

Fig. 136. *Dardanus fucosus* Biffar and Provenzano. Male: *a*, anterior part of body in dorsal view; *b*, left chela and carpus, external view; *c*, second left walking leg, propodus and dactyl, lateral view; *d*, same, dactyl, ventral view; *a-d*, 5 mm indicated (USNM 103342).

Variation.—Prominence of surface ornamentation varies individually and increases somewhat with age. Variations include tuberculation of the major palm, and density of the fringe of setae and tuberculation of the external surface of the second walking leg (Biffar and Provenzano 1972).

Color.—Palm of large cheliped basically purple or reddish purple, tubercles dark purple or blue. First and second walking legs with narrow bands of brown-orange on merus, carpus, and propodus, width of band on carpus or propodus about 0.2–0.3 length of segment. Cornea, in life, bluish or greenish with broad black bar running horizontally when viewed from front (paraphrased from Biffar and Provenzano 1972).

Habitat.—The species occurs on a variety of mud, shell, and coral bottoms at depths ranging from that of an eel grass bed in the moat at Ft. Jefferson, Loggerhead Key, Tortugas, to 134 m off Tobago (Young 1978 reported it to 365 m). Specimens from the Carolinas are often in the bryozoan, *Hippoporida*, “Texas longhorn shells” (Deichmann 1954).

Type-locality.—Off French Guiana-Brazil border, 5°29'N, 51°37'W, 64 m, Oregon Stn. 4202.

Known range.—Near Cape Hatteras, N. C., 35°02'N, 75°26'W, to off Amapá, extreme northern Brazil, 4°2'N, 50°33'W.

Remarks.—*Dardanus* contains species of such remarkable similarity that identification is a problem. The newly described *D. fucosus* was formerly called *D. venosus*, which is a strictly tropical western Atlantic species (Biffar and Provenzano 1972). These authors pointed out morphological differences in both adults and larvae. The best character for separating adults is presence of a shallow ventral groove on the dactyl of the second left walking leg in *D. fucosus*, and lack of this in *D. venosus*. Nowhere in the Carolinian Province should the two species normally occur together.

Ovigerous females are known more or less year round: in February from the Guianas and extreme northern Brazil, May from Guyana, June from Florida, July from Panama to French Guiana, September from North Carolina and the Guianas, October from Venezuela, and in November from extreme northern Brazil (Biffar and Provenzano 1972), also July to September in Georgia.

The glaucothoe described by Provenzano (1963b) as that of *Petrochirus diogenes* was later found to be *D. fucosus* (Provenzano 1968; Biffar and Provenzano 1972).

Dardanus insignis (Saussure)

Fig. 137

Pagurus insignis Saussure 1858:453, pl. 3, figs. 20, 20a.

Dardanus insignis.—Verrill 1908a:446, text-fig. 60; pl. 26, figs. 4b, c, 5b.—Williams 1965:124, fig. 100.

Recognition characters.—Anterior shield of carapace longer than width of front, with scattered clumps of setae, roughened slightly near anterior and anterolateral margins. Anterior margin lacking rostrum; lateral projections on front triangular, thickened, prominent, surmounted by blunt spinule, and hairy on frontal edge. Eystalks stout, slightly constricted in middle, exceeding tips of antennal peduncles, tuft of hairs at base of dilated cornea; eye scales prominent, well separated, serrated distally with strong mesial pair of spines separated somewhat from smaller more lateral series of 4 spines by notch often obscured by tuft of setae. Antennal peduncles somewhat exceeding eystalks. Acicles long, reaching to base of cornea, with few spines and hairs arranged in spiral line

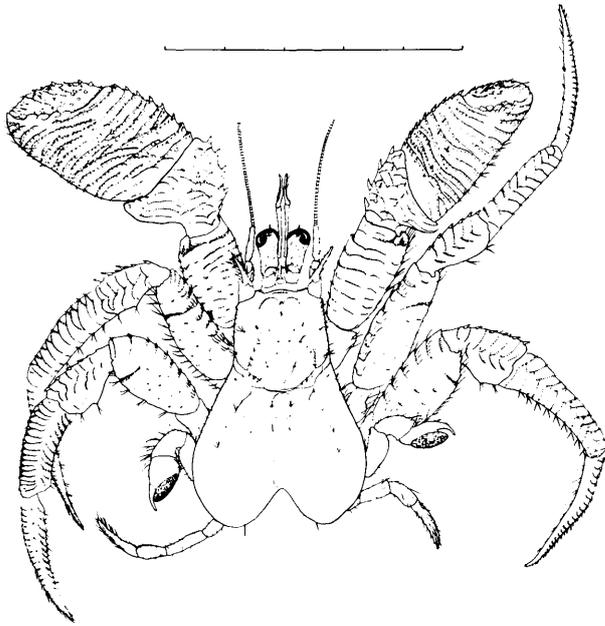


Fig. 137. *Dardanus insignis* (Saussure). Anterior part of male in dorsal view, 5 mm indicated (from Williams 1965).

originating on inner surface at base and curving across dorsal surface to termination on lateral surface near tip.

