7–5.0	RSMAS
21°10′N 86°19′W	173–206	GERDA 894 USNM 270140	10 Sep 1967	1		3	3.0–4.0	RSMAS
21°10′N 86°21′W	132–175	GERDA 893 PMcL	10 Sep 1967	3	3	1	3.4–5.0	RSMAS
21°10′N 86°18′W	458–284	PILLSBURY 582 USNM 270148	23 May 1967	2			3.7–4.0	RSMAS
21°07′N 86°21′W	155–205	PILLSBURY 598 USNM 270149, PMcL	15 Mar 1968	3			2.5–3.5	RSMAS
21°07′N 86°20′W	252–292	PILLSBURY 591 PMcL	14 Mar 1968	15	7	5	2.3–4.1	RSMAS
21°06′N 86°28′W	107–402	GERDA 950 USNM 270144	28 Jan 1965	2			3.6–4.0	RSMAS
21°06′N 86°28′W	192–307	GERDA 951 USNM 270146	28 Jan 1968	16	9	2	2.1–4.8	RSMAS
21°05′N 86°23′W	348–357	PILLSBURY 580 USNM 270151	22 May 1967	10	5		2.1–4.1	RSMAS
21°05′N 86°21′W	—	GERDA 944 NHRM	27 Jan 1968	2	1		2.8–3.3	RSMAS
21°04′N 86°19′W	338–366	GERDA 898 UMML	10 Sep 1967	2			3.7	RSMAS
21°00′30″N 86°23′W	307–329	PILLSBURY 594 USNM 270150	15 Mar 1968	7	4	2	1.8–4.2	RSMAS
21°02′N 86°29′W	123–240	GERDA 1275 PMcL	21 Aug 1970	3			4.3–4.9	RSMAS
21°00′N 86°25′N	345	GERDA 879 USNM 270143	9 Sep 1967	1			1.6	RSMAS
20°59′N 86°24′W	210–292	GERDA 897 RMNH D46270	10 Sep 1967	2	2		3.3–3.5	RSMAS
20°55′N 86°28′W	219–177	GERDA 889 USNM 270141	10 Sep 1967	2			2.6–2.8	RSMAS
15°17.8′N 81°21.9′W	247–256	70-A10-26 PMcL	13 Jul 1970	2			5.6, 7.4	TAM

with closely-spaced, crenulate platelets; cutting edge of fixed finger with row of small calcareous teeth and 1 prominent tooth in distal half; lateral and ventral surfaces of palm and fixed finger with scattered tufts of setae. Carpus approximately ⅔ length of merus; dorsomesial margin with row of acute spines, dorsal surface with transverse rows of low ridges and tufts of stiff setae, dorsolateral margin not well delimited, lateral and mesial faces and ventral surface with scattered tufts of setae. Merus triangular, dorsal surface, lateral and mesial faces each with short, transverse rows of tufts of setae; ventromesial margin with row of strong spines, ventrolateral spinulose, ventral surface with few small spines. Ischium with row of spines on ventromesial margin.

Left cheliped elongate, chela more than 2 times as long as broad. Dactyl usually twice length of palm, unarmed but with numerous tufts of moderately long and stiff setae. Dorsolateral margin of palm and fixed finger with row of broad bi- or trifid spines, dorsal surfaces partially to completely covered with closely-spaced platelets except near dorsomesial margin of palm where numerous tufts of long, stiff setae usually present, dorsal midline occasionally slightly spinulose proximally; mesial and ventral surfaces with tufts of long, moderately stiff setae. Carpus short, approximately ⅔ length of merus, dorsomesial and dorsolateral margins with spinules or protuberances, stronger spinules distally and often also on dorsal surface, lateral and mesial faces with scattered transverse ridges and tufts of setae, ventral surface often slightly spinulose. Merus triangular; dorsal surface with transverse rows of tufts of long, stiff setae, extending onto lateral and mesial faces; ventrolateral and ventromesial margins each with long stiff setae and row of moderately strong spines, more prominent mesially, ventral surface with scattered spines. Ischium with row of strong spines on ventromesial margin and 1 or 2 spines on ventrodistal margin.

Second and 3rd pereopods generally similar from left to right. Dactyls long, usually exceeding propodi by ⅓ to ½ own length; compressed laterally, but without noticeable twisting; terminating in slender claw; dorsal surfaces each with row of moderately long and stiff setae; ventral margins each with row of 7–12 corneous spines, increasing in size distally, mesial faces slightly concave, but without clearly defined sulcus. Propodi approximately as long as carpi; dorsal surfaces with tufts of long setae; ventral surfaces with 3 widely-spaced corneous spinules and tufts of setae; mesial and lateral faces with scattered setae. Carpi ⅔ to ¾ length of meri; unarmed, surfaces with row of tufts of long, stiff setae. Meri with tufts of stiff setae on dorsal surfaces; ventral margins with protuberance, stronger on 2nd, and with tufts of long setae. Ischia with tufts of long setae and row of acute spines (2nd) on ventral margins.

Sternite of 3rd pereopods with anterior lobe subquadrate, and with capsulate setae. Sternite of 4th and 5th pereopods also with several capsulate setae. Telson with subequal posterior lobes, separated by shallow, broad median cleft; terminal margins oblique, each with 2 or 3 small spines; lateral margins also oblique, with narrow marginal plate and scattered long setae; anterior lobes with few long, marginal setae.

Color.—Shield and basal antennal segments tinged with orange. Ambulatory legs with one or two patches of light orange dorsally; carpus tinged with orange; propodi and dactyls each with band of light orange in proximal half (A. J. Provenzano, Jr., notes).

Distribution.—Straits of Florida and western Caribbean; 37–1,016 m.

Etymology.—The specific name is derived from Actiniaria, the order of sea anemones, and *phoreus*, to bear or carry, reflecting the association of this species with anemones.

Affinities.—*Anisopagurus actinophorus* shares with *A. bartletti* and *A. hopkinsi* the closely-packed, contiguous tubercles on the dorsal surfaces of the palms of the chelipeds. In *A. bartletti* these tubercles, particularly on the right chela, tend to be subconical and spiniform, a condition not seen in either of the other species. The left cheliped of *A. actinophorus* is distinctive in having a row of spines on the dorsomesial surface of the carpus and a noticeably elongate, slender chela.

Remarks.—*Anisopagurus actinophorus* is found living symbiotically with actinians that produce a chitinous carcinoecium somewhat similar to that observed in some species of the family Parapaguridae (see Lemaitre, 1989). As previously mentioned, *Anisopagurus bartletti* frequently is also found living in association with actinians; however, the actinian associated with *A. bartletti* does not produce a chitinous carcinoecium.

Anisopagurus hopkinsi new species
Figures 6c, d, 7

Holotype.—♀ (SL 2.0 mm), USNM 267678; type locality: off west coast of Florida, 27°49′56″N, 84°31′W.

Material Examined.—See Table 3.

Description.—Shield slightly to considerably longer than broad; anterior margin between rostrum and lateral projections somewhat concave; anterolateral margins sloping; posterior margin truncate. Rostrum broadly rounded, unarmed. Lateral projections broadly rounded, usually with distinct marginal or submarginal terminal spine. Shield with few scattered tufts of setae. Ocular peduncles moderately long and slender (about same length as shield), corneae only slightly dilated, few tufts of setae on dorsomesial or mesial surfaces; ocular acicles triangular, terminating subacutely, with strong submarginal spine, dorsal surface concave; acicles separated by basal width or more than basal width of 1 acicle.

Antennular peduncles overreaching ocular peduncles by approximately ⅓ to ½ length of ultimate segment. Ultimate and penultimate segments with few scattered setae; basal segment with 1 spine on lateral face.

Antennal peduncles equaling or slightly shorter than ocular peduncles. Fifth and fourth segments with few scattered setae. Third segment usually with small spine on ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in simple or bifid spine and with 1–3 additional spines on mesial margin and occasionally also 1 on lateral margin; dorsomesial distal angle with small spine. First segment with 2 spines on lateral margin distally. Antennal acicle arcuate, reaching to base of cornea, terminating in small spine, mesial and lateral margins with numerous setae. Antennal flagella moderately long, with 1–3 long (4 or 5 article length) every 2–4 articles, and occasionally also 1 or 2 short setae.

Right cheliped suboperculate. Dactyl slightly shorter to slightly longer than palm, with row of blunt spines on dorsomesial margin, dorsal surface elevated in midline and covered with flattened, marginally muricate tubercles, ventral surface with few scattered setae; cutting edge with row of calcareous teeth, terminating in small corneous claw. Palm approximately as long as carpus; dorsomesial margin with row of subacute or blunt, simple spines, dorsomesial distal angle produced, prominently so in larger specimens; dorsolateral margin also with row of

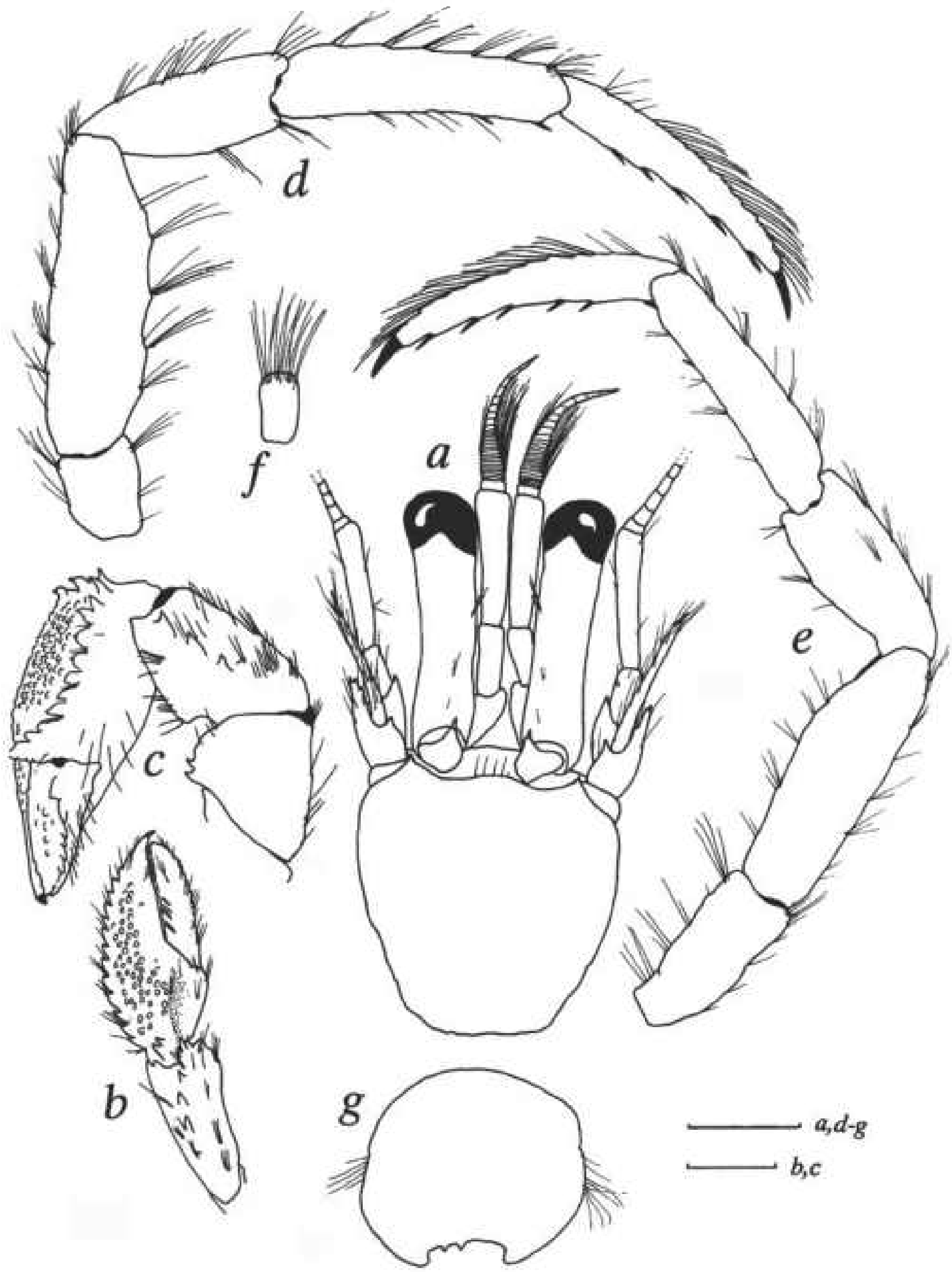

Figure 7. *Anisopagurus hopkinsi* n. sp.: a, shield and cephalic appendages; b, left cheliped; c, right cheliped, mesial view; d, right 2nd pereopod, lateral view; e, left 3rd pereopod, lateral view; f, anterior lobe of sternite of 3rd pereopod; g, telson. Scales equal 1 mm (a–e), and 0.5 mm (f, g). All from DISL 0001: a, d–g, male, USNM 267679; b, c, holotype female, USNM 267678).

Table 3. *Anisopagurus hopkinsi* n. sp. material examined

Locality	Depth (m)	Station deposition	Date	Sex ♂	Sex ♀	Sex ♀♀ (ovigerous)	SL (mm)	Collector
Eastern United States								
32°54′N 78°07′W	91	SILVER BAY 2154 USNM 267680	15 Jul 1960			1	2.2	NMFS
Gulf of Mexico								
25°00′N 84°00′W	132	65-A-9-20 PMcL	14 Jul 1965	3			2.7–3.2	TAM
27°49′56″N 84°41′56″W	165	0002 USNM 267681	5 Feb 1978	1	1		1.0, 1.6	DISL
27°49′56″N 84°31′W	95	0001 USNM 267678, 267679	5 Feb 1978		2		2.0, 2.1	DISL
26°24′57″N 83°49′58″	97	2105 PMcL	2 Feb 1978	1	1		1.6, 2.2	DISL

simple, subacute or blunt spines, dorsal surface of palm and fixed finger covered with contiguous, low, flattened, marginally muricate tubercles; cutting edge of fixed finger with row of strong calcareous teeth, terminating in small corneous claw; dorsal midline of palm weakly elevated, with 2 or 3 spines near proximal margin, cluster of several blunt spines proximally mediad of midline and 1 or 2 laterad; mesial, lateral and ventral surfaces with scattered tufts of setae. Carpus approximately equal to length of merus; dorsomesial margin with row of acute spines, dorsolateral margin not delimited; dorsal, lateral, mesial and ventral surfaces with scattered tufts of setae. Merus triangular; dorsal margin with few tufts of setae, mesial and lateral distal margins often with row of long setae; ventromesial margin with 2 or 3 prominent spines proximally, ventrolateral margin with 1 or 2 spines near distal angle and occasionally few small spines or spinulose tubercles proximally. Ischium with row of small spines or spinules on ventromesial margin.

Left cheliped with propodal-carpal articulation approximately 45° from perpendicular. Dactyl nearly half length of palm; dorsomesial margin with row of low protuberances and tufts of setae, dorsal, mesial and ventral surfaces with scattered tufts of setae; cutting edge with row of small corneous teeth, terminating in small corneous claw. Chela at most twice as long as broad. Palm elevated in midline, with 2 or 3 prominent spines at posterior margin, dorsolateral margin with row of simple, blunt or subacute spines, dorsal surface covered, at least in lateral half, with contiguous, low, flattened, marginally muricate tubercles; cutting edge of fixed finger with row of very small calcareous teeth, interspersed distally with few corneous denticles, terminating in small corneous claw. Carpus approximately equaling merus in length; dorsal surface with row of strong, acute spines, row curving mesially in distal third, dorsomesial margin unarmed, but with tufts of setae; mesial and ventral surfaces with tufts of long setae, lateral face with few scattered setae, laterodistal margin with 2 small spines dorsally. Merus subtriangular; dorsal margin with few tufts of setae; ventromesial margin with 2 strong, widely-spaced spines proximally, ventrolateral margin with row of widely-spaced acute spines and few tufts of setae. Ischium with row of small spines on ventromesial margin.

Second and 3rd pereopods generally similar from left to right. Dactyls equaling or exceeding propodi by less than ⅓ own length; somewhat laterally compressed, but not twisted; terminating in moderately long corneous claws; dorsal surfaces each with row of long, stiff setae, mesial faces each with row of widely-spaced tufts of stiff setae dorsally; ventral margins each with 5 or 6 corneous spines. Propodi appreciably longer than carpi; each with 1 corneous spine at ventrodistal margin and 1 additional spine in distal ⅓; dorsal and ventral surfaces with tufts of moderately long or long setae. Carpi with tufts of setae on dorsal surfaces but without spine at dorsodistal margin. Meri unarmed but with low protuberances and tufts of long setae dorsally and ventrally. Ischia with long setae on ventral margins.

Sternite of 3rd pereopods with terminal tuft of setae on subovate anterior lobe. Sternites of 3rd–5th pereopods without capsulate setae. Telson with terminal margin rectangularly excavated, unarmed or with 1 or 2 small spines on each side of weakly developed or nearly obsolete median cleft; lateral margins rounded, with narrow corneous marginal plate.

Color.—Unknown.

Distribution.—Eastern coast of United States (off Georgia), and Gulf of Mexico; 91–165 m.

Etymology.—This species is named for Dr. Thomas S. Hopkins, director of the Bureau of Land Management's Flower Garden Banks survey, where this species was first recognized.

Affinities.—As previously noted, this species bears considerable superficial similarities to *A. bartletti* and *A. actinophorus.* It is distinguished from both species by its more elongate, slender ocular peduncles and single row of spines on the carpus of the left cheliped. *Anisopagurus hopkinsi* n. sp. may also be recognized by the frequently distinctive development of the dorsomesial distal angle of the palm of the right chela into a prominent "horn-like" protuberance (Figs. 6d, 7c); however, this development does appear to be variable.