Chelipeds heavy, left larger than right, covered with ciliated, tuberculate rugosities becoming bolder and more diagonal distally on hands and fixed fingers; dactyl of major chela with ciliated rugosities somewhat diagonal, those on minor dactyl irregularly arranged; opposed edges of fingers with heavy white teeth, tips dark; spine on crest of meri, outer surface of carpi, and hands, largest spines on upper mesial border; row of spines on lower mesial border of merus and ischium. Walking legs (legs 2 and 3) strong, with rugose pattern similar to chelipeds and forming herringbone pattern on outer surface of propodus of large second left walking leg; dactyls of walking legs with crest of spines dorsally, that of left second with crest of spines also ventrally and continued on propodus.

Measurements in mm.—Anterior shield: male, length 17.5, width 15.5; ovigerous female, length 10.6, width 10.6.

Color.—Ground color yellowish; rugosities tan near body becoming maroon on chelipeds and first two pairs of walking legs distally, proximal rugae on hands with reticulate maroon pattern on yellowish background; anterior shield mottled tan; eyestalks banded alternately with maroon, yellow, and tan.

Habitat.—In both shells and calcareous worm tubes (Hazlett 1966); some specimens have been found in the bryozoan "Texas longhorn shells"

(Deichmann 1954); 22 to 260 m (Wenner and Boesch 1979; Wenner and Read 1982).

Type-locality.—Guadeloupe.

Known range.—Off Oregon Inlet, N. C., 31 m (Cerame-Vivas, et al. 1963), to Port Aransas, Tex.; through West Indies to Guadeloupe.

Remarks.—Until the above northern record, another NE of Cape Hatteras, 35°21'N, 74°53'W, 101 m (Musick and McEachren 1972) and a third on the reef SE of Cape Lookout, 70–90 m (Cain 1972) were established, this species was known only from beyond the 183-m curve in the Carolinas. Ovigerous females are known from Georgia in June, and Florida in March, April, June–August.

Provenzano (1963b) described the glaucothoe stage of *D. insignis* in plankton from south Florida, comparing it to glaucothoes of similar species. Hazlett (1966a) described aspects of the behavior of *D. insignis*, an active species, comparing cheliped and leg displays, body posture and shell fighting to those of *Petrochirus diogenes*. Kellogg (1971) observed *D. insignis* kill and remove a *Fasciolaria hunteri* from its shell prior to using the shell for new housing.

Genus *Petrochirus* Stimpson 1858

Stimpson 1858:233 (71).

Petrochirus diogenes (Linnaeus)

Fig. 138

Cancer Diogenes Linnaeus 1758:631.

Petrochirus bahamensis.—Hay and Shore 1918:410, pl. 30, fig. 6.—Schmitt 1935a:206, fig. 66.—Provenzano 1959:378, fig. 8.—1961:153.

Petrochirus diogenes Holthuis 1959:151.—Williams 1965:122, fig. 98.—Provenzano 1968:147, figs. 1–12.

Recognition characters.—Anterior shield of carapace flattened, about as broad as long, rough, uneven, and with scattered tufts of hairs; front trilobate, rostrum about as long as lateral projections. Eyestalks straight, moderately dilated distally, with tuft of setae above corneal surface and scanty tufts along length; eye scales broad basally, acute anteriorly with indistinct serrations. Antennular peduncles equaling or exceeding eyestalks. Antennal peduncles shorter than eyestalks; acicle slender, hairy, and minutely spined.

Chelipeds massive, subequal, right slightly larger; hands and carpi coarsely roughened with grouped tubercles separated by appressed setae on upper and, to some extent, lower surfaces, becoming spi-

nose along inner margin; fingers opening obliquely, major chela with fingers tuberculate on crushing edges, minor chela with fingers somewhat spooned, cutting edges sharp, tips corneous. Walking legs (legs 2 and 3) with carpus ornamented above as chelae; propodi similar with clusters of hairs beneath; dactyls with slightly twisted rows of spines and dense setae; propodi and carpi, especially of first walking legs, with dorsal row of dark-tipped spines.

Measurements in mm.—Anterior shield: male, length 36, width 34; female, length 20, width 20.

Color.—Generally reddish; chelipeds reddish except between fingers, and white spots on carpal articles; antennal and antennular peduncles longitudinally striped with red and white, antennal flagella transversely banded with red and white (Provenzano 1959).

Habitat.—Mud, mud and shell, and sand bottoms. Common on shrimping grounds near Tortugas, Fla. (Provenzano 1959), off Mississippi between 18 and 92 m (Franks, et al. 1972), in the western Gulf of Mexico (Hildebrand 1954, 1955), and southeast of Cape Lookout, N. C., in about 33 m, but young are found also in Beaufort, N. C., harbor (Kellogg 1971); in *Thalassia* beds in Belize (B. Kensley, personal communication); to 128 m off South Carolina (Wenner and Read 1982).

Type-locality.—Near shores of Bahama Islands (Catesby 1743 [1754 ed. in Holthuis 1959]).

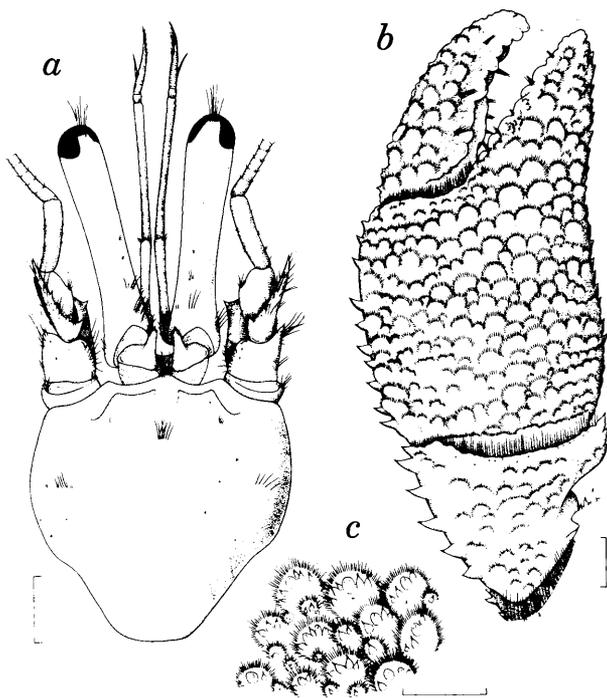


Fig. 138. *Petrochirus diogenes* (Linnaeus). Female: *a*, anterior part of body in dorsal view; *b*, right chela and carpus, external view, and *c*, grouped tubercles enlarged; *a-c*, 5 mm indicated (USNM 136870).

Known range.—Off Cape Lookout, N. C., through Gulf of Mexico and West Indies to off Ilha de São Sebastião, Brazil, 23°42.5'S, 45°14.5'W (Forest and de Saint Laurent 1967).

Remarks.—The genus *Petrochirus* has a reported fossil record extending from the Cretaceous to the present in North America (Rathbun 1935). Toulou (1911) considered the Miocene form from Panama to be conspecific with the living species in the West Indies region, but Rathbun (1918a) considered it as distinct (*P. bowwieri*) and possibly ancestral to the modern species.

Petrochirus diogenes is the largest hermit crab in the Carolinian fauna and this feature, plus its coarsely tuberculate, ruddy appendages, makes it conspicuous. The species inhabits tun and murex shells on the North Carolina scallop ground offshore, but the young in harbor channels are usually in *Polynices* or *Terebra dislocata* shells in poor condition (Kellogg (1971). Kellogg observed a *P. diogenes* inhabiting a tun shell tear off the operculum of a *Busycon carica*, kill the mollusk and remove it from its shell in 24 hours and then adopt the shell as new housing. Caine (1975) found that scavenged material constituted 45%, prey 40% of diet, plus algae which may or may not be incidentally ingested. Kensley (personal communication) observed *P. diogenes* sifting through coarse sediments in Belize, and feeding on the exposed polychaetes. A common commensal is the porcellanid crab, *Porcellana sayana*, and other commensals on the shells carried by the crab, such as *Crepidula plana* (Say), bryozoans (*Scrupocellaria* sp.), tubicolous worms (*Hydroides* sp. and *Spirorbis* sp.) as well as other species, are mentioned by Pearse (1932b). An association between the sea anemone *Calliactis tricolor* in this and other crabs was discussed by Cutress and Ross (1969), and Cutress, et al. (1970) from studies in Puerto Rico. Randall (1967) reported *P. diogenes* from stomach contents of the Nassau grouper, *Epinephelus striatus*.