Anisopagurus pygmaeus (Bouvier, 1918)
Figures 8, 9a–c

Eupagurus pygmaeus Bouvier, 1918: 11, fig. 4 (type locality: La Socapa, Bahía de Santiago de Cuba, Cuba).

Pagurus pygmaeus: Gordan, 1956: 335 (lit.).—Provenzano, 1959: 410, fig. 19.—Hazlett and Provenzano, 1965: 619.—Williams, 1965 (in part), fig. 106, not p. 131.—Hazlett, 1966a: 91; 1966b: 72.—Forest and De Saint Laurent, 1968: 116.

Pylopagurus pygmaeus: McLaughlin, 1975: 373.

Anisopagurus pygmaeus: McLaughlin, 1981a: 6 (by implication).—Williams, 1984 (in part): 223, fig. 159a, b, not fig. 159c (see remarks).—Gómez-Hernández and Martínez-Iglesias, 1986: 27 (list).—Abele and Kim, 1986: 31, 361 (key), 368, 369 unnumbered fig. a.

not *Pagurus pygmaeus:* Young, 1978: 177 [=*Pagurus carolinensis* McLaughlin, 1975, or *Pagurus brevidactylus* (Stimpson, 1859)]. (See remarks.)

Holotype.—♀ no longer extant (J. Forest, pers. comm.).

Material examined.—See Table 4.

Diagnosis.—Shield slightly longer than broad; rostrum triangular, with small terminal spinule; lateral projections broadly triangular, with strong, terminal marginal or submarginal spine. Ocular peduncles moderately long, with corneae only slightly dilated; ocular acicles somewhat ovate, with multispinose distal and distomesial margin; separated basally by approximately ¾ basal width of 1 acicle.

Right cheliped with row of acute to blunt spines on dorsomesial margin of dactyl and 2 or 3 irregular rows of spines on dorsal surface; palm with row of

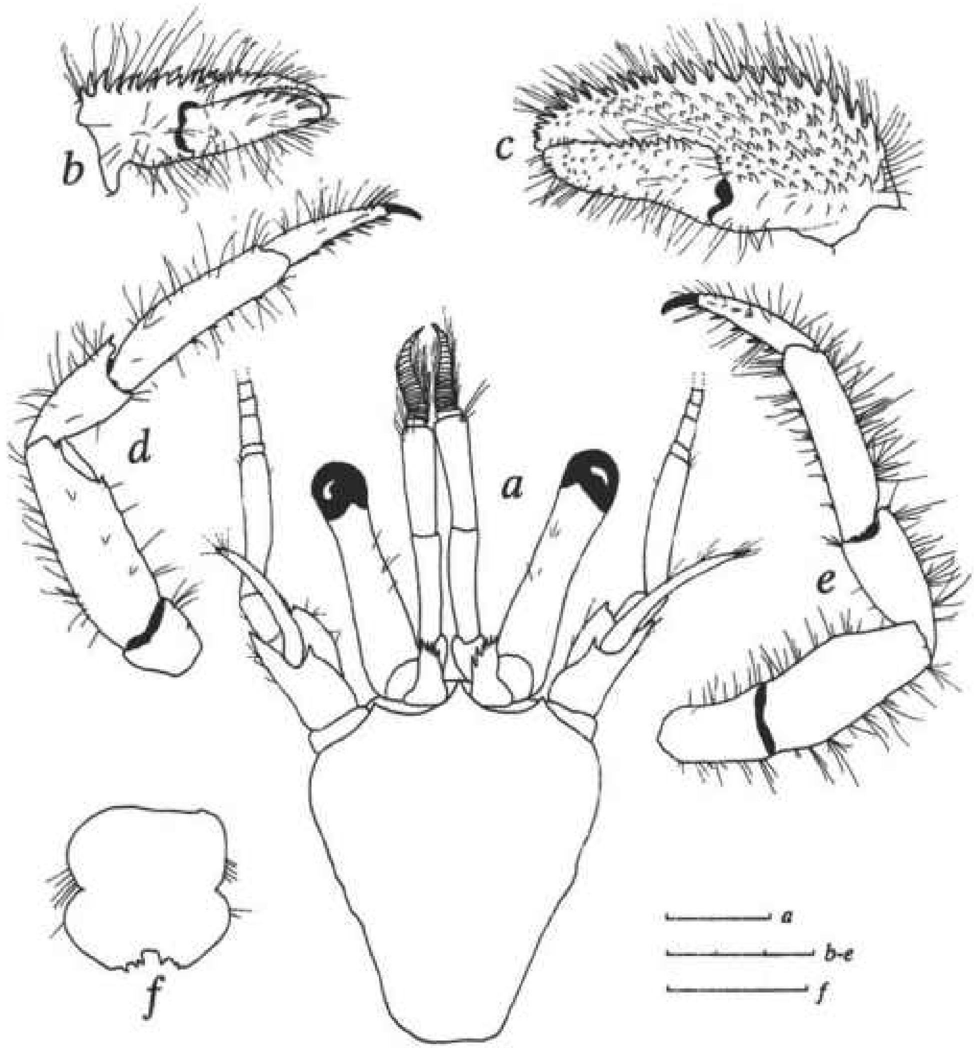

Figure 8. *Anisopagurus pygmaeus* (Bouvier): a, shield and cephalic appendages; b, left chela, mesial view; c, right chela, mesial view; d, right 2nd pereopod, lateral view; e, left 3rd pereopod, lateral view; f, telson. Scales equal 1 mm (a, f), and 3 mm (b–e). (Male, Curaçao, USNM).

acute or blunt spines on dorsomesial margin, dorsal surface with 6–9 irregular rows of acute spines (smaller specimens) or blunt tubercles (large specimens), extending onto fixed finger, dorsolateral margin also with row of acute or blunt spines; carpus with row of strong spines on dorsomesial margin, dorsal surface with few spines or protuberances, dorsolateral margin not distinctly delimited. Merus with 1 or 2 spines on dorsodistal margin, ventromesial margin with few spines distally, ventrolateral margin with row of acute spines, decreasing in strength with increased animal size.

Left cheliped appreciably smaller than right. Dactyl with row of small spines or protuberances on dorsomesial margin and on dorsal midline. Palm subtriangular with dorsal midline slightly elevated; row of strong spines on dorsolateral margin extending almost entire length of fixed finger, dorsal surface with 2 rows of spines

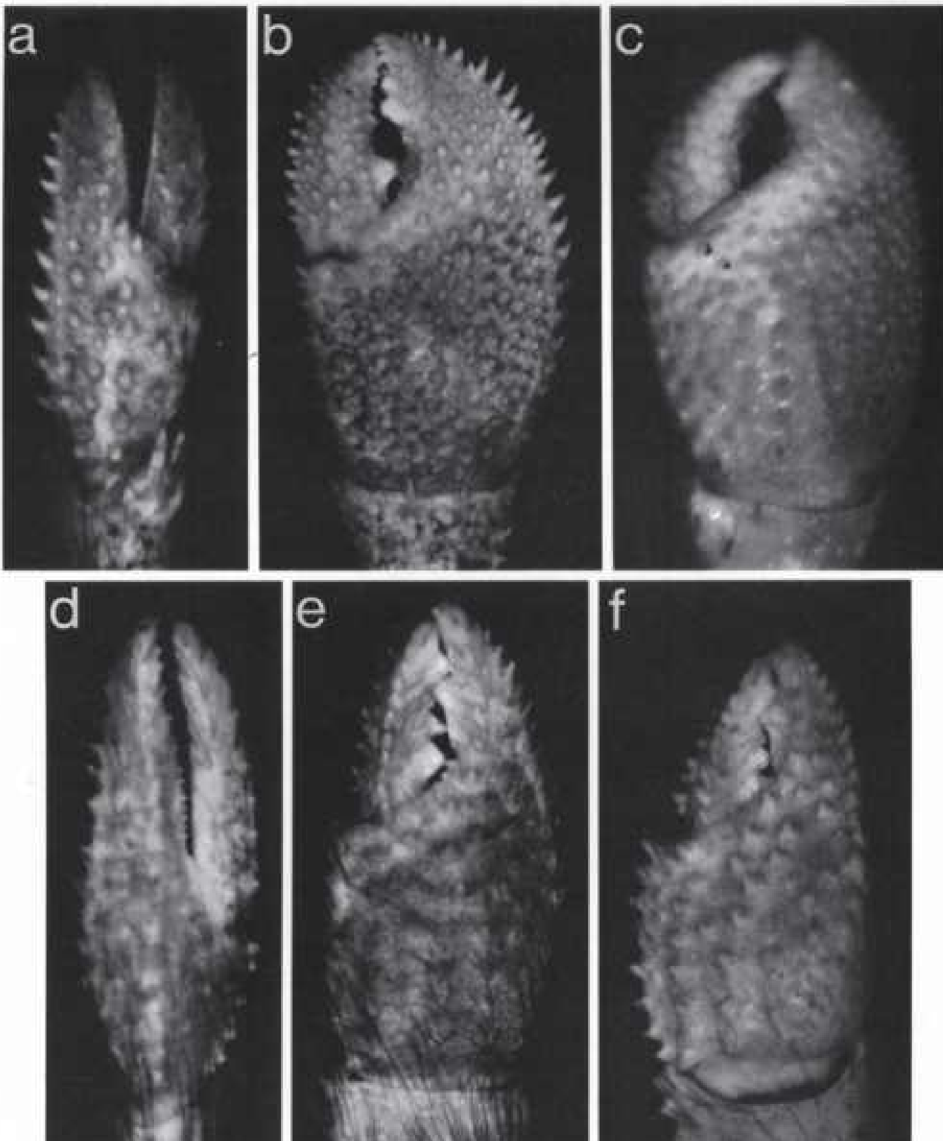

Figure 9. Chelae of *Anisopagurus pygmaeus* (Bouvier) (a–c), and *A. vossi* n. sp. (d–f): a, left (19.2×); b, right (9.1×); c, right (9.3×); d, left (15.2×); e, right (15.0×); f, right (15.3×). (a, b, male from Curaçao, USNM; c, another male from Curaçao, USNM; d, e, holotype male, Barbados, NR-12-4, USNM 267682; f, female, Barbados, NR-4, PMcL).

laterally and 1 in midline, all extending onto fixed finger, dorsomesial surface and margin each with spinulose protuberances. Carpus with row of very strong spines on dorsomesial and on dorsolateral margins; ventrolateral distal angle with prominent acute spine. Merus with row of strong acute spines on ventrolateral margin, ventromesial margin with 1 or 2 small spines proximally.

Ambulatory legs similar. Dactyls short and moderately broad, dorsal surfaces with scattered setae; ventral margins each with 4–6 strong corneous spines. Pro-

Table 4. *Anisopagurus pygmaeus* (Bouvier) material examined

Locality	Depth (m)	Station deposition	Date	Sex ♂	Sex ♀	Sex ♀♀	SL (mm)	Collector
Florida Keys								
Long Reef	—	— UMML 32:1135	29 Jun 1958	1			2.3	G.L. Voss
Southern Caribbean								
Curaçao	—	— USNM 122457	1963		1		2.6	B.A. Hazlett
Curaçao	—	— USNM	24 Sep 1963	2	6		1.8–2.2	B.A. Hazlett
Curaçao	—	— USNM, PMcL	1963	5	8		1.7–3.1	B.A. Hazlett
Boca St. Michael, Curaçao	—	— USNM, RMNH D46269	5 Aug 1963	2			2.4, 2.7	B.A. Hazlett
Boca St. Michael, Curaçao	—	— RMNH D46269	28 Aug 1963	1	1	3	2.5–2.9	B.A. Hazlett

podi each with row of corneous spines on ventral margin; dorsal surfaces with tufts of setae. Carpi each with small spine at dorsodistal margin. Meri unarmed.

Sternite of third pereopods with subovate or subtriangular anterior lobe. Telson with posterior lobes separated by small median cleft; lateral margins rounded, with weakly calcified marginal plate; terminal margins oblique, each with 2–5 small spines.

Color.—"The antennules are light, transparent blue; the antennae faintly purple with white bands; eyestalks clear; cephalothorax creamish with a green tinge; chelipeds and the first two proximal segments of each walking leg a brilliant vivid scarlet (#4-D6 in Maerz and Paul, *A Dictionary of Color*); and the distal segments of the ambulatories are colored by sequential bands of light blue-orange-dark blue-orange-yellow-dark blue-light blue yellow. The bands of color go completely around the legs. The tips of the cheliped dactyls are light scarlet to white" (Hazlett, 1966b).

Distribution.—Florida Keys (Provenzano, 1959), Cuba to Curaçao; depth range uncertain.

Remarks.—Provenzano's (1959) description and illustration of a male of *A. pygmaeus* (as *Pagurus*) from Florida was the first report of this species following Bouvier's (1918) original description of a single female from Cuba. Subsequently, Hazlett and Provenzano (1965), Williams (1965, 1984), Hazlett (1966b), Young (1978), and Abele and Kim (1986), reported this taxon from as far south as Curaçao, and as far north as South Carolina. Except for Williams (1984) and Abele and Kim (1986), these other carcinologists, like Bouvier (1918), assigned the species to *Pagurus*.

Bouvier's (1918) female type specimen from Cuba is no longer extant. We have examined Provenzano's (1959) male from Long Reef, Florida (UMML 32:1135), and confirmed its identity. We also have examined the other material upon which literature reports of either *Pagurus* or *Anisopagurus pygmaeus* have been based, as well as all additional specimens deposited in the national collections under those names. With the exception of specimens reported as *Pagurus pygmaeus* by

Hazlett and Provenzano (1965) and Hazlett (1966a, b) from Curaçao, other carcinologists have confounded Bouvier's taxon with two unrelated, but superficially similar, species of the *provenzanoi* group of *Pagurus* (cf. Lemaitre et al., 1982) that, like *A. pygmaeus*, have multifid ocular acicles, i.e., *P. carolinensis* McLaughlin, and *P. brevidactylus* (Stimpson). Gómez-Hernandez and Martínez-Iglesias (1986) listed *Anisopagurus pygmaeus* from Cuba, based on the type locality.

Reports by Williams (1965) and Young (1978) of *A. pygmaeus* (as *Pagurus*) from South Carolina are based on specimens of *P. carolinensis* (USNM 90075). The indication by these authors that the range of Bouvier's species included Puerto Rico was based on specimens of *P. brevidactylus* (USNM 102611). Williams' (1965) fig. 106, was reproduced from Provenzano (1959, fig. 19), and as such represents Bouvier's species; however, his description appears to have been based at least in part on his South Carolina specimens of *P. carolinensis*. In that report, Williams indicated that his identification was tentative. Williams (1984: 223) again reported *A. pygmaeus*, and updated the range of this species to include the Tortugas and Cuba. However, the specimens used by Williams from these two localities are *P. brevidactylus* (USNM 102612, 102613, 102753). Williams' (1984, fig. 159) illustration of *A. pygmaeus* is a composite of parts from two specimens, one from Curaçao (USNM 122457, fig. 159a, b), and another from Cuba (USNM 48763, fig. 159c); the Cuban specimen is actually *P. brevidactylus*.

McLaughlin (1975) called attention to the presence of paired first pleopods in females of this species, and transferred it to *Pylopagurus*. However, her reference to Bouvier's (1898, fig. 1) figure of "*Eupagurus pygmaeus*" is obviously a typographical error. This earlier paper by Bouvier dealt entirely with decapods collected in "Lower California" (Baja California, Mexico) and was not accompanied by figures.

Abele and Kim's (1986: 369, unnumbered fig. a) illustration of *Anisopagurus pygmaeus* is a generalized copy of Provenzano's (1959: 411, fig. 19), as is their key characters extracted from Provenzano's description.

Among the species currently assigned to *Anisopagurus*, *A. pygmaeus* is the only species with multispinous ocular acicles. Although rare in pylopagurid-like genera, this condition is not uncommon in pagurid, diogenid, and parapagurid genera alike. For example, multispinose ocular acicles occur in several, but not all species of the *Provenzanoi* group of *Pagurus*, in *Micropagurus*, and *Xylopagurus*, as well as in some, but again not all, species of *Paguristes*, *Dardanus*, *Diogenes*, *Calcinus*, and *Sympagurus*. As suggested by McLaughlin (1975) the presence of multispinose ocular acicles may not have phylogenetic significance.

Anisopagurus vossi new species
Figures 9d–f, 10

Holotype.—♂ (SL 2.4 mm), USNM 267682; type locality: Barbados.

Material Examined.—See Table 5.