Ovigerous females are known in March from the Virgin Islands (Provenzano 1961), June from Texas, and in August from west Florida (Provenzano 1968). The complete larval development, showing some adaptability to environmental conditions, has been studied in the laboratory (Provenzano 1968). Five or six zoeal stages and a glaucothoe were described. Starved stage I larvae were not able to survive to molt to the next stage, but they survived longer at 20°C than at higher or lower temperatures. At 10° and 15°C larvae fed *Artemia* were also unable to molt and died in about the same time as starved siblings; but at 20°, 25°, and 30°C, fed larvae molted and grew. Viable glaucothoes were not obtained at 20°C; at 25°C they were obtained after

five and six zoeal stages, and at 30°C nearly all glaucothoes developed after five zoeal stages. At all temperatures the first zoeae had a longer mean duration than immediately following stages, but duration increased again in last stages, reaching a maximum in the glaucothoe. Duration of zoeal stages was 50 days at 20°C, and 25 days at the higher temperatures used. Potential planktonic life is estimated to vary from 31 to 43 days at 30°C, 37 to 50 days at 25°C, and 72 to 84 days at 20°C.

Pearse (1932a) determined the freezing point of *P. diogenes* blood (range -1.90° to -2.32°C).

Holthuis (1959) reviewed the complex nomenclatural history of the species, designated the type, restricted the type-locality, and outlined the geographic range.

Genus *Paguristes* Dana 1852

Provenzano 1959:381.—China 1966:256.—Forest and de Saint Laurent 1967:67.

Diagnosis.—Rostrum usually well developed. Eyestalks long and usually slender; eye scales usually spiniform. Chelipeds equal or subequal, left may be somewhat larger; fingers in horizontal plane, tips usually corneous, occasionally calcareous. Fourth legs with dactyl terminal, fifth pair chelate. Male with pair of modified uniramous pleopods on first 2 abdominal segments; female with pair of uniramous pleopods on first abdominal segment only.

Key to Species

(After Provenzano 1959)

1. Rostrum broadly rounded or pointed, but not advanced beyond level of lateral projections on front of anterior shield of carapace 2
Rostrum slender and definitely advanced beyond level of lateral projections on front of anterior shield of carapace 4
2. Eye scales separated, ending in an acuminate tip 3
Eye scales adjacent, ending in more than 1 terminal spine *P. hummi*
3. Anterolateral sides of anterior shield of carapace not spiny *P. lymani*
Anterolateral sides of anterior shield of carapace definitely spiny *P. moorei*
4. Anterior shield of carapace not noticeably longer than broad 5
Anterior shield of carapace noticeably longer than broad 6
5. Anterior and lateral margins of shield meeting at almost right angle
. *P. sericeus*
Anterior and lateral margins of shield meeting at broadly obtuse or rounded angle *P. triangulatus*
6. Eye scales ending in acuminate tip *P. spinipes*
Eye scales ending in more than 1 terminal spine *P. tortugae*

Paguristes hummi Wass

Fig. 139

Paguristes hummi Wass 1955:148, figs. 1–4.

Recognition characters.—Anterior shield of carapace longer than wide, surface with few setose tubercles. Rostrum obtuse and shorter than lateral projections, each projection often surmounted by minute spinule. Eyestalks slender, slightly constricted in midlength; eye scales mesially adjacent except for shallow indentations near bases and variably divergent tips armed with 4–7 spines anterolaterally, largest spine at tip. Antennular peduncles reaching almost to tip of eyestalks; acicles with 5 spines on inner margin, smooth laterally.

Chelipeds equal, similar, moderately spined, and

ornamented with plumose hairs longest and most dense at margins of hands; hands twice as long as wide, armed with longitudinal rows of spines on upper surface, outer marginal row with many more spines than intermediate and mesial ones; fingers agape slightly, opposed edges with few small teeth and calcareous denticles, tips corneous; carpus with spine on margins longest and densest distally; merus crested dorsally with spinules and plumose hairs. Walking legs (legs 2 and 3) with propodi $\frac{3}{4}$ length of dactyls, propodus and merus of first pair crested with spinules, second pair with tubercles only; both pairs hairy except for lateral surfaces of meri and inner surfaces of propodi.

Measurements in mm.—Anterior shield: male, length 3.8, width 3.4; ovigerous female, length 2.2, width 2.0.