Description.—Shield slightly longer than broad; anterior margin between rostrum and lateral projections somewhat concave; anterolateral margins sloping; posterior margin roundly truncate. Rostrum broadly triangular, overreaching lateral projections little if at all, terminating acutely and usually with small terminal spinule. Lateral projections obtusely triangular or bluntly rounded, usually with small marginal or submarginal spinule. Ocular peduncles moderately short, approximately $\frac{4}{5}$ shield length, stout, with corneae slightly dilated, few setae on dorsal and mesial faces; ocular acicles triangular, terminating acutely or subacutely and with strong

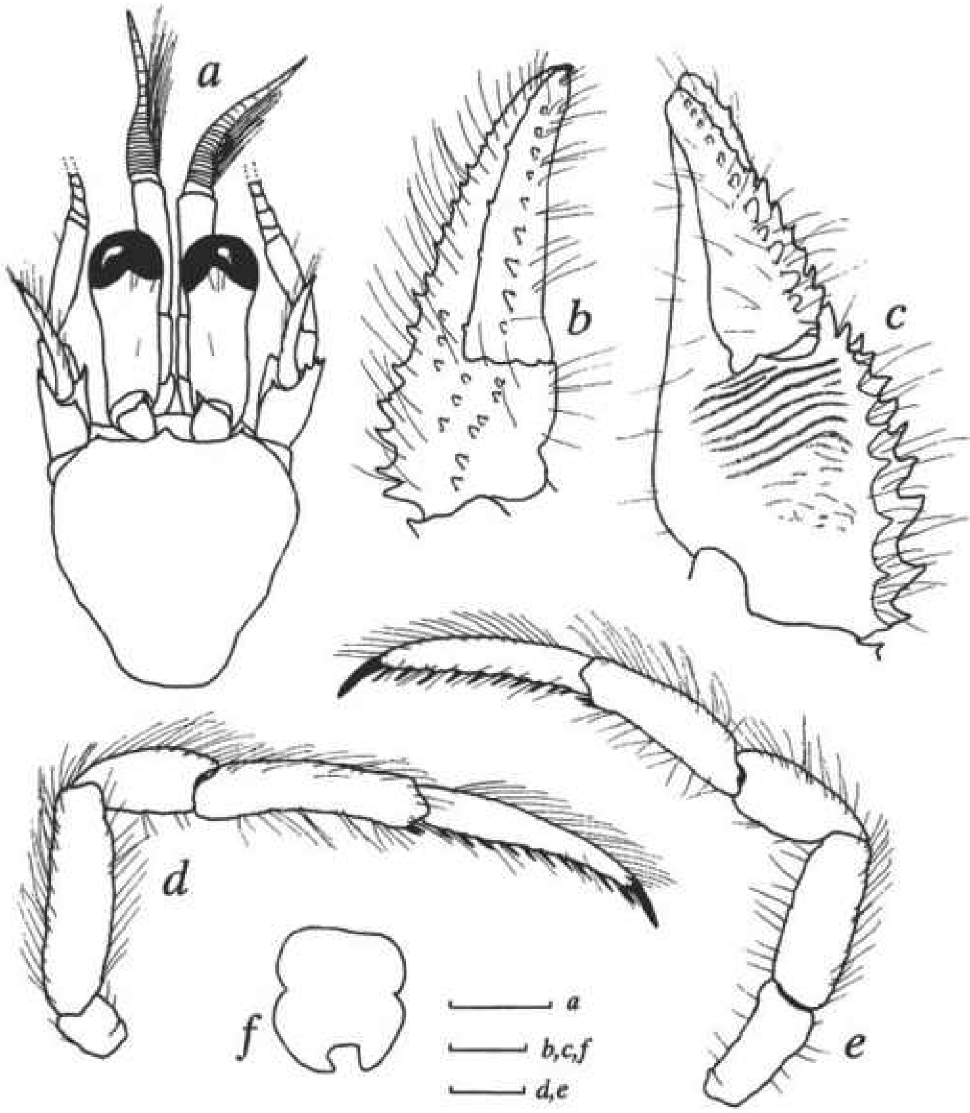

Figure 10. *Anisopagurus vossi* n. sp.: a, shield and cephalic appendages; b, left chela, mesial view; c, right chela, mesial view; d, right 2nd pereopod, lateral view; e, left 3rd pereopod, lateral view; f, telson. Scales equal 1 mm (a, d, e), and 0.5 mm (b, c, f). (Holotype male, NR-12-4, USNM 267682).

submarginal spine; separated basally by slightly less to slightly more than basal width of 1 acicle.

Antennular peduncles overreaching ocular peduncles by ⅓ to ½ length of ultimate segment. Ultimate and penultimate segments unarmed; basal segment with prominent spine on lateral face.

Antennal peduncles equaling or slightly overreaching ocular peduncles. Fifth and fourth segments unarmed. Third segment with small spine at ventrodistal margin. Second segment with dorsolateral distal angle produced, terminating in simple or bifid spine, and usually with 1 accessory spine on mesial margin; dor-

Table 5. *Anisopagurus vossi* n. sp. material examined

Locality	Depth (m)	Station deposition	Date	Sex ♂	Sex ♀	Sex ♀♀	SL (mm)	Collector
Caribbean								
21°13′N 86°25′W	248–86	GERDA 947 PMcL	27 Jan 1968	1	1		1.5, 1.7	RSMAS
21°00′30″N 86°28′W	307–29	PILLSBURY 594 USNM 267684, PMcL	15 Mar 1968	2			1.6, 1.9	RSMAS
Barbados	—	NR-12-4 USNM 267682, 267683	—	5	2	1	1.2–2.4	J. Lewis
Barbados	—	NR-4 PMcL	—			1	1.6	J. Lewis

somesial distal angle with small spine. First segment with 1 or 2 prominent spines on lateral surface ventrally. Antennal acicle arcuate, not reaching distal margin of cornea, terminating in small spine and with few setae on mesial margin. Antennal flagellum short, with 1 or 2 long (>4 articles) every 4–8 articles. Sternite of 3rd maxillipeds with strong spine on either side of midline.

Right cheliped stronger but not appreciably longer than left. Dactyl approximately equaling length of palm; cutting edge with several strong calcareous teeth, terminating in small corneous claw; dorsomesial margin with row of strong spines, dorsal midline slightly elevated and with row of prominent spines; all surfaces with scattered long setae. Palm approximately ⅔ length of carpus; dorsomesial margin with row of strong spines, dorsal surface slightly convex, armed with 4 or 5 rows of moderately strong spines, 2 extending onto fixed finger, dorsolateral margin with row of strong spines, surface and margins with numerous long, fine setae; mesial face with presumably stridulatory mechanism in distal half formed by 8 or 9 vertical ridges (Fig. 10c); lateral and ventral surfaces with scattered long setae. Carpus slightly longer than merus; dorsomesial margin with row of strong spines, dorsal surface with numerous short, transverse ridges and long setae, dorsolateral margin not delimited; mesial, lateral and ventral surfaces all with short, transverse rows of long setae. Merus with long setae on dorsodistal margin, dorsal surface with short, transverse rows of long setae; mesial, lateral and ventral surfaces with few setae, ventromesial and ventrolateral margins unarmed. Ischium unarmed.

Left cheliped moderately long, slender; dactyl and fixed finger directed somewhat ventrally. Dactyl twice length of palm; dorsomesial margin with row of small spines, decreasing in size distally; dorsal midline with row of widely-spaced small spinules, surface with numerous long setae; cutting edge with row of small corneous teeth. Palm somewhat triangular in cross-section, approximately half length of carpus; dorsal midline with row of spines extending almost to tip of fixed finger, dorsolateral surface with row of moderately strong spines, dorsolateral margin with row of strong spines and long, fine setae; dorsomesial surface with few spinules, dorsomesial margin with several small spines or spinulose tubercles; mesial, lateral and ventral surfaces unarmed, but with scattered long setae. Carpus slightly shorter than merus; dorsomesial and dorsolateral margins sometimes weakly spinulose, each also with short, transverse rows of long setae, 1 small spine on dorsolateral distal margin and 1 or 2 small spines on dorsomesial distal margin; mesial, lateral and ventral surfaces with long setae, most numerous on ventral surface. Merus with short, transverse rows of setae on dorsal surface and mesial and lateral faces; ventrolateral margin with few low protuberances and long setae, 1 small spine distally; ventromesial margin with few low protuberances and long setae. Ischium with row of very small tubercles or spinules on ventromesial margin.

Second and third pereopods similar from left to right. Dactyls slightly longer than propodi; in dorsal view, straight; in lateral view, slightly curved ventrally; terminating in long, corneous claws; dorsal surfaces each with row of low protuberances and long setae, ventral margins each with row of 9–12 strong, corneous spines. Propodus of left 3rd shorter than propodi of 2nd and 3rd right; dorsal surfaces all with low protuberances and long setae; mesial and lateral faces with few scattered setae; ventral surfaces each with low protuberances and long setae, 1 or 2 corneous spines at ventral distal margin. Carpi unarmed, but with long setae dorsally and few setae ventrally. Meri also unarmed, but with long setae ventrally. Ischia unarmed. Fourth pereopods with moderately long dactyls, small preungual process at base of claw; propodal rasp with 3 or 4 rows of corneous scales.

Sternite of 3rd pereopods with anterior lobe subrectangular, usually with capsulate setae. Sternites of 4th and 5th pereopods usually without capsulate setae. Telson with subequal posterior lobes separated by very deep, broad median cleft; terminal margins perpendicular, unarmed; lateral margins rounded, lateral plate not well delineated.

Color.—Ocular peduncles with yellowish tint. Basal segment of antennular peduncles and second segment of antennal peduncles with patches of red. Chelipeds pinkish orange with flecks of red. Ambulatory legs with flecks of red, particularly prevalent on ischia, meri and carpi; each of these segments also circumscribed by 1 or 2 faint yellow bands. (A. J. Provenzano, Jr., notes).

Distribution.—Caribbean Sea; 76–307 m.

Etymology.—This species is dedicated to the late Dr. Gilbert L. Voss, who, during his tenure as Chairman of Biology at the Rosenstiel School of Marine and Atmospheric Science, strongly supported the pagurid systematic research that forms the basis of this report.

Remarks.—Stridulatory structures have been reported in species of the semiterrestrial genus *Coenobita* and in species of the diogenid genus *Trizopagurus* sensu lato. The stridulatory mechanism consists of a series of ribs on the lateral face of the propodus of the left cheliped in *Coenobita.* Sound is produced by rubbing the dactyl of the 2nd or 3rd pereopod across these ribs. In *Trizopagurus* species, the ribs occur as patches of transverse ribs on the mesial faces of the dactyls and propodi of both chelipeds. Sound is produced by the crab rubbing the chelipeds together (Field et al., 1987). In *Anisopagurus vossi* the presumably stridulatory mechanism consists of a series of vertical ridges on the palm of the right cheliped. No opposing ridges were found of the palm of the left; however, the sloping dorsomesial surface and margin are armed with small spinules and tubercles.

Manucomplanus McLaughlin, 1981

Pylopagurus A. Milne Edwards and Bouvier, 1891: 104 (in part); 1893: 74 (in part).
Elassochirus Benedict, 1892: 1 (in part); not *Elassochirus:* McLaughlin, 1974: 308. Founded as a subgenus of *Eupagurus* Brandt, 1851.
Nylopagurus: Balss, 1921: 46 (misspelling of *Pylopagurus*).
Manucomplanus McLaughlin, 1981a: 6. Type species by original designation: *Eupagurus (Elassochirus) corallinus* Benedict, 1892. Gender masculine.

Diagnosis.—Eleven pairs of phyllobranch gills. Rostrum broadly triangular or rounded. Lateral projections obtusely triangular or broadly rounded, usually unarmed. Ocular acicles broadly triangular with mesial margins expanded in proximal half and with strong submarginal spine; separated basally by slightly less to slightly more than basal width of 1 acicle. Ultimate antennular segment frequently with single or double row of long setae on ventral margin. Maxillule (Fig. 1d) with external lobe of endopod moderately well developed, not recurved, internal lobe with 1 terminal bristle. Maxilla (Fig. 1e) with proximal lobe of scaphognathite moderately broad. First maxilliped (Fig. 1f) with moderately slender exopod. Third maxilliped with well developed crista dentata and 1 accessory tooth; merus with or without spine on dorsodistal margin; carpus unarmed. Sternite of 3rd maxillipeds with strong spine on either side of midline.

Right cheliped exhibiting pronounced sexual dimorphism; propodal-carpal articulation perpendicular; posteroventral surface of chela with deep concavity to accommodate ventrodistal portion of carpus when cheliped is flexed. Chela subovate or ovate in females and small males, with dactyl and fixed finger appreciably elongate in large males; carpus and merus usually produced ventrally. Left cheliped with dactyl and fixed finger broad, dorsoventrally flattened, with prominent hiatus; propodal-carpal articulation 15°–45° from perpendicular; dactyl with numerous tufts of long setae on ventral surface. Sternite of 3rd pereopods with anterior lobe elongate and slender to acutely triangular, margins usually spinulose in males. Fourth pereopods with propodal rasp consisting of several rows of corneous scales; dactyl very short, claw short; preungual process usually well developed at base of claw.

Abdomen generally flexed. Uropods usually asymmetrical. Telson with transverse suture; posterior lobes subquadrate to roundly triangular, subequal; separated by moderate to deep median cleft; terminal margins oblique to rounded, with few to numerous moderately strong spines, often interspersed with smaller spines. Males with paired gonopores, vas deferens not protruded; 3 unpaired biramous pleopods with endopods reduced. Females with paired 1st pleopods modified as gonopods, with four unpaired biramous pleopods, 2nd–4th with both rami well developed, 5th with endopod reduced.

Distribution.—Atlantic: southeastern United States from North Carolina to Florida; Gulf of Mexico and Caribbean; West and South Africa. Pacific: Baja California and Gulf of California, Mexico, to off Colombia; Cocos and Galápagos Islands. Depth range: 30–225 m.

Etymology.—*Manucomplanus* is from the Latin *manus* meaning hand, and *complano* to make level, and refers to the flattened dactyls and fixed fingers of the chelipeds.

Remarks.—As previously noted, all five species currently assigned to *Manucomplanus* are extremely similar in morphology, and it is often only with difficulty that specific determinations can be made. Of the two Atlantic species, *M. ungulatus* appears to have an extremely broad geographical distribution, whereas *M. spinulosus* apparently is found more commonly only off the Caribbean coast of northern South America to northern Brazil. *Manucomplanus ungulatus* does not appear to have an analog species in the Gulf of California. In contrast, *M. spinulosus* may be considered an analog of *M. cervicornis* and/or *M. longimanus*; however, neither of these Pacific species appears to have a restricted range. The Atlantic *M. ungulatus* is distinctive in having a cluster of closely-packed, teardrop-shaped spinules on the fixed finger of the right chela. The Pacific *M. varians* is distinctive in having the right cheliped armed with flattened or mushroom-shaped tubercles.

Key to the Species of *Manucomplanus*

1a. Ultimate segment of antennular peduncle with sparse setae on ventral margin (Atlantic species) 2
1b. Ultimate segment of antennular peduncle with regular row(s) of long setae on ventral margin (Pacific species) 3
2a. Fixed finger of right chela with cluster of closely-packed, tear-drop-shaped spines on dorsal surface (at least proximally) .... *M. ungulatus*
2b. Fixed finger of right chela with scattered or widely-spaced, small, slender spinules on dorsal surface .... *M. spinulosus*
3a. Dorsal surface of right chela with densely arranged, flattened or mushroom-shaped tubercles (at least on fixed finger); dorsal surface of propodi of left 2nd pereopod with row of calcareous spines .... *M. varians*
3b. Dorsal surface of right chela with scattered simple or teardrop-shaped spines; dorsal surface of propodi of left 2nd pereopod with low protuberances or spinules 4
4a. Dorsal surface of palm with tear-drop-shaped spines; terminal margins of posterior lobes of telson oblique; dactyls of 3rd pereopods short and broad (less than 7 times as long as broad) .... *M. cervicornis*
4b. Dorsal surface of palm with spines or spinules; terminal margin of posterior lobes of telson horizontal; dactyls of 3rd pereopods long and moderately slender (7 or more times as long as broad) .... *M. longimanus*

Manucomplanus ungulatus (Studer, 1883)
Figures 11, 12a–d

Eupagurus ungulatus Studer, 1883: 26, pl. 2, fig. 13a–c (type locality: entrance to Table Bay, Cape of Good Hope).—Balss, 1911: 106 (footnote).
Pylopagurus ungulatus: Milne Edwards and Bouvier, 1891: 110; 1893: 80, pl. 4, figs. 15–18.—Alcock, 1905: 189 (list).—Stebbing, 1910: 359.—Balss, 1911: 106 (by implication); 1921: 46.—Barnard, 1950: 454.—Gordan, 1956: 340 (lit.).—Kensley, 1981: 33 (list).
Eupagurus corallinus Benedict, 1892: 23 (type locality: off Key West Florida, herein restricted by lectotype selection to Albatross station 2318).—Alcock, 1905: 181 (list).—André and Lamy, 1936: 98, fig. 4S, pl. 1, figs. 1, 2.
Pagurus corallinus: Hay and Shore, 1918: 412, pl. 30, fig. 4.—Schmitt, 1931: 222, fig. 43.—Gordan, 1956: 328 (lit.).
"Hermit crab": Schmitt, 1965: 143, fig. 61.
Pylopagurus corallinus: Williams, 1965: 134, fig. 110.—Young, 1978: 177.—Wenner and Read, 1982: 187.
Manucomplanus corallinus: McLaughlin, 1981a: 7 (by implication).—Williams, 1984: 224, fig. 160.—Abele and Kim, 1986: 32, 360 (key), 387, unnumbered figs. g, h.

Holotype.—Eupagurus ungulatus Studer: ♀ (SL 2.8 mm), ZMB 5682.

Lectotype.—Eupagurus corallinus Benedict, herein selected: ♂ (SL 3.5 mm), USNM 16941.

Material Examined.—See Table 6.

Diagnosis.—Shield approximately as long as broad to slightly longer than broad; rostrum obtusely triangular. Ocular peduncles moderately short, corneae somewhat dilated; ocular acicles separated basally by basal width of 1 acicle. Ultimate segment of antennular peduncle slightly overreaching ocular peduncles, ventral margins with spare, long setae.

Right cheliped with 1 to 3 small spines on dorsodistal margin of merus, ventrolateral margin with row of granules or tiny spinulose tubercles; dorsolateral and dorsomesial margins of carpus each with row of acute or subacute spines or spinulose tubercles, becoming increasingly less distinct with increasing animal size; dorsal surface with moderately closely-spaced blunt or spinulose tubercles; dorsal surfaces of palm, fixed finger and dactyl armed with closely-spaced, small

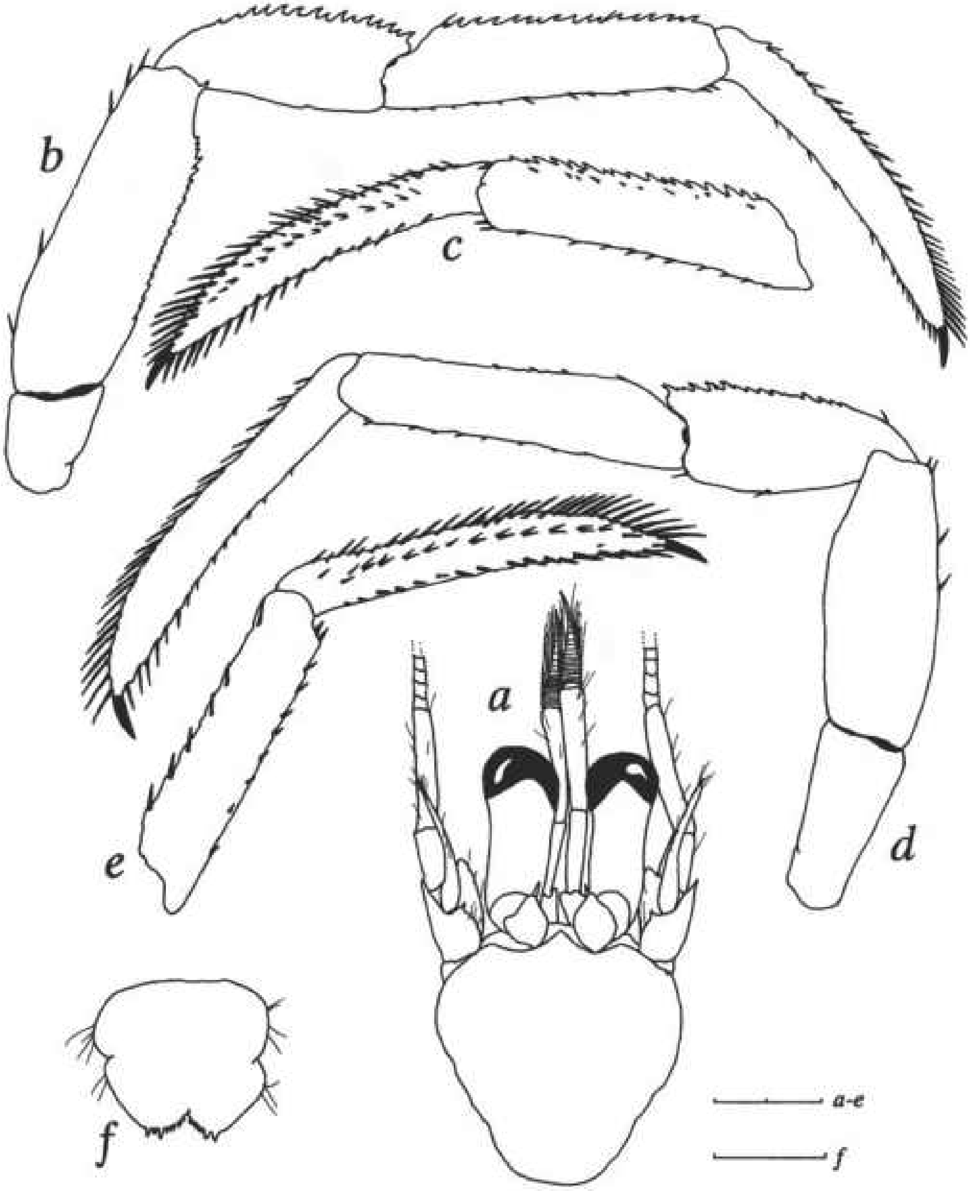

Figure 11. *Manucomplanus ungulatus* (Studer): a, shield and cephalic appendages; b, right 2nd pereopod, lateral view; c, propodus and dactyl of same, mesial view; d, left 3rd pereopod, lateral view; e, propodus and dactyl of same, mesial view; f, telson. Scales equal 2 mm (a–e), and 1 mm (f). (Male, DISL 0002, USNM).

to moderately strong, often tear-drop-shaped spines, most prominent and closely-packed on fixed finger (Fig. 12a, c), dorsomesial and dorsolateral margins each with row of irregular, strong, acute spines.

Left cheliped often with 1 very small spine at ventrolateral distal angle of merus, particularly in small specimens; dorsolateral margin of carpus with row of strong, acute spines, dorsomesial margin with row of spinules or small spines

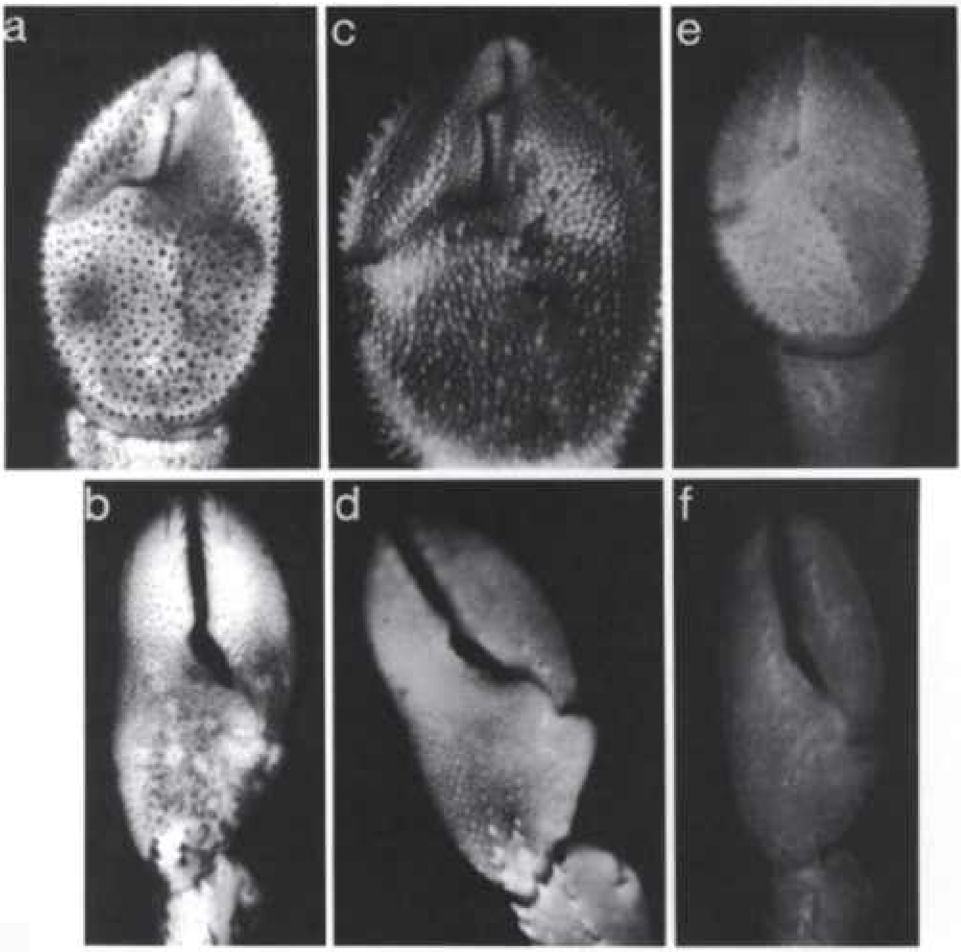

Figure 12. Chelae of *Manucomplanus ungulatus* (Studer) (a–d), showing variations, and *M. spinulosus* (Holthuis) (e, f). a, right (2.4×); b, left (4.8×); c, right (1.8×); d, left (4.2×); e, right (5.9×); f, left (12.1×). (a, b, male, DISL 0002, USNM; c, d, male, BLAKE 38, MCZ 4016; e, f, female, PILLSBURY 767, USNM).

extending onto mesial face distally; propodal-carpal articulation 30° clockwise from perpendicular, slightly elevated in midline proximally and often armed with 2–4 small spines, dactyl with granular or minutely spinulose surface, dorsolateral margin with row of tiny granules or spinules.

Dactyls of 2nd and 3rd pereopods moderately long, 2nd moderately broad, somewhat twisted, dorsal margins and mesial faces dorsally each with row of strong corneous spines; ventral margins each with 8–14 corneous spines, increasing in size distally; propodi each with row of strong spines on dorsal surface (2nd pereopod) or small spines or corneous spinules (3rd pereopod); carpi each with row of strong spines on dorsal surface; ventral margins of meri each with single or double row of small spines or spinules giving margins serrate appearances.

Sternite of 3rd pereopods with anterior lobe elongate, slender, often slightly enlarged and spinulose near tip. Telson with oblique terminal margins, each with

Table 6. *Manucomplanus ungulatus* (Studer) material examined. (*: specimens not measured or sexed, left in bryozoan housing)

Locality	Depth (m)	Station deposition	Date	Sex ♂	Sex ♀	Sex ♀♀	SL (mm)	Collector
Eastern coast of United States								
off Cape Hatteras	—	L-1 PMcL	Sep 1962	1			2.9	—
off South Carolina	—	DOLPHIN USNM 188328, 188338	—	2			2.9, 3.2	E.L. Wenner
off South Carolina	—	DOLPHIN USNM 186443, 188199	1979	3		1	3.2–4.0	E.L. Wenner
34°12′N 76°04′56″W	86	FISH HAWK D-8249 USNM 51059		1			2.8	USFC
33°49′18″N 76°34′18″W	62	— USNM 209668	11 Aug 1981	1			1.8	DU
33°31′36″N 77°23′54″W	32	MS04 USNM 220874	7 Feb 1981	1			3.3	E.L. Wenner
33°20′N 77°13′W	73	SILVER BAY 2159 USNM	16 Jul 1960	1			3.1	NMFS
33°12′N 77°36′W	44	Texas Instruments 1E USNM 174384	17 Aug 1977		1		1.8	R.W. Heard
32°50′36″N 78°36′18″W	37	DOLPHIN USNM 188196	20 Apr 1979	1			2.8	E.L. Wenner
32°50′06″N 78°36′18″W	35	DOLPHIN USNM 188326	21 Sep 1979	1			3.3	E.L. Wenner
32°49′48″N 78°36′W	35	DOLPHIN USNM 188327	21 Sep 1979	1			4.2	E.L. Wenner
32°45′N 78°56′W	27	Texas Instruments 2D USNM 174252	18 Aug 1977	1			3.5	R.W. Heard
32°40′N 78°47′W	37	Texas Instruments 2E USNM 174483	14 Feb 1977		1		2.7	B. Boothe
32°40′N 78°47′W	37	Texas Instruments 2E USNM 174382	18 Aug 1977	3	1		3.1–3.6	K. Shaw
32°34′N 79°05′W	35	PELICAN 194-10 USNM 103429	9 Mar 1940	4		1	2.9–4.0	RSMAS
32°24′42″N 78°53′18″W	91	DOLPHIN USNM 186436, 186437	28 Jan 1976			2	2.9–3.3	E.L. Wenner
31°31′48″N 79°44′36″W	58	OS01 USNM 225796	5 Aug 1981	1			3.4	M. Dojiri
31°31′48″N 79°44′36″W	56	OS01 USNM 225797	4 May 1981	2			2.8, 2.9	M. Dojiri
31°31′48″N 79°44′42″W	54	OS01 USNM 225795	9 Mar 1981			1	3.9	M. Dojiri
31°27′N 79°46′W	64	Texas Instruments USNM 174383	22 Nov 1977	1			2.4	K. Shaw
31°26′32″N 79°42′13″W	298	— USNM 150222	6 Aug 1963	4	1	1	2.2–3.1	M. Gray
31°24′30″N 80°01′W	42	PELICAN 179-1 USNM	1 Feb 1940			1	3.3	RSMAS
31°13′N 80°44′W	20	PELICAN 178-8 USNM	31 Jan 1940	1			3.3	RSMAS

Table 6. Continued

Locality	Depth (m)	Station deposition	Date	Sex ♂	Sex ♀	Sex ♀♀	SL (mm)	Collector
Umbrella Creek, Georgia	—	— USNM 102794	10 Jun 1932	1	2		2.5–50	W. Anderson
30°44′N 80°14′W	43	DOLPHIN USNM 188197	17 Sep 1975	1			3.0	E.L. Wenner
30°28′N 80°48′30″W	27	PELICAN 176-7 USNM 102792, MNHN	25 Jan 1940	1		1	2.7–3.5	RSMAS
30°26′12″N 80°12′18″W	61	OS03 USNM 214891	11 Mar 1980	2		1	3.7–4.2	E.L. Wenner
29°30′N 80°15′W	73	SILVER BAY 3171 USNM, MNHN	10 May 1961	3	1		2.8–4.2	NMFS
29°06′N 80°31′W	24	SILVER BAY 1909 USNM	18 Apr 1960			1	4.3	NMFS
28°59′N 80°04′W	91–183	PELICAN 204-3 USNM	29 Mar 1940	1			3.8	RSMAS
28°09′30″N 80°12′W	33	PELICAN 168-3 USNM	17 Jan 1940				*	RSMAS
off Palm Beach, Florida	55	— USNM	Jun 1951			1	3.8	T.L. McGinty
off Miami, Florida	55	— USNM 45620	May 1912	3			2.4–2.7	J. B. Henderson
Gulf of Mexico								
18 mi S by W of Destin, Florida	33–37	— MCZ 12015	Oct 1941			2	2.2, 2.5	T.L. McGinty
30°14′N 86°19′W	43	dredge a USNM	8 Mar 1977	6		2	1.8–2.7	T.S. Hopkins
30°13′N 86°10′W	27	PELICAN 151-2 USNM 102793	9 Mar 1939			2	2.3, 3.7	RSMAS
30°01′30″N 85°54′54″W	27	DC-42-134 NHRM	6 Jun 1974	2	1		2.9–3.4	DISL
29°56′N 86°09′W	55	OREGON 13062 USNM	5 Apr 1973	2			2.2, 3.7	NMFS
29°56′N 86°06′30″W	37	DC-42-34 NHRM	3 Jun 1974	7			1.7–3.7	DISL
29°55′42″N 86°06′29″W	36	A USNM	28 Jun 1976	12	5	3	1.7–3.8	DISL
29°51′N 86°06′30″W	39	— USNM	4 Jun 1974	1			2.4	DISL
29°48′N 86°03′30″W	39	DC-42-37 RMNH D46271	4 Jun 1974	11	7	3	1.4–4.2	DISL
29°47′30″N 85°54′30″W	35	DC-42-41 USNM	6 Jun 1974	1			3.3	DISL
29°27′30″N 87°48′30″W	55	ALBATROSS 2390 USNM 9706	4 Mar 1885				*	USFC
29°24′N 88°04′W	59	ALBATROSS 2387 USNM 9690	4 Mar 1885	1			3.0	USFC
29°15′30″N 85°29′30″W	49	ALBATROSS 2372 USNM 16942	7 Feb 1885	1			2.5	USFC

Table 6. Continued

Locality	Depth (m)	Station deposition	Date	Sex ♂	Sex ♀	Sex ♀♀	SL (mm)	Collector
29°14′N 85°29′15″W	46	Albatross 2373 USNM 16943	—				*	USFC
29°11′30″N 85°29′00″W	48	Albatross 2374 USNM 9633	7 Feb 1885		1	1	1.7, 2.2	USFC
28°47′30″N 84°37′00″W	44	Albatross 2407 USNM 9807	15 Mar 1885	4			2.4–2.8	USFC
28°46′N 84°49′W	48	Albatross 2406 USNM 16940	15 Mar 1885	1	2	2	2.4–3.7	USFC
28°46′N 93°25′W	27	Pelican 100-3 USNM 102796	16 Jan 1939				*	RSMAS
28°46′N 84°49′W	48	Albatross 2406 USNM	15 Mar 1885	1			2.9	USFC
28°45′N 85°02′W	55	Albatross 2405 USNM	15 Mar 1885	1			3.1	USFC
28°44′N 85°01′W	46	Oregon 728 USNM 94445	16 Dec 1952	2			3.3–3.4	NMFS
28°28′N 84°25′W	38	Albatross 2405 USNM 16939	16 Mar 1885	3		1	2.1–3.5	USFC
28°26′30″N 84°23′30″W	45	DC-42-44 USNM	18 Jun 1974	1			1.8	DISL
28°24′N 84°21′W	45	DC-42-49 USNM	18 Jun 1974	1			3.5	DISL
27°50′N 84°21′W	34	DC-42-62 MNHN	16 Jun 1974		1		3.7	DISL
27°49′56″N 84°41′56″W	165	DISL 0002 USNM	5 Feb 1978	3			2.9–4.8	DISL
27°47′N 83°56′W	51	Oregon 4087 USNM	4 Dec 1962				*	NMFS
27°45′30″N 83°25′30″W	30	DC-42-65 USNM	15 Jun 1974				*	DISL
26°33′30″N 83°15′30″W	49	Albatross 2411 USNM 9829	18 Mar 1885		1		2.5	USFC
25°23′00″N 82°54′30″W	49	Grampus 5070 USNM 16944	26 Feb 1889	1			3.4	USFC
25°17′11″N 83°02′04″W	52	— USNM 211827	Jul 1981	1			3.3	—
West Florida	35	— MCZ 4084, 12962	—	1	2	1	2.1–3.5	W. Stimpson
23°10′N 88°35′W	37	Blake 38 MCZ 4016	—	1			5.0	A. Agassiz
22°28′N 87°02′W	49	Albatross 2366 USNM 9593	30 Jan 1885		1		3.9	USFC
22°07′30″N 87°06′W	38	Albatross 2363 USNM 9577	30 Jan 1885	3	1	2	2.7–4.3	USFC
Bahamas, Straits of Florida, and Florida Keys								
Nassau, Bahamas	—	Albatross USNM 11511	1886	4			2.0–2.8	USFC
25°05′00″N 80°15′00″W	102	Albatross 2640 USNM 11518, 11519	9 Apr 1886	3	1		1.9–2.7	USFC
25°04′30″N 82°59′15″W	48	Albatross 2414 USNM 102616	19 Nov 1885				*	USFC

Table 6. Continued

Locality	Depth (m)	Station deposition	Date	Sex ♂	Sex ♀	Sex ♀♀	SL (mm)	Collector
Key West, Florida	110	State University of Iowa Expedition USNM 102614	19 Jun 1893			1	2.4	—
Tortugas, Florida	46	3 USNM 102615	16 Aug 1924	1			2.8	W.L. Schmitt
24°26′N 81°48′15″W	68	ALBATROSS 2315 USNM 94607	15 Jan 1885			1	2.6	USFC
24°25′45″N 81°46′W	82	ALBATROSS 2318 USNM	15 Jan 1885	4		2	2.4–3.7	USFC

2–4 moderate to strong spines and often also few spinules, lateral margins unarmed or with few spinules proximally.