Variation.—The largest specimen in the USNM collection (paratype 95594, Alligator Harbor, Fla.) is much less ornamented with spines and hairs on the chelae than is normal for other specimens in the series.

Color.—Most distinguishing mark, merus of cheliped with blue patch on inner surface bordered anteriorly by a narrow black line, followed by a similar yellow line (Wass 1955).

Habitat.—Usually found in small sponges, occasionally in *Murex*, and also in the bryozoan "Texas longhorn shell," *Hippoporidea edax*. At the mouth of Tampa Bay, Wass (1955) found it in intertidal pools in mid-October only on the south side of Mullet Key, housed in a variety of small gastropod shells, mostly *Terebra*, but some in *Olivella*, and one in a scaphopod shell.

Type-locality.—Alligator Harbor, Franklin County, Fla.

Known range.—Newport River, N. C., to off Sapelo Island, Ga.; Marco Beach, southwestern Fla., to off Isles Dernieres, La. (28°38'N, 90°55'W); intertidal to 22 m.

Remarks.—Two males, paratypes of nearly identical size (USNM 95595), occur side by side in the same opening of a sponge from Alligator Harbor, Fla. The species is found occasionally in Beaufort, N. C., harbor in shells of *Terebra dislocata* with a

good deal of fouling attached, primarily in shelly areas. It is much more abundant offshore there on rocky outcrops where a variety of sponges and algae thrive, and may feed primarily on algae (Kellogg 1971).

Ovigerous females are known from southwest Florida in February (Provenzano 1959) and northwest Florida in October (Wass 1955).

***Paguristes lymani* A. Milne Edwards and Bouvier**

Fig. 140

Paguristes lymani A. Milne Edwards and Bouvier 1893:49, pl. 4, figs. 13–22.—Williams 1965:116, fig. 92.

Recognition characters.—Anterior shield of carapace slightly broader than long, sides a little hairy and roughened by spiny granules. Rostrum often a rounded lobe falling far short of pointed lateral projections; anterior margin thickened and rounding gradually to lateral margins from lateral projections, posterolateral corners apparently notched in adults. Eystalks somewhat dilated at base and longer than distance between apices of lateral projections of front; eye scales singly acuminate or with up to 3 unequal spines on anterior border, long hairs somewhat obscuring tip. Antennular peduncles highly variable, exceeding eystalks by less than half to entire length of terminal article. Tips of antennular peduncles extending $\frac{2}{3}$ – $\frac{3}{4}$ length of eystalks, slightly exceeding acicles; acicles terminated by spiny fork and often with 3 to 5 spinules on internal or external borders, external spine at base of acicle also spinulose on outer margin.

Chelipeds subequal and similar; hands about twice as long as broad, upper surface covered with rather large, well separated, tubercular granules, many with corneous tips, 4 spines on internal margin of palm; lower margin of palm concave at base of fixed finger; fingers slightly agape, terminated by corneous tips preceded by finely denticulate cutting edges, dactyl with 4 or 5 small teeth behind corneous portion; carpus with 3 rows of spines on upper surface, 4 or 5 larger ones on inner margin, about 6 on outer margin (distalmost largest), and about 6 more on upper surface near inner margin; superior border of merus armed with more or less pointed projections, feebly rugose externally; spines on palm, carpus and merus obscured by long hairs. Walking legs (legs 2 and 3) with long hairs, particularly on upper and lower borders of dactyls; spines on crest of carpus, propodus and base of dactyl, and somewhat reduced ones on inner and outer

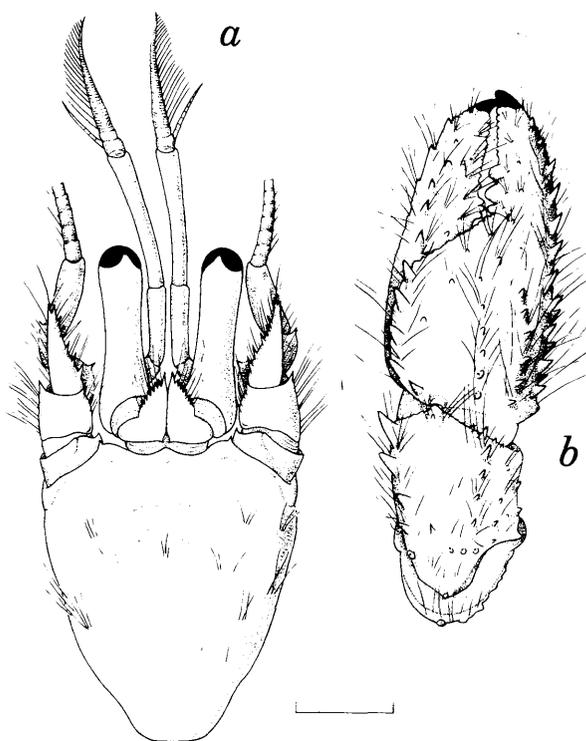


Fig. 139. *Paguristes hummi* Wass. Male: a, anterior part of body in dorsal view; b, right chela and carpus, external view; paratype, 1 mm indicated (USNM 98954).