Color.—Shield with splotches of reddish orange, particularly laterally and posteriorly. Chelipeds with splotches of orange or red on base color of white or faint orange; ambulatory legs with bandings of same color.

Distribution and Habitat.—Eastern United States from North Carolina (off Cape Hatteras) to Florida; Bahamas and Straits of Florida; Gulf of Mexico; South and West Africa; 20–298 m. Frequently inhabiting "Texas long-horn" bryozoans (Williams, 1984), and less frequently sponge-covered gastropod shells.

Affinities.—The two Atlantic species of *Manucomplanus* are very similar in general appearance, but may be quickly distinguished from one another by the characteristic tear-drop-shaped spines of the fixed finger of the right chela of *M. ungulatus*. This species also reaches a considerably larger size than does *M. spinulosus*.

Variations.—*Manucomplanus ungulatus* exhibits a broad range of morphological variations on the right cheliped. In particular, the shape of the carpus and the dorsal armature of the chela, are influenced considerably by sex and size of the individuals. With growth, males tend to develop a carpus more elongated than in females of similar size. In small specimens (SL < 2.0 mm) of both sexes, the carpus is approximately 1.4 times as long as broad. In larger male specimens (SL > 4.0 mm), the carpus is frequently twice as long as broad, whereas in females it is at most 1.5 times as long as broad. On the dorsal surface of the chela, the density and shape of the spines vary with growth similarly in males and females. In smaller specimens (SL < 2.0 mm), the spines are widely separated, often scattered, and the characteristic tear-drop shape of the spines on the fingers of this species is only weakly discernible. In contrast, larger specimens (SL > 4.0 mm) have closely-packed, often prominent tear-drop-shaped spines on one or both fingers (Fig. 12a, c).

Remarks.—Studer (1883) based his description of *Eupagurus ungulatus*, on a single specimen collected in South Africa during the GAZELLE expedition. In his remarks, Studer related his species to *Eupagurus discoidalis* A. Milne Edwards. Shortly thereafter, A. Milne Edwards and Bouvier (1891) published "preliminary observations" on pagurid species collected by the BLAKE and HASSLER in waters of the Gulf of Mexico and Caribbean. *Pylopagurus* was among the new genera briefly described in this account, and while Milne Edwards and Bouvier indicated that six species belonged in the genus, only *E. discoidalis* and *E. ungulatus* were formally assigned. A complete report of the BLAKE expedition was subsequently published (A. Milne Edwards and Bouvier, 1893) in which these authors redescribed *Pylopagurus ungulatus* and compared Studer's (1883) description and illustrations with specimens collected by the BLAKE and previously by Stimpson from west Florida. Although they noted some differences between their material and Studer's published report, they believed these not sufficient to justify the description of a new western Atlantic species. They did note, however, that if the BLAKE specimens were identical with that of the GAZELLE, this species would have a very extended geographical range.

Despite the fact that Studer (1883) had not indicated the sex of his specimen, Milne Edwards and Bouvier (1893) believed that there was no doubt that their assignment of Studer's species to *Pylopagurus* was correct. This belief was confirmed by Balss (1911) who, in a footnote, remarked that the type had the paired abdominal appendages characteristic of the genus. Two additional specimens collected by the GAZELLE Expedition from the type locality, but presumably not seen by Studer are also in the collection of the Zoologisches Museum, Berlin. It is believed that these were subsequently identified by Balss (Gruner, pers. comm.), but are not the specimens referred to by Balss (1921) from Lagos, Nigeria. It appears that all subsequent references to *Pylopagurus ungulatus* from African waters have been based upon Studer's (1883) and Balss' (1911, 1921) citations.

Prior to the detailed descriptions of species collected by the BLAKE (A. Milne Edwards and Bouvier, 1893), Benedict (1892) described a large number of new hermit crab species from the collections of the United States National Museum, among them *Eupagurus corallinus* from Key West, Florida. Although Benedict's description was based upon both males and females, he made no mention of the paired 1st pleopods in the females and his assignment of the species to *Eupagurus* suggests that he overlooked them. Hay and Shore (1918) extended the range of Benedict's species, but only when it was redescribed by Williams (1965) was its relationship to *Pylopagurus* recognized.

McLaughlin (1981a) reexamined A. Milne Edwards and Bouvier's (1893) specimen of *P. ungulatus* from BLAKE station 38, off the Yucatán Bank (♂ SL 5.0 mm, MCZ 4016). After comparing it with the syntypes of Benedict's *P. corallinus,* McLaughlin (1981a) concluded that Milne Edwards and Bouvier's (1893) specimens were misidentified specimens of *P. corallinus.* We have now had the opportunity to critically examine both Studer's (1883) holotype of *E. ungulatus* and the two additional specimens from the type locality subsequently identified by Balss. Additionally, we have examined the remaining Milne Edwards and Bouvier (1893) specimens of *P. ungulatus* and several hundred specimens identifiable as *P. corallinus* from the Gulf of Mexico, east coast of Florida and Caribbean. As previously indicated, this highly variable species is subject to considerable sexual dimorphism. In no characters were we able to find distinctions in the African specimens that were not well within the range of variation of the eastern Atlantic taxon. Therefore, we must conclude that *Manucomplanus ungulatus* is the senior subjective synonym of *M. corallinus.*

Manucomplanus spinulosus (Holthuis, 1959)
Figures 12e, f, 13

Pylopagurus spinulosus Holthuis, 1959: 154, figs. 29, 30 (type locality: 20 mi. N of Suriname coast between mouths of Nickerie and Coppename Rivers).
Pagurus impressus zilchi Türkay, 1968: 250, fig. 5a, b.
Manucomplanus spinulosus: McLaughlin, 1981a: 7 (by implication).

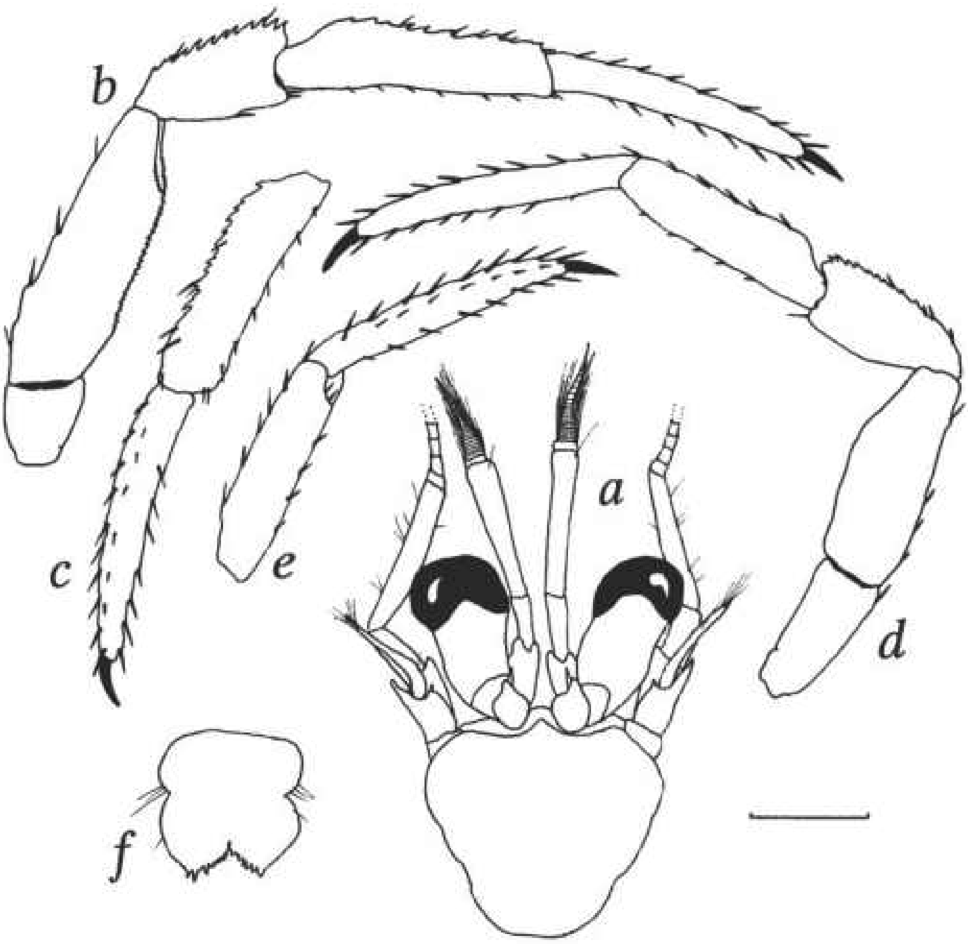

Figure 13. *Manucomplanus spinulosus* (Holthuis): a, shield and cephalic appendages; b, right 2nd pereopod, lateral view; c, propodus and dactyl of same, mesial view; d, left 3rd pereopod, lateral view; e, propodus and dactyl of same, mesial view; f, telson. Scale equals 1 mm (a–e), and 0.5 mm (f). (Female, PILLSBURY 767, USNM).

Holotype.—Pylopagurus spinulosus Holthuis: ♀♀ (SL 3.0 mm), RMNH 11901.

Holotype.—Pagurus impressus zilchi Türkay: ♂ (SL 3.4 mm), SMF 4351.

Material Examined.—See Table 7.

Diagnosis.—Shield slightly broader than long; rostrum produced as small, acute lobe, without terminal spine. Ocular peduncles short, moderately stout, with corneae strongly dilated; ocular acicles separated basally by approximately basal width of 1 acicle. Ultimate segment of antennular peduncle approximately equal to length of ocular peduncle, ventral margin with sparse, long setae. Right cheliped with ventral surface and margins of merus minutely tuberculate; carpus with dorsomesial and dorsolateral margins each delimited by row of small spines, dorsal surface with numerous small spines; dorsal surfaces of palm, fixed finger and dactyl all with scattered small, slender spines and few larger, often blunt spines, margins spinose.

Left cheliped with 1 or 2 acute spines on ventrolateral distal angle of merus;

Table 7. *Manucomplanus spinulosus* (Holthuis) material examined

Locality	Depth (m)	Station deposition	Date	Sex ♂	Sex ♀	Sex ♀♀	SL (mm)	Collector
Straits of Florida								
24°36′36″N 81°06′42″W	42	Gerda 1033 USNM	26 Feb 1969	1		2	1.6–2.4	RSMAS
Southern Caribbean								
12°17′N 71°03′18″W	24–26	Pillsbury 767 USNM	28 Jul 1968		6		1.7–2.0	RSMAS
11°11′N 63°17′W	24–27	Pillsbury 712 USNM	19 Jul 1968	21	5	24	1.6–3.7	RSMAS
11°07′N 64°23′24″W	26–27	Pillsbury 721 USNM	21 Jul 1968		4		1.5–19	RSMAS
10°47′36″N 62°56′W	46–48	Pillsbury 710 UMML 32:4969	19 Jul 1968		1		1.5	RSMAS
Northeastern South America, off Suriname								
between Nickerie and Coppename Rivers	27	Coquette RMNH 11901	15–20 Apr 1957			1	3.0	—
08°12′N 58°33′W	37	Pillsbury 695 NHRM	15 Jul 1968	1		2	2.3–2.6	RSMAS
07°19′N 56°51′W	101–108	Pillsbury 684 USNM	14 Jul 1968	1			2.2	RSMAS
07°00′N 57°08′W	26–27	Pillsbury 686 USNM, PMcL	15 Jul 1968	2			1.9, 2.3	RSMAS
06°12′N 57°58′W	38	Pillsbury 653 USNM	9 Jul 1968		1		2.5	RSMAS
06°07′N 52°19′W	84–92	Pillsbury 650 USNM	8 Jul 1968	13	5	8	1.6–2.8	RSMAS
05°56′N 52°20′W	57–51	Oregon 2307a-b USNM 119889	11 Sep 1958			1	2.9	NMFS

carpus with row of moderately strong spines on dorsolateral margin, dorsomesial margin with tufts of long stiff setae and row of tiny spinules (in larger individuals); dorsal surfaces of palm, fixed finger and dactyl each with scattered small spinules and few larger spines, margins each with row of small, closely-spaced spinules.

Dactyls of 2nd pereopods slightly shorter and broader than those of 3rd pereopods, each with dorsal, ventral and mesial rows of corneous spines; propodi each with row of calcareous spines (2nd) or corneous spinules (3rd) on dorsal surfaces; carpi each with row of strong spines on dorsal surface; ventral margins of meri unarmed or minutely spinulose.

Sternite of 3rd pereopod with anterior lobe elongate and slender. Telson (missing from holotype) with terminal margins of posterior lobes obtusely triangular or rounded, each with several small spinules mesially.

Color.—In preservative, scattered red dots on right cheliped (Holthuis, 1959).

Distribution.—Straits of Florida (apparently rare), and Caribbean coast of northern South America to Suriname; 24–108 m.

Affinities.—As previously stated, in the Atlantic, *M. spinulosus* is generally quite similar to *M. ungulatus*; however, it bears many more morphological similarities with the Pacific species *M. cervicornis* and *M. longimanus*, particularly in the spination of the right chela. In the absence of geographical data, these species may be distinguished primarily by the sparse setation of the ventral margin of the ultimate peduncular segment, and the shortness of its length in *M. spinulosus*.

Remarks.—The fact that the monotypic subspecies *Pagurus impressus zilchi* was based on a male specimen may account for Türkay's (1968) assignment of this taxon to *Pagurus*. There are general similarities in the shape of the right chelipeds of *Pagurus impressus* (Benedict) and Türkay's taxon; however, our reexamination of *P. i. zilchi* has shown that it clearly should be assigned to *Manucomplanus*. In all characters this taxon falls within the range of variation exhibited by *M. spinulosus* and, therefore, *P. i. zilchi* must be considered a junior subjective synonym.

Manucomplanus cervicornis (Benedict, 1892)
Figures 14, 15a, b

Eupagurus cervicornis Benedict, 1892: 25 (type locality: Gulf of California, restricted by lectotype selection to ALBATROSS station 2829, off Cape St. Lucas, Baja California, Mexico).—Alcock, 1905: 180 (list).

Pylopagurus cervicornis: Glassell, 1937: 253.—Walton, 1954: 154, pl. 42A–D.—Gordan, 1956: 340 (lit.).—Snyder-Conn, 1980: 285.

Manucomplanus cervicornis: McLaughlin, 1981a: 7 (by implication).—Cairns and Barnard, 1984: 2.

Lectotype.—Herein selected: ♀ (SL 3.2 mm), USNM 16700.

Material Examined.—Table 8.

Diagnosis.—Shield slightly broader than long to approximately as long as broad; rostrum produced, terminating acutely or subacutely. Ocular peduncles moderately short to short, corneae strongly dilated; ocular acicles separated basally by slightly less than basal width of 1 acicle. Ultimate segment of antennular peduncle exceeding ocular peduncle by approximately ⅓ own length, ventral margin with regular row of closely-spaced, long setae.

Right cheliped with ventromesial and ventrolateral margins of merus minutely serrate and with 1 or 2 spines on lateral margin ventrally; carpus with closely-spaced spinules on dorsal surface, dorsomesial and dorsolateral margins each with row of small spines, strongest mesially; dorsal surfaces of palm, fixed finger and dactyl often with tear-drop-shaped spines or spinules varying in density and strength from large and closely-spaced (Fig. 14b) to small and moderately spaced (Fig. 14c), spines or spinules each usually terminating in corneous bristle, dorsomesial and dorsolateral margins each with row of small spines.

Left cheliped with acute spine at ventrolateral margin of merus, ventromesial margin weakly serrate; carpus with row of acute spines on dorsolateral and dorsomesial margins, strongest laterally, dorsodistal margin with 1 or 2 strong spines, ventrolateral margin with acute spine distally; dorsal surfaces of palm, fixed finger and dactyl all minutely spinulose, margins each with row of very small, bead-like tubercles.

Dactyls of 2nd and 3rd pereopods moderately short and broad, each usually with low spines (2nd) or low, sometimes spinulose protuberances (3rd) on dorsal surfaces, mesial faces each with row of strong corneous spines, ventral margins each with 8–10 corneous spines increasing in size distally; propodi each with row of small spines (2nd) or low protuberances (3rd) on dorsal margin, ventral surfaces each with row of corneous spines or spinules; carpi each with row of moderately

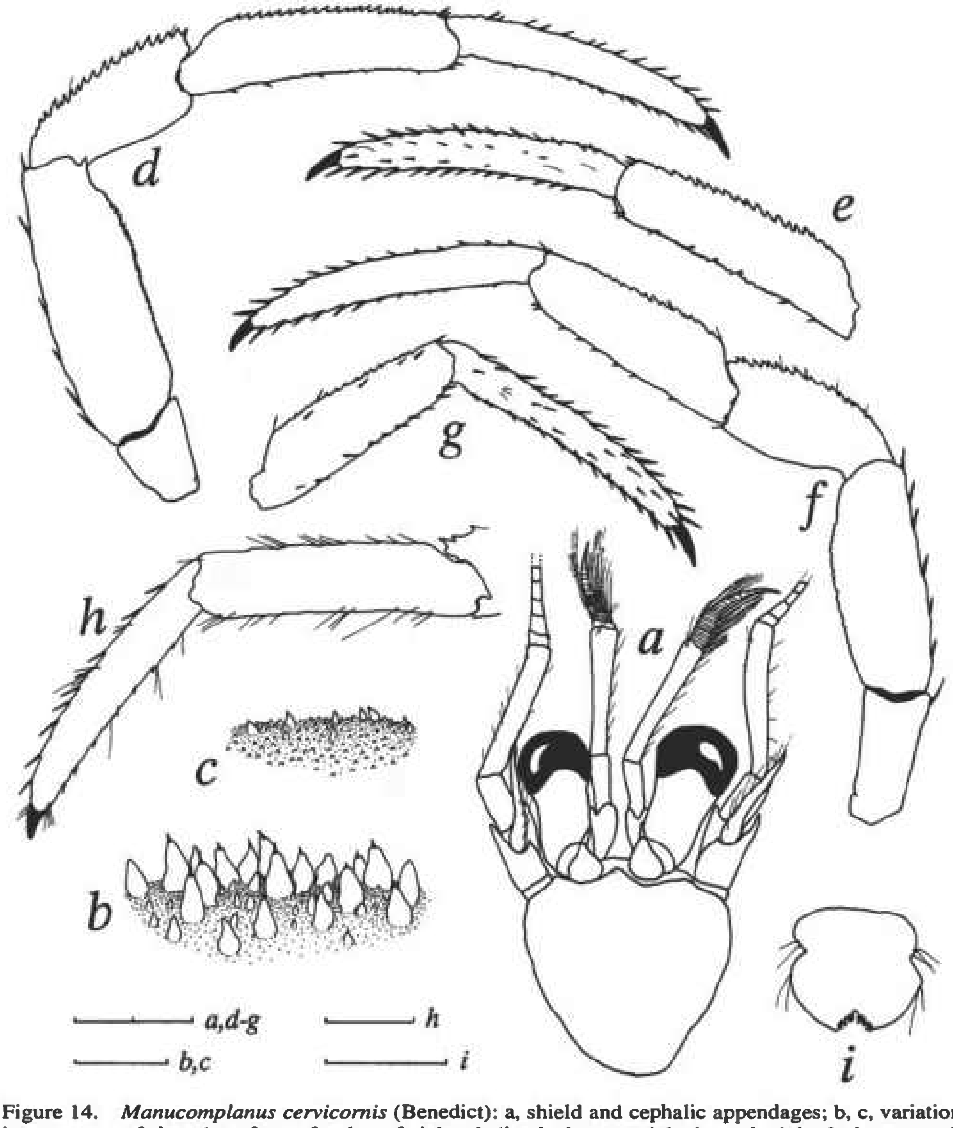

Figure 14. *Manucomplanus cervicornis* (Benedict): a, shield and cephalic appendages; b, c, variation in armature of dorsal surface of palm of right cheliped, dorsomesial view; d, right 2nd pereopod, lateral view; e, propodus and dactyl of same, mesial view; f, left 3rd pereopod, lateral view; g, propodus and dactyl of same, mesial view; h, propodus and dactyl of left 3rd pereopod, lateral view; i, telson. Scales equal 2 mm (a, d–g), 0.5 mm (b, c), and 1 mm (h, i). (a, d–g, i, male, VELERO IV 1055-40, AHF(LACM); b, female, ALBATROSS 2829, USNM 16700; c, female, VELERO IV 1725-49, AHF(LACM)).

strong spines on dorsal surface; meri each with single or double row of small spinules (2nd) or low protuberances (3rd) on ventral margin.

Sternite of 3rd pereopods with anterior lobe elongate, ovate or triangular, terminating acutely or with small spinule, surface and margins often spinulose in males. Telson with terminal margins oblique, each with row of spines, lateral margins somewhat rounded, unarmed.

Color.—Unknown.

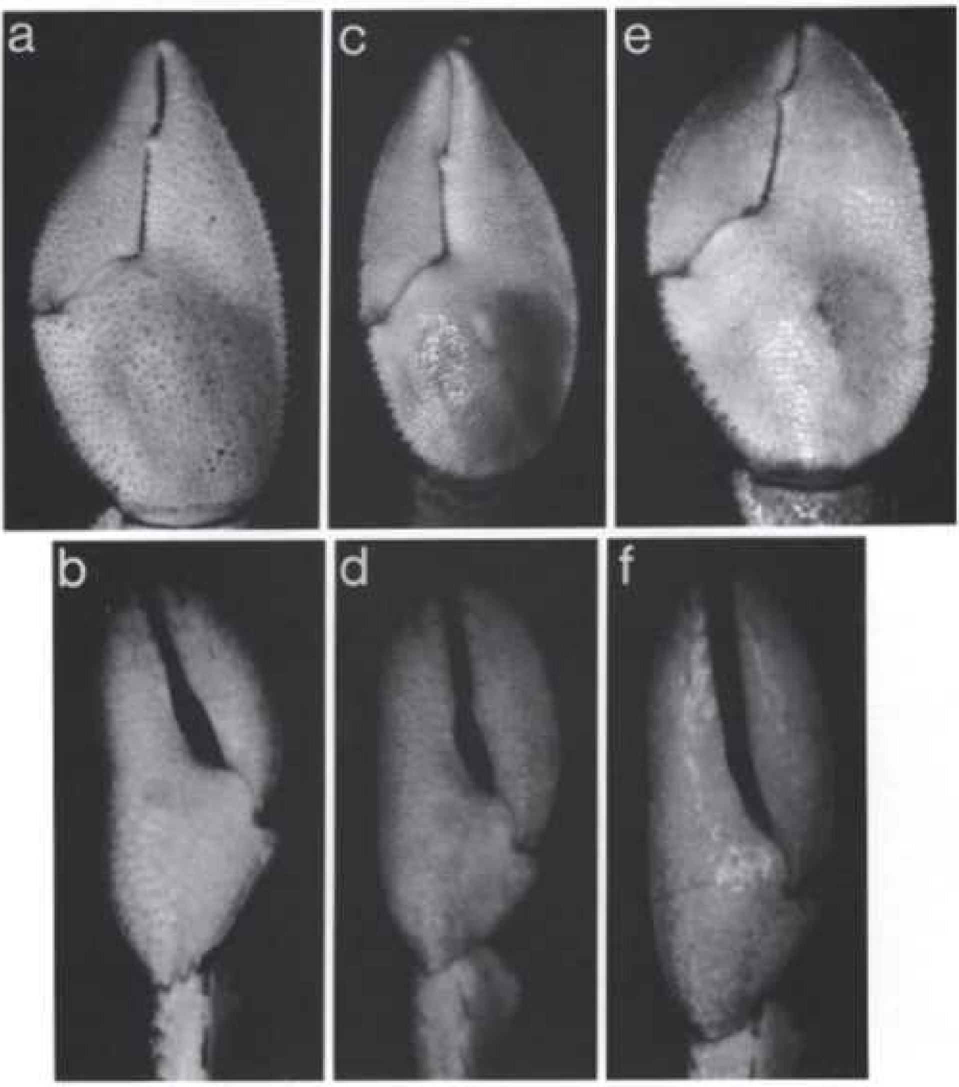

Figure 15. Chelae of *Manucomplanus cervicornis* (Benedict) (a, b), *M. varians* (Benedict) (c, d), and *M. longimanus* (Faxon) (e, f). a, right (3.7×); b, left (7.4×); c, right (4.3×); d, left (6.9×); e, right (5.2×); f, left (9.6×). (a, b, male, VELERO III 1055-40, AHF(LACM); c, d male, VELERO III 712-37, AHF(LACM); e, f, female, VELERO III 773-38, AHF(LACM)).

Distribution and Habitat.—Eastern Pacific: from Baja California and the Gulf of California, Mexico, to Panamá; 37–203 m. Typically found inhabiting gastropod shells encrusted by the calcified hydroid *Janaria mirabilis* Stechow (Cairns and Barnard, 1984).

Affinities.—Walton (1954) distinguished *M. cervicornis* from *M. varians* by the shape of the spines of the right cheliped and by the armature of the telson, and these characters indeed can be used to distinguish the two species. However, in small specimens of the latter species, the flattened shape of the tubercles may not be readily observed. Additionally, the orientation of the terminal margin of the

Table 8. *Manucomplanus cervicornis* (Benedict) material examined

Locality	Depth (m)	Station deposition	Date	Sex ♂	Sex ♀	Sex ♀♀	SL (mm)	Collector
Baja California, Gulf of California and Mexico (Pacific)								
N of Granite Is., Angel de la Guardia Is.	104	Velero III 1055-40 AHF(LACM)	28 Jan 1940	2	1		2.5–4.3	AHF
S of Pond Is., Angel de la Guardia Is.	113–155	Velero III 1080-40 AHF(LACM)	5 Feb 1940	3	7		1.7–3.3	AHF
E of Angel de la Guardia Is.	73	Velero III 594-36 AHF(LACM)	6 Mar 1936	1			4.2	AHF
Puerto Refugio, Angel de la Guardia Is.	119	Velero III 544–36 AHF(LACM)	4 Mar 1936	2	3		2.9–4.0	AHF
Puerto Refugio, Angel de la Guardia Is.	143–165	Velero III 1054-40 AHF(LACM)	28 Jan 1940		1		2.2	AHF
Puerto Refugio, Angel de la Guardia Is.	110	Velero III 708-37 AHF(LACM)	21 Mar 1937		1		3.7	AHF
San Pedro Nolasco Is.	170–203	Velero III 1084-40 AHF(LACM)	6 Feb 1940	1			3.1	AHF
off San Pedro Nolasco Is.	201	Velero III 735-37 AHF(LACM)	29 Mar 1937		1		3.8	AHF
San Ignacio Bay, Sinaloa	55–91	Velero III 742-37 AHF(LACM)	31 Mar 1937	2	5	6	2.3–3.1	AHF
1¼ mi. SW of Cabeza Ballena	55	Velero IV 1726-49 AHF(LACM)	11 Mar 1949	10	1		2.7–4.0	AHF
1¼ mi. SW of Cabeza Ballena	37	Velero IV 1725-49 AHF(LACM)	11 Mar 1949	2	1	3	1.7–3.7	AHF
Arena Bank	82	Crocker Expedition USNM	3 Apr 1936	2			3.2, 3.3	W. Beebe
22°52′00″N 109°55′00″W	57	Albatross 2829 USNM 16700, 108267, 110996	1 May 1888	5	9	1	2.7–3.8	USFC
off Navidad Head, near Tenacatita Bay, Jalisco	46–64	275-34 USNM	4 Mar 1934	2	1		2.5–3.3	W.L. Schmitt
Panamá (Pacific)								
Secas Is.	128	Velero III 251-34 AHF(LACM)	22 Feb 1934	1		1	2.3–2.4	AHF

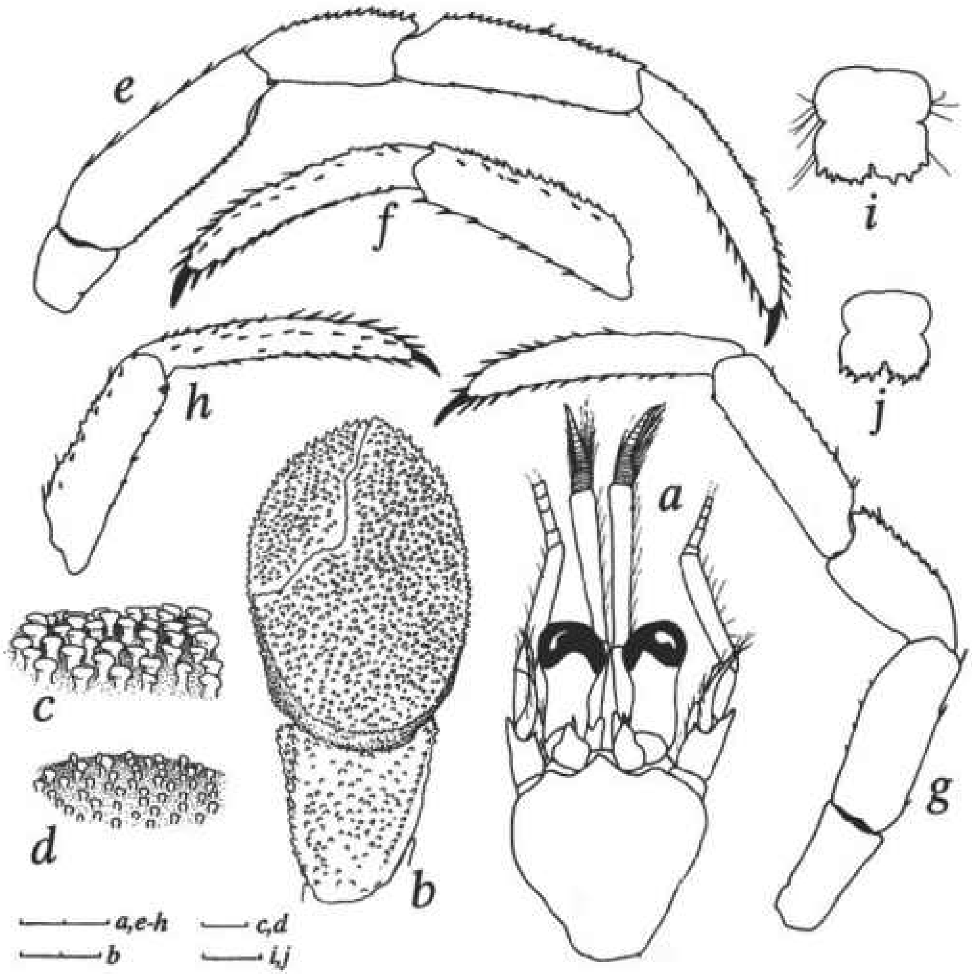

Figure 16. *Manucomplanus varians* (Benedict): a, shield and cephalic appendages; b, right cheliped; c, d, variation in armature of dorsal surface of palm of right cheliped, dorsomesial view; e, right 2nd pereopod, lateral view; f, propodus and dactyl of same, mesial view; g, left 3rd pereopod, lateral view; h, propodus and dactyl of same, mesial view; i, j, telson. Scales equal 2 mm (a, b, e–h), 0.25 mm (c, d), and 1 mm (i, j). (a, e–i, male, VELERO III 712-37, AHF(LACM); j, female, same station; b, c, male, ALBATROSS 2929, USNM 108263; d, male, ALBATROSS 3014, USNM 16735).

telson in relation to its longitudinal axis can be used to differentiate *M. cervicornis* from *M. varians*. In *M. cervicornis* the terminal margin is strongly oblique (Fig. 14i), whereas in *M. varians* the margin is nearly horizontal (Fig. 16i, j).

Manucomplanus varians (Benedict, 1892)
Figures 15c, d, 16

Eupagurus varians Benedict, 1892: 24 (type locality: Gulf of California; restricted by lectotype selection to ALBATROSS station 2999, Gulf of California, 24°54′30″N, 110°39′W).—Bouvier, 1898: 382.—Alcock, 1905: 180 (list).—Abel, 1920: 72, fig. 78.—Stechow, 1921: 30.—Balss, 1924: 779.—André and Lamy, 1936: 96, pl. 1, figs. 3, 4.
Pagurus varians: Stechow, 1962: 424.—Gordan, 1956: 336 (lit.).

Pylopagurus varians: Glassell, 1937: 253.—Walton, 1954: 152, pl. 42E–H.—Gordan, 1956: 340 (lit.).—Ball and Haig, 1974: 102.—Snyder-Conn, 1980: 284, pl. 11.—Ingle, 1982: 468, unnumbered photo.—Anonymous, 1985, inside front cover, unnumbered photo by Alex Kerstitch.
"Stag-horn": Smith, 1966: 30, 2 text figs.
Manucomplanus varians: McLaughlin, 1981a: 7 (by implication).—Cairns and Barnard, 1984: 2.

Lectotype.—Herein selected: ♂ (SL 4.1 mm), USNM 16734.

Material Examined.—See Table 9.

Diagnosis.—Shield slightly longer than broad; rostrum obtusely triangular, terminating acutely but without terminal spine or spinule; lateral projections obtusely triangular or broadly rounded. Ocular peduncles short, moderately stout, with corneae strongly dilated; ocular acicles separated basally by slightly less than basal width of 1 acicle.

Right cheliped with single or double row of small spines on ventromesial and ventrolateral margins of merus, dorsodistal margins with several small spinules; carpus with row of moderately strong spines on dorsomesial margin, dorsolateral margin only weakly delimited by row of small spines or spinules, surfaces all with closely-spaced blunt to sharp spinules; palm, fixed finger and dactyl with closely-spaced flattened or mushroom-shaped tubercles or spinules (Fig. 16b–d) on dorsal surfaces, dorsomesial and dorsolateral margins each with row of strong, acute spines.

Left cheliped with row of small spines on ventromesial and ventrolateral margins of merus; carpus with row of strong spines on dorsolateral margin, dorsomesial margin with row of small spinules, ventrodistal margin with row of denticles mesially and few spinules or spines laterally; palm, fixed finger and dactyl with scattered small spinules or spinulose tubercles on dorsal surfaces, margins each with row of spinules.

Dactyls of 2nd and 3rd pereopods moderately long and broad, each with row of small spines (2nd) or low, sometimes spinulose protuberances (3rd) on dorsal margins, mesial faces each with row of strong corneous spines dorsally and in midline, ventral margins each with row of 10–15 corneous spines, increasing in size distally; propodi each with row of strong, calcareous spines on dorsal margins, ventral margins each with row of corneous spines; carpi each with row of strong spines on dorsal margin, 1 or 2 corneous spinules on ventrodistal margin; meri with stiff corneous bristles or spinules on dorsal margins, ventral margins each with double row of acute spines (2nd) or with row of spinules mesially (3rd).