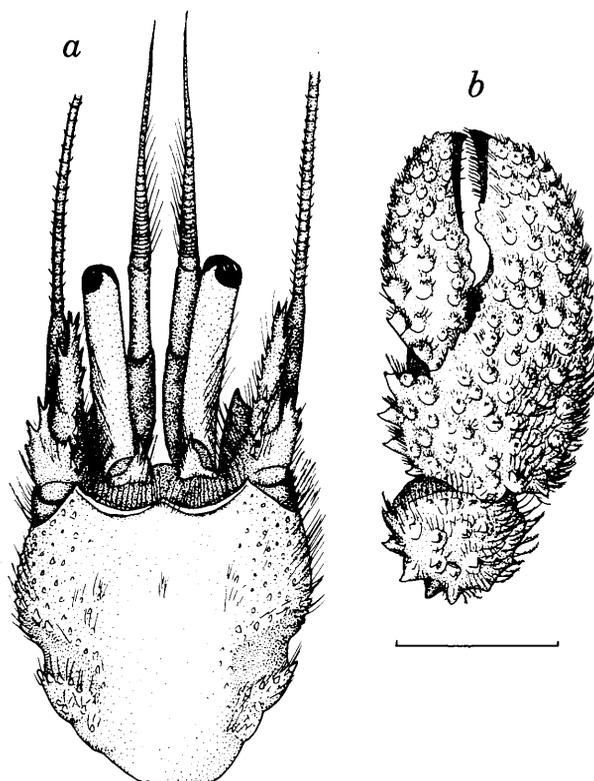


Fig. 140. *Paguristes lymani* A. Milne Edwards and Bouvier. *a*, Anterior part of body in dorsal view; *b*, right chela and carpus, external view; 5 mm indicated (from Williams 1965).

sides of propodus and carpus where rows appear mixed with hairs; dactyls arched, somewhat shorter than combined length of 2 preceding articles, and each terminated by conical claw.

Measurements in mm.—Anterior shield: male, length 7.5, width 7.9; ovigerous female, length 6.4, width 7.0.

Variation.—The spination of the chelipeds may vary in strength and density. Length of the antennular peduncles, in relation to the eyestalks, is highly variable. The eye scales become more dentate with age. The rostrum and lateral projections of the front may reach a common level, and small individuals tend to be hairier than large ones (Milne Edwards and Bouvier 1893). Proportion of the anterior shield changes with age; in young individuals it may be longer than wide.

Habitat.—Museum and published records show that this species has been found housed in small to medium-sized shells belonging to the families Cassididae, Dentaliidae, Nassariidae, Ovulidae, Muriidae, Trochidae, Turridae, and Volutidae; 27 to 1600 m.

Type-locality.—Sand-Key [Fla.], 27 m.

Known range.—Southeast of Cape Lookout, N. C. (150–180 m); Florida Keys to Swan Island off Honduras; through West Indies to Guyana.

Remarks.—Ovigerous females have been taken in February from North Carolina and Florida, May and June from Florida, and November from Guyana.

Paguristes moorei Benedict

Fig. 141

Paguristes moorei Benedict 1901c:144, pl. 4, fig. 3.—Williams 1965:115, fig. 91.

Recognition characters.—(Taken from female holotype.) Anterior shield of carapace slightly longer than broad; upper surface of carapace with few scattered hairs and irregular punctations, more or less iridescent. Rostrum short, obtusely pointed, slightly less advanced than more acute lateral projections. Eyestalks slender, slightly dilated distally, slightly longer than width of anterior shield (8.6 mm); eye scales not adjacent, anterior process acute. Antennular peduncle slightly exceeding eyestalk when extended. Antennal peduncle extending slightly beyond middle of eyestalk; flagellum not exceeding tips of legs, with scattered setae; acicles bispinose at tip (right spine on right acicle broken), row of 4 strong spines on proximal $\frac{2}{3}$ of inner side (right acicle with single external spine).