Sternite of 3rd pereopods with anterior lobe slender, elongate, with simple or bifid terminal spine and spinulose protuberances marginally (males) or subtriangular, unarmed and terminating subacutely (females). Telson with terminal margins horizontal and slightly convex, 1 strong spine at each lateral angle and 1 to 4 strong spines interspersed with smaller spines marginally, lateral margins each also with 1 to several small spines.

Color.—Shield orange. Ocular peduncles reddish-brown; corneae bright orange. Basal segments of antennular peduncles clear, distal segment with alternating reddish-brown areas and dorsal white spots; flagellum reddish-brown. Segments of antennal peduncle transparent; acicle with alternating transverse bands of white and reddish-brown; flagellum with 3–5 reddish-brown segments alternating with 1 white segment. Right cheliped with mottled red and white merus; carpus pink with few deep red tubercles; chela reddish-brown to orange. Merus and chela of left cheliped mottled red and white; carpus with distinct transverse red and white bands. Ambulatory legs generally reddish-brown with white area distally on each segment (after Ball and Haig, 1974).

Distribution and Habitat.—Baja California and Gulf of California, Mexico to Panamá; Galápagos Islands; 17–717 m. *Manucomplanus varians,* similarly to *M. cervicornis,* is commonly found inhabiting gastropod shells encrusted by the calcified hydroid *Janaria mirabilis* (see Cairns and Barnard, 1984).

Affinities.—As previously indicated, *M. varians* is most closely allied to *M. cervicornis.* The former is distinctive in the dorsal armature of the right chela with flattened or mushroom-shaped tubercles, and in possessing calcareous spines on the dorsal surfaces of the propodi of the ambulatory legs.

Variations.—In *M. varians,* the shape and armature of the right chela can vary considerably. The tubercles or spinules on the dorsal surface, the strength and sharpness of the spines on the dorsolateral and dorsomesial margins, and the elongation of the chela, all tend to increase with increasing size of the individuals. The tubercles can be dense and distinctly mushroom-shaped (Fig. 16c), or consist of widely-spaced, small, flattened tubercles or spinules (Fig. 16d). The dorsolateral and dorsomesial margins can be defined by small, blunt to sharp spines, or by strong sharp spines. The chela tends to become more elongate with growth, particularly in larger males (e.g., Fig. 15c). In the material examined, the chela varied from 1.4 to 2.1 times as long as broad.

Manucomplanus longimanus (Faxon, 1893)
Figures 15e, f, 17

Pylopagurus longimanus Faxon, 1893: 168 (type locality: ALBATROSS station 3368, off Panamá, 05°32'45"N, 86°54'30"W, MCZ 4520); 1895: 61, pl. 12, figs. 1–1e.—Alcock, 1905: 189 (list).—Walton, 1954: 156.—Gordan, 1956: 340 (lit.).
Manucomplanus longimanus: McLaughlin, 1981a: 7 (by implication).

Syntypes.—5 ♂ (SL 2.4–5.6 mm), MCZ 4520.

Material Examined.—See Table 10.

Diagnosis.—Shield longer than broad; rostrum triangular, terminating subacutely; lateral projections obtusely triangular or broadly rounded, without submarginal spine. Ocular peduncles moderately short, with corneae somewhat dilated; ocular acicles separated basally by slightly less than basal width of 1 acicle. Antennular peduncle with double row of long setae on ventral margin of ultimate segment.

Right cheliped with ventromesial and ventrolateral margins each with row of often blunt spines, ventral surface with closely-spaced spinulose protuberances; carpus with row of moderately strong acute spines on dorsomesial margin, dorsolateral margin with row of blunt spinules, dorsal surface with closely-spaced small spinules; dorsal surfaces of palm, dactyl and fixed finger with small, usually blunt tubercles and granules (Fig. 17b), margins spinose.

Left cheliped with row of small spines or spinules on ventrolateral and ventromesial margins of merus; carpus with row of acute spines on dorsolateral and dorsomesial margins, strongest mesially, ventrolateral margin with strong spine distally; dorsal surfaces of palm, fixed finger and dactyl with numerous small spines or spinules, slightly larger on dactyl, dactyl also with row of tufts of long setae on ventral surface.

Dactyls of 2nd and 3rd pereopods moderately long, moderately narrow, each with row of corneous spines or bristles on dorsal margins and mesial surfaces,

Table 9. *Manucomplanus varians* (Benedict) material examined

Locality	Depth (m)	Station deposition	Date	Sex ♂	Sex ♀	Sex ♀♀	SL (mm)	Collector
Baja California, Gulf of California and Mexico (Pacific)								
Santa María Bay	18–36	— USNM	22 Jan 1938		1		3.7	S.A. Glassell
31°21′15″N 113°59′00″W	17	ALBATROSS 3025 USNM 16736	25 Mar 1889	1			4.6	USFC
South Bay, Cedros Is.	18–27	VELERO III 287-34 AHF (LACM)	10 Mar 1934			1	1.8	AHF
Puerto Refugio, Angel de la Guarda Is.	91–137	VELERO III 712-37 AHF(LACM)	21 Mar 1937	1	1		2.2, 3.5	AHF
Puerto Refugio, Angel de la Guarda Is.	38	VELERO III 1051-40 AHF(LACM)	27 Jan 1940		1		2.2	AHF
between Partida Is. and Angel de la Guarda Is.	37	VELERO III 555-36 AHF(LACM)	8 Mar 1936	1	1		2.2, 2.3	AHF
E of Angel de la Guarda Is.	15–18	VELERO III 551-36 AHF(LACM)	6 Mar 1936	1			1.9	AHF
San Lorenzo Channel	9–27	VELERO III 498-36 AHF(LACM)	19 Feb 1936		1	1	2.3, 2.7	AHF
28°28′N 112°04′30″W	53	ALBATROSS 3014 USNM 16735	25 Mar 1889	1	1		3.0–3.6	USFC
28°23′45″N 111°58′00″W	26	ALBATROSS 3013 USNM 42559	23 Mar 1889		2		2.7, 2.8	USFC
off San Pedro Nolasco Is.	137	VELERO III 734-37 AHF(LACM)	29 Mar 1937	4	4		1.8–5.0	AHF
N of Punta Belcher	15	SEARCHER 286 AHF(LACM) 1971-1	31 Oct 1971	1	1		5.4, 5.7	AHF
off San Francisco Is.	91–189	VELERO III 513-36 AHF(LACM)	24 Feb 1936	1			2.7	AHF
24°54′30″N 110°39′00″W	71	ALBATROSS 2999 USNM 16734, 108263, 265356	16 Mar 1888	11	7	11	2.5–5.1	USFC
off Punta Tosca	27	SEARCHER 34 AHF(LACM) 1972-17	1 Feb 1971	2	1	1	2.5–4.4	AHF
24°16′N 110°22′W	38	ALBATROSS 2822 USNM 16732	30 Apr 1888	1			4.3	USFC
San Ignacio Bay, Sinaloa	55–91	VELERO III 742-37 AHF(LACM)	31 Mar 1937			4	3.0–3.1	AHF

Table 9. Continued

Locality	Depth (m)	Station deposition	Date	Sex ♂	♀	ovig. ♀♀	SL (mm)	Collector
22°52′N 109°55′W	57	ALBATROSS 2829 USNM 16733	1 May 1888	10	1	2	3.1–4.8	USFC
Gulf of California	—	HASSLER USNM	28 May 1881	1			4.9	H.E. Nichols
Panamá								
Secas Is.	46	VELERO III 449-35 AHF(LACM)	5 Feb 1935		3	1	2.5–3.1	AHF
07°57′N 78°55′W	60	ALBATROSS 2795 USNM 16731	5 Mar 1888	1			2.7	USFC
Galápagos Islands								
off James Bay, James Is.	55	VELERO III 182-34 AHF(LACM)	24 Jan 1934	3	2		2.0–3.1	AHF
00°29′S 89°54′30″W	717	ALBATROSS 2818 USNM 42614	15 Apr 1888		1		2.2	USFC
E of Wreck Bay, Chatham Is.	59	VELERO III 170-34 AHF(LACM)	21 Jan 1934	1	1	1	1.7–3.6	AHF
Post Office Bay, Charles Is.	27	VELERO III 167-34 AHF(LACM)	19 Jan 1934	2	1		1.5–4.0	AHF
N of Hood Is.	91–189	VELERO III 816-38 AHF(LACM)	29 Jan 1938	2	2		2.0–3.2	AHF

ventral margins each with row of 10–12 strong corneous spines; propodi each with row of small spines and row of corneous spinules on dorsal surface (2nd) or only with row of corneous spinules (3rd), ventral surfaces each with row corneous spinules; carpi each with row of strong spines on dorsal surface; meri of 2nd each with single or double row of spines on ventral surface, 3rd each with short row of spinules on ventromesial margin distally and extending onto mesiodistal margins.

Sternite of 3rd pereopods with anterior lobe narrowly and acutely triangular, terminating in acute simple or bifid spine and with small spines or spinules marginally (males) or terminating subacutely and with margins unarmed (females). Telson with terminal margins of posterior lobes horizontal and slightly convex, each with 4 or 5 strong spines, interspersed with small spinules; posterolateral margins unarmed or with few spinules on left.

Color.—Unknown.

Distribution.—Gulf of California, Mexico, to off Panamá; 37–121 m.

Affinities.—Faxon (1893) compared his species to *M. ungulatus*, but remarked that it was readily distinguished from the latter by the great size of the right cheliped. Since all of Faxon's specimens were males, the shapes of the chelipeds were indeed distinct from the female specimen illustrated by Studer (1883) or the

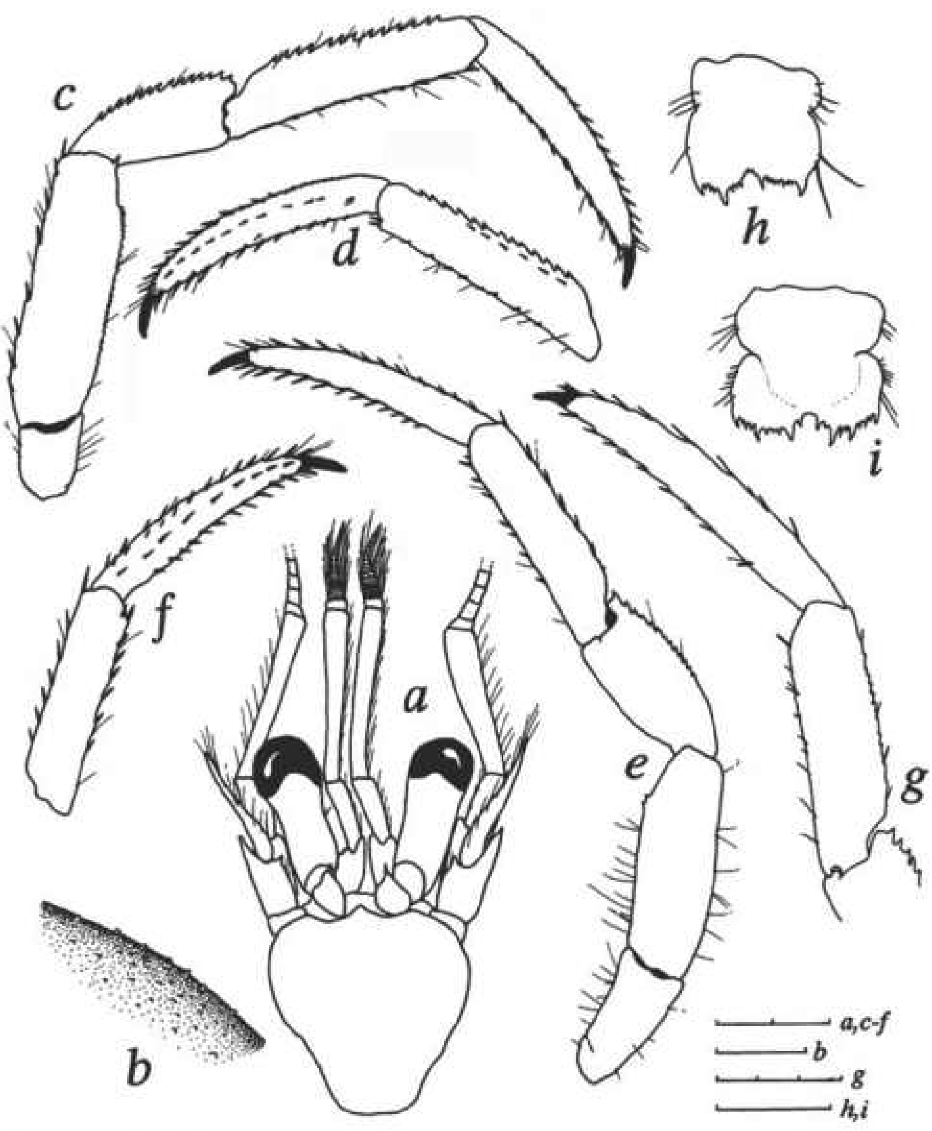

Figure 17. *Manucomplanus longimanus* (Faxon): a, shield and cephalic appendages; b, armature of dorsal surface of palm of right cheliped, dorsomesial view; c, right 2nd pereopod, lateral view; d, propodus and dactyl of same, mesial view; e, left 3rd pereopod, lateral view; f, propodus and dactyl of same, mesial view; g, propodus and dactyl of left 3rd pereopod, lateral view; h, i, telson. Scales equal 2 mm (a, c–f), 0.5 mm (b), 3 mm (g), and 1 mm (h, i). (a, c–f, female, VELERO III 773-38, AHF(LACM); b, g, h, male, "Velero III" 275-34, AHF(LACM); i, female, same station).

small male illustrated by A. Milne Edwards and Bouvier (1893). It would appear that Walton (1954) used this same criterion, plus the addition of the direction of the corneous bristles of the spines, to distinguish between *M. longimanus* and *M. cervicornis*. The former is not a distinguishing character when specimens of similar sizes and sexes are compared; the latter are frequently broken off in preserved material. The only characters at present that appear to distinguish these two taxa are the length-breath relationship and the number of spines on the ventral margins

Table 10. *Manucomplanus longimanus* (Faxon) material examined

Locality	Depth (m)	Station deposition	Date	Sex ♂	Sex ♀	Sex ♀♀	SL (mm)	Collector
Gulf of California and Mexico (Pacific)								
1¼ mi SW of Cabeza Ballena	37	VELERO IV 1725-49 AHF(LACM)	11 Mar 1949	1			4.0	AHF
Tenacatita Bay, Jalisco	46–73	— AHF(LACM)	18 Feb 1938	10	10		2.2–3.2	S.A. Glassell
Acapulco	—	— USNM	Apr 1930			1	2.0	H.N. Lowe
off Navidad Head, near Tenacatita Bay, Jalisco	46–64	275-34 USNM	4 Mar 1934	1		2	2.8–3.1	W.L. Schmitt
Costa Rica (Pacific)								
off San Nuez Is., Cocos Is.	57–91	VELERO III 772-38 AHF(LACM)	13 Jan 1938	3	10	2	1.7–4.7	AHF
off San Nuez Is., Cocos Is.	57–91	VELERO III 773-38 AHF(LACM)	13 Jan 1938		1		3.9	AHF
Chatham Bay, Cocos Is.	73–86	VELERO III 780-38 AHF(LACM)	14 Jan 1938	4	2		2.7–5.2	AHF
Off Panamá (Pacific)								
05°32'45"N 86°54'30"W	121	ALBATROSS 3368 MCZ 4520	28 Feb 1891	5			2.4–5.6	USFC

of the dactyls of the ambulatory legs, and the terminal margins of the telsons. In *M. cervicornis* the dactyls are much shorter and broader than they are in specimens of similar size and sex of *M. longimanus*; the spines on the ventral margins range from 8–10 in the former species and from 10–12 in the latter. In *M. longimanus* the terminal margin of the telson is horizontal (Fig. 17h, i), whereas in *M. cervicornis* the terminal margin is strongly oblique (Fig. 14i).

Protoniopagurus new genus

Diagnosis.—Eleven pairs of phyllobranch gills. Ocular acicles acutely triangular, with simple or bifid terminal spine, and sometimes 1 accessory smaller spine; separated basally by approximate width of 1 acicle. Maxillule (Fig. 1g) with external lobe of endopod slightly produced, not recurved, internal lobe with 2 terminal bristles. Maxilla (Fig. 1h) with proximal lobe of scaphognathite moderately broad. First maxilliped (Fig. 1i) with exopod of moderate breadth basally. Third maxilliped with well developed crista dentata and 1 accessory tooth. Sternite of 3rd maxillipeds with spine on either side of midline.

Chelipeds subequal, right slightly larger, both suboperculate; propodal-carpal articulation approximately 15° (right) to 30° (left) from perpendicular. Sternite of 3rd pereopods with small, subquadrate anterior lobe. Fourth pereopods with rasp of dactyl consisting of few slender corneous scales; no preungual process apparent; propodal rasp of numerous (10–12) rows of long, slender, overlapping corneous scales. Sternites of 4th and 5th pereopods with capsulate setae.

Abdomen short, not flexed. Uropods symmetrical or nearly so; protopods each with prominent, unarmed posterior projection; both rami elongate, slender. Telson with faint transverse suture; posterior lobes not clearly delineated, terminal margin entire, unarmed but with long setae. Males without paired or unpaired pleopods (A. J. Provenzano, Jr., notes). Females with paired first pleopods modified as gonopods, with 3 unpaired pleopods (2nd–4th), with both rami well developed.

Distribution.—Caribbean Sea; 91–585 m.