Chelipeds subequal but of similar form, mesial margins nearly straight; hands short and thick,

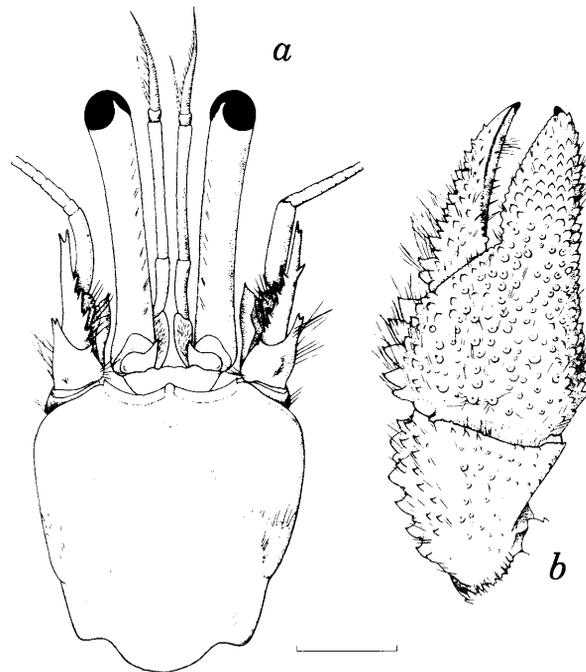


Fig. 141. *Paguristes moorei* Benedict. Female: *a*, anterior part of body in dorsal view; *b*, right chela and carpus, external view; 3 mm indicated (USNM 29207, holotype).

covered dorsally with many tubercles and hairs, but nearly smooth ventrally, row of strong spines on upper mesial border of palm, edges of fingers fitting closely; carpus similar to hands but with fewer tubercles in 2 rows, largest tubercles on mesial upper border; merus prismatic with tubercles on angles. First walking legs (leg 2) with row of spines along upper margin of carpus and propodus.

Measurements in mm.—Anterior shield: holotypic female, length 8.5, width 8.3.

Color.—Yellowish, eyestalks deep orange or crimson below and white above (Hay and Shore 1918).

Habitat.—From near edge of continental shelf.

Type-locality.—Puerto Rico.

Known range.—Edge of continental shelf off Cape Lookout, N. C.; Florida Straits (Hazlett 1966a); Puerto Rico.

Remarks.—*Paguristes moorei* was recorded by Cerrame-Vivas and Gray (1966) as a tropical form occurring off North Carolina. Hazlett (1966a) noted aspects of behavior, comparing the species' displays with those of *P. spinipes* as most active at 15°C, and shell fighting as similar to that of *Clibanarius anomalus*.

Paguristes sericeus A. Milne Edwards

Fig. 142

Paguristes sericeus A. Milne Edwards 1880:44.—Milne Edwards and Bouvier 1893:46, pl. 3, figs. 14–22.—Provenzano 1961:155.—Williams 1965:117, fig. 93.—Provenzano and Rice 1966:54, figs. 1–10.—Pequegnat and Ray 1974:242, fig. 44.

Paguristes tenuirostris Benedict 1901b:143, pl. 4, fig. 1.

Paguristes rectifrons Benedict 1901b:145, pl. 4, fig. 7.

Recognition characters.—Anterior shield of carapace nearly as broad as long, flattened, with several spines on each side; anterior margin as long as ocular peduncles, making nearly right angle with lateral margins; lateral projections low but each terminating in small spine. Rostrum with acute tip often reaching along approximately $\frac{1}{2}$ length of eye scales. Eyestalks slightly narrowed in middle; eye scales small, acuminate at tip. Antennular peduncles extending almost to tips of eyestalks. Antennal peduncles slightly exceeding acicles, terminal article armed with 2 spines; acicles straight, terminated by spiny fork and with 2 or 3 spines on internal and external borders.

Chelipeds subequal, rather short and broad; upper surface of hands and carpi with soft, silky, yellow hairs nearly obscuring surface, many strong granulations becoming corneous at tips scattered