Etymology.—This genus is named for its discoverer, Dr. Anthony J. Provenzano, Jr., fondly referred to by his carcinological students as "Tony Pro."

Remarks.—We have not personally been able to examine the male specimen of the only species in this genus; however, A. J. Provenzano's notes and figures indicate that pleopods are lacking and no sexual tubes are present. *Protoniopagurus* n. gen. differs from all other pylopagurid-like genera in several characters, the most important of which are the absence of all pleopods in the males, and loss of the unpaired 5th pleopod in the female. The phenomenon of loss of male pleopods has arisen independently several times in the Paguridae, e.g., *Pagurus prideaux* Leach; *Paguridium* Forest. Loss of male pleopods and the accompanying reduction of female pleopods has been reported in species of *Paguritta* Melin (cf. McLaughlin and Lemaitre, 1993); *Ostraconotus* A. Milne Edwards, *Porcellanopagurus* Filhol, *Solitariopagurus* Türkay, *Alainopagurus* Lemaitre and McLaughlin (cf. Lemaitre and McLaughlin, 1995; Poupin and McLaughlin, 1996); and *Forestopagurus drachi* (Forest) (cf. García-Gómez, 1994). The well calcified, laterally expanded shield, the distinctively developed propodal rasps of the 4th pereopods, and the elongate uropodal rami with posteriorly produced protopods are suggestive of a specialized habitat (e.g., Lemaitre, 1993, 1994); however, habitat data for *Protoniopagurus* n. gen. are not as yet available.

The phylogenetic relationship of *Protoniopagurus* n. gen. to other pylopagurid-like genera is seen particularly in the paired female first pleopods modified as gonopods. In having the dorsal surfaces of the chelae covered with low spinose or tuberculate, mushroom-shaped tubercles with erose margins, *Protoniopagurus* n. gen. bears some similarity to *Agaricochirus erosus* (A. Milne Edwards). A further relationship with *Agaricochirus* McLaughlin, is suggested by the short, straight, somewhat inflated abdomen, and the development of the telson. As in *Agaricochirus*, the transverse suture in *Protoniopagurus* n. gen. is very faintly delineated; the median cleft of the terminal margin is indicated only by a very slight depression.

Protoniopagurus bioperculatus new species
Figures 18, 19

Holotype.—♀♀ (SL 6.0 mm), USNM 267686; type locality: off west coast of Puerto Rico, JSDS 37, 18°11′55″N, 67°42′50″W.

Material Examined.—See Table 11.

Description.—Shield very well calcified, appreciably broader than long; anterior margin between rostrum and lateral projections slightly concave; anterolateral margin sloping and extending laterally onto upper fourth of lateral surface; posterior margin roundly truncate; dorsal surface with scattered tufts of short to moderately long setae. Rostrum broadly triangular, rounded or with acute terminal spine. Lateral projections obtusely triangular, with prominent terminal marginal spine. Ocular peduncles approximately 3/4 shield length; corneae not noticeably

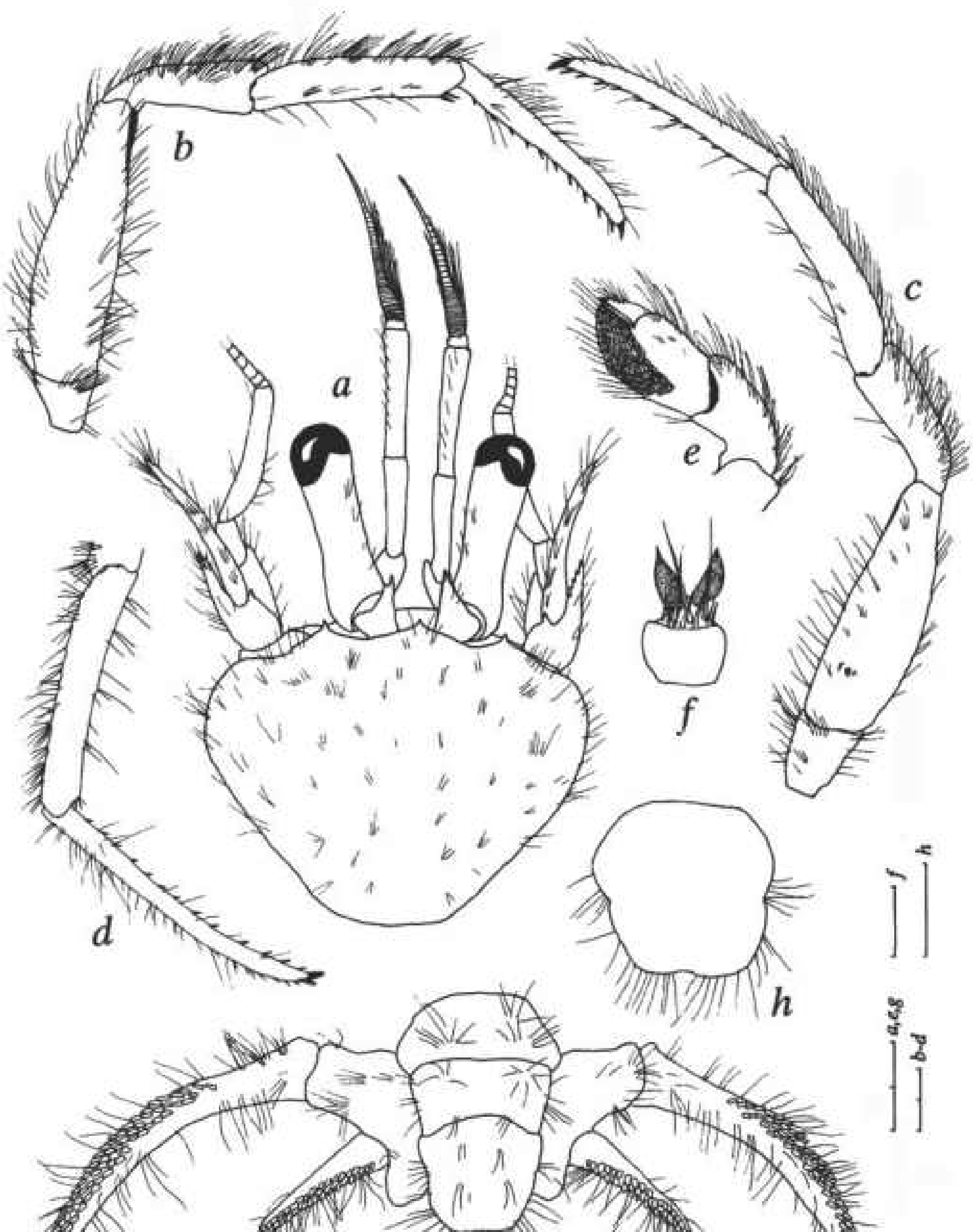

Figure 18. *Protoniopagurus bioperculatus* n. gen., n. sp.: a, shield and cephalic appendages; b, right 2nd pereopod, lateral view; c, left 3rd pereopod, lateral view; d, propodus and dactyl of 3rd left pereopod, lateral view; e, carpus, propodus, and dactyl of left 4th pereopod, lateral view; f, anterior lobe of sternite of 3rd pereopods; g, 6th abdominal segment, uropods, and telson. Scales equal 2 mm (a–d, e, g), 0.5 mm (f), and 1 mm (h). (a–c, e, g, h, female, OREGON 4834, USNM 267687; d, male, GERDA 952, [deposition unknown]; f, female holotype, JSDS, 37, USNM 267686).

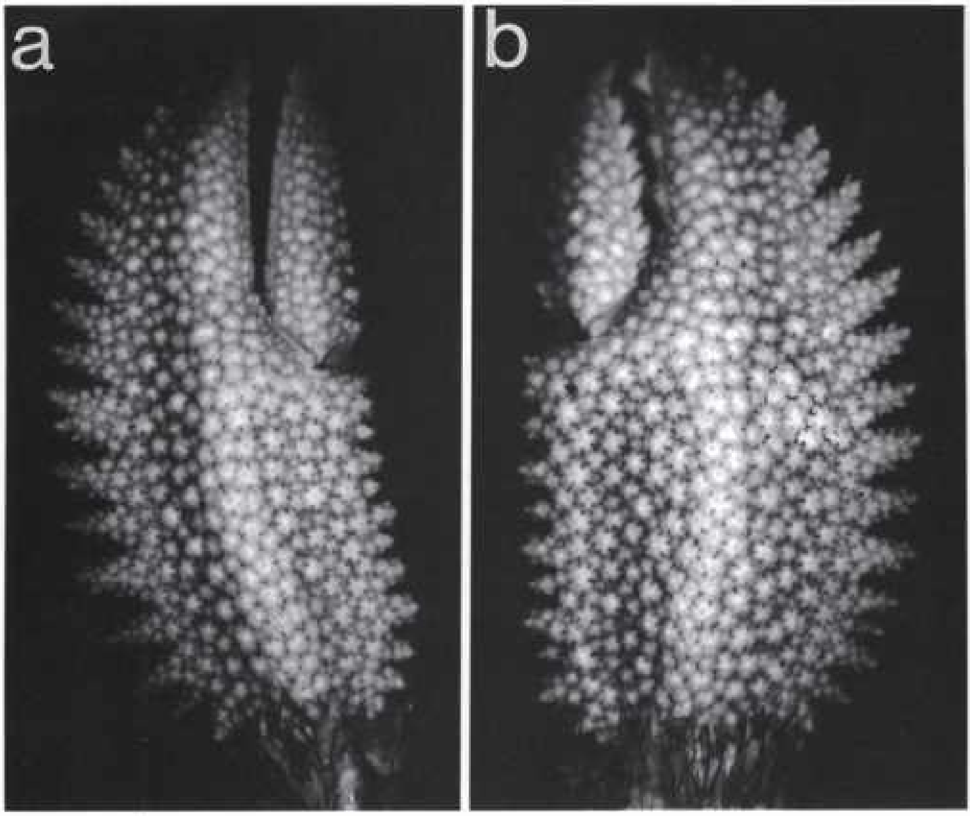

Figure 19. Chelae of *Protoniopagurus bioperculatus* n. gen., n. sp.: a, left (5.0×); b, right (5.9×). (Female, OREGON 4834, USNM 267687).

dilated, few tufts of setae on dorsomesial face; ocular acicles moderately long and acutely triangular, terminating in strong, simple or bifid spine and with lateral spine or spinule; separated basally by approximately entire length of 1 acicle.

Antennular peduncles overreaching ocular peduncles by half length of ultimate segment; ultimate segment with row of setae on dorsal surface; penultimate and basal segments unarmed.

Antennal peduncles slightly overreaching ocular peduncles. Fifth, 4th and 3rd segments unarmed but with few scattered setae. Second segment with dorsolateral

Table 11. *Protoniopagurus bioperculatus* n. gen., n. sp. material examined

Locality	Depth (m)	Station deposition	Date	Sex ♂	Sex ♀	Sex ♀♀	SL (mm)	Collector
Caribbean								
21°02′N 86°26′W	91–585	GERDA 952 —	28 Jan 1968	1			7.8	RSMAS
18°11′55″N 67°42′50″W	329	JSDS 37 USNM 267686	10 Feb 1933			1	6.0	—
14°15′30″N 80°28′30″W	274–293	OREGON 4834 USNM 267687	12 May 1964		1		6.4	NMFS

distal angle produced, terminating in small spine and with 2 spines on mesial margin; dorsomesial distal angle with prominent spine. First segment with strong spine on ventrolateral surface. Antennal acicle slightly arcuate, slightly overreaching distal margin of cornea, terminating in small spine and with tufts of setae on mesial and lateral surfaces. Antennal flagella long, with 1 or 2 long setae every 4–12 articles and occasional shorter setae.

Right cheliped elongate, but only slightly longer and stronger than left; chelae dorsoventrally compressed. Dactyl of right chela slightly shorter than palm, with row of irregular simple and/or multidentate spines, strongest proximally, dorsal surface slightly elevated in midline, almost fully covered with flattened or weakly spinulose, mushroom-shaped tubercles, most with erose margins; cutting edge with row of strong calcareous teeth, terminating in strong calcareous tooth; ventral surface with scattered tufts of setae and with 2 auxiliary rows of small calcareous teeth of denticles adjacent to cutting edge. Palm nearly twice length of carpus; dorsomesial margin with row of strong, usually trifid spines, dorsolateral margin with similar row of spines, decreasing in size and extending to distal end of fixed finger; dorsal surface of palm and fixed finger elevated in midline, surfaces entirely covered with closely-spaced, flattened, tuberculate or spinose, mushroom-shaped tubercles, most with erose margins; cutting edge of fixed finger with row of strong, calcareous teeth, terminating in strong calcareous tooth, dorsomesial margins of palm and dactyl and dorsolateral margins of palm and fixed finger each with row of tufts of setae; lateral and ventral surfaces of palm and fixed finger with scattered tufts of setae. Carpus short, approximately 2/3 length of merus; dorsomesial margin with raised, short, transverse, spinulose and setose ridges proximally and strong spine distally, dorsodistal margin laterally and medially each with cluster of spines, dorsodistal margin laterally with 1 strong and few small spines, dorsal midline with longitudinal row of short, transverse, sometimes spinose ridges and tufts of setae, dorsal surface laterally with numerous low, short, transverse ridges and setae, dorsolateral margin not delimited; ventral, proximal, ventrolateral, and ventromesial margins with continuous row of small, blunt spines or tubercles. Merus subtriangular; dorsal margin with row of short transverse ridges and short setae; lateral face with few short transverse ridges and setae distally and ventrally, ventrolateral margin with row of strong acute spines; mesial face with scattered setae, ventromesial margin with row of very small spinules or tubercles; ventral surface minutely spinulose. Ischium with row of spinules and scattered setae on ventromesial margin.

Left cheliped elongate; dactyl approximately equaling palm in length; dorsomesial margin with row of moderately strong, usually simple spines, dorsal surface covered with closely-spaced, raised, mushroom-shaped tubercles, usually with erose margins; cutting edge with few small calcareous teeth at proximal angle and row of small, corneous teeth distally, terminating in calcareous tooth with small corneous tip. Dorsolateral margin of palm and fixed finger with row of strong relatively long, multidentate spines, decreasing in size on fixed finger, dorsal midlines elevated, dorsal surfaces covered with closely-spaced, flattened, spinulose or tuberculate, mushroom-shaped tubercles, most with erose margins, dorsomesial margin of dactyl and palm and dorsolateral margins of palm and fixed finger with tufts of setae; ventral surfaces of palm, fixed finger and dactyl with scattered tufts of setae, short row of denticles on inner margins of latter; cutting edge of fixed finger with row of small calcareous teeth, terminating in stronger calcareous tooth. Carpus short, approximately 2/3 length of merus; dorsomesial margin with row of strong spines, dorsomesial distal angle with cluster of strong spines, dorsodistal margin mesially and laterally each with 1 strong spine and 1 or 2 small spines, dorsal midline with short, transverse, occasionally spinulose ridges and setae, dorsolateral margin not delimited; lateral surface with short transverse ridges and setae in distal half; ventral, mesial, and lateral distal margins with continuous row of spines, strongest laterally. Merus subtriangular; dorsal margin with row of short transverse ridges and setae; ventrolateral margin with row of strong, acute spines, ventromesial margin with row of quite small spines, ventral surface minutely spinulose. Ischium with row of spinules on ventromesial margin.

Ambulatory legs similar from left to right. Dactyls long, slender, equaling or slightly longer than propodi; dorsal surfaces each low protuberances and tufts of short or long stiff setae; mesial faces each with row of small corneous spines dorsally; lateral faces with few corneous spinules near dorsal margins; ventral margins each with 10–12 corneous spines. Propodi 1/4 to 1/3 longer than carpi; dorsal surfaces each with low protuberances and tufts of stiff setae; mesial and lateral surfaces with scattered setae; ventral margins with 1 or 2 corneous spines at distal margins. Carpi with dorsodistal margins unarmed, dorsal and lateral faces dorsally with short transverse rows of stiff setae. Meri approximately twice length of carpi; unarmed, but with tufts of setae dorsally, ventrally and laterally. Ischia with few tufts of setae. Fourth pereopods with slender dactyls armed with few corneous spinules distally; propodal rasp of numerous rows of overlapping long, slender scales.

Sternite of 3rd pereopods with subquadrate anterior lobe, unarmed, but with capsulate setae. Sternites of 4th and 5th pereopods with capsulate setae. Telson with weakly marked transverse suture; posterior lobes with median cleft marked only by very faint concavity, terminal margins horizontal, unarmed, but with long setae.

Color.—Dactyls, propodi and carpi of ambulatory legs longitudinally striped orange and white (A. J. Provenzano, Jr., notes).

Distribution.—Caribbean Sea: so far known only from the western Caribbean, and west of Puerto Rico; 91–585 m.

Etymology.—The name "bioperculatus" reflects the operculate structure of both chelipeds of this species.

Affinities.—*Protoniopagurus bioperculatus* is a singularly distinct species; however, as previously indicated it shares a few characters with species of *Agaricochirus.* For example, the erose mushroom-shaped tubercles of the chelae are similar to those of *A. erosus*; the general configuration of the left chela resembles that of *A. alexandri* (A. Milne Edwards and Bouvier).

Acknowledgments

This study could not have been successfully completed without the cooperation and help of the curators of the several museums and/or institutions that made their collections available for study, and to them all we express our gratitude. We owe special acknowledgement and thanks to Dr. Anthony J. Provenzano, Jr., whose work with western Atlantic hermit crabs continues to provide the foundation for all regional studies; who first recognized the majority of the new species described herein, and whose artists provided invaluable morphological information and documentation on coloration. Photographs are the work of E. J. McGeorge. This is a scientific contribution from the Smithsonian Marine Station at Link Port, Fort Pierce, Florida (number 377), and Shannon Point Marine Center, Western Washington University.

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