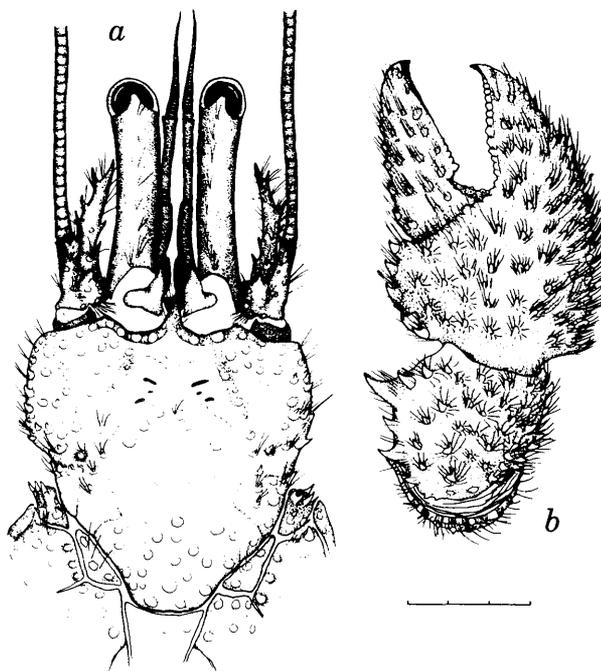


Fig. 142. *Paguristes sericeus* A. Milne Edwards. *a*, Anterior part of body in dorsal view; *b*, right chela and carpus, external view; 3 mm indicated (from Williams 1965).

over upper surface; cutting edges of fingers finely and evenly toothed, terminal parts corneous. Walking legs (legs 2 and 3) reaching beyond extended chelipeds; dactyls regularly curved, dactyl of first walking leg 1.5 times length of propodus, of second as long as propodus and carpus combined.

Measurements in mm.—Anterior shield: male, length 11.7, width 9.7; ovigerous female, length 5.9, width 5.8.

Variation.—Provenzano and Rice (1966) pointed out that shape of both the anterior carapace and eyestalks change through development, being quite different even in adults of different sizes. In these, the anterior margin becomes straighter and the eyestalks longer and more slender with increasing age. These differences led Benedict (1901b) to describe *P. tenuirostris* and *rectifrons* as distinct. Spines on sides of the cephalic shield may be worn off occasionally.

Color.—Body orange-red with numerous irregular white spots having darker border of red than general body color; eyestalks usually solid red, occasionally with white spots distally, cornea azure, almost green (from live specimens, and Provenzano 1959, 1961; Provenzano and Rice 1966).

Habitat.—Coral rubble and sand, found in *Strombus*, *Murex*, and *Oliva* (Provenzano 1961, and various authors); 9 to 145 m.

Type-locality.—23°34'N, 83°16'W [near Dry Tortugas, Fla.], 66 m.

Known range.—Off Cape Lookout, N. C.; West Flower Garden Bank, NW Gulf of Mexico to Virgin Islands.

Remarks.—Ovigerous females are known from the Virgin Islands in April (Provenzano 1961) and Florida in May and July (Rice and Provenzano 1965). Illustrations in Milne Edwards and Bouvier (1893) are inaccurate in a number of features; details of the telson and anterior carapace are not shown clearly (Provenzano and Rice 1966).

In addition to their work on allometric changes in body form, Rice and Provenzano (1965) reared and described two zoeal stages and the glaucothoe. In 36–38‰ water at 15°–25°C, half of the larvae were starved, half fed. At 15°C none survived first zoea; at 20° and 25°C both fed and starved larvae survived second zoea. The fed larvae proceeded through glaucothoe and three crab stages at 25°C, and to second crab in 20°C. Starved larvae survived to the glaucothoe stage at 25°C. Total mean time for development to first crab was about 50% greater at 20°C (16.1 days) than at 25°C (10.9 days).

Paguristes spinipes A. Milne Edwards

Fig. 143

Paguristes spinipes A. Milne Edwards 1880:44.—Williams 1965:118, fig. 95.—Forest and de Saint Laurent 1967:68.

Paguristes visor Henderson 1888:78, pl. 8, fig. 3.

Paguristes armatus Hay 1917:73.

Recognition characters.—Anterior shield of carapace convex, considerably longer than broad; frontal margin thickened and drawn out into almost straight-sided, acute rostrum, with tip considerably exceeding rather obtuse lateral projections. Eystalks considerably longer than greatest width of front but not quite so long as length of anterior shield, somewhat contracted in middle and slightly bent laterally, not much dilated distally; eye scales acuminate. Antennular peduncles extending nearly to tips of, or a little beyond, eystalks. Antennal peduncles extending about $\frac{1}{2}$ – $\frac{1}{3}$ length of eystalks; acicles straight, terminated by spiny fork, and with 2 or 3 spines on internal and external borders.

Chelipeds subequal and similar in form, narrow but massive; hands less than half as broad as long; upper surface of hands and carpi covered with conical spines, many with corneous tips, strongest on superointernal border, fingers more than half as long as whole of propodus and terminating in corneous tips, opposed edges with numerous small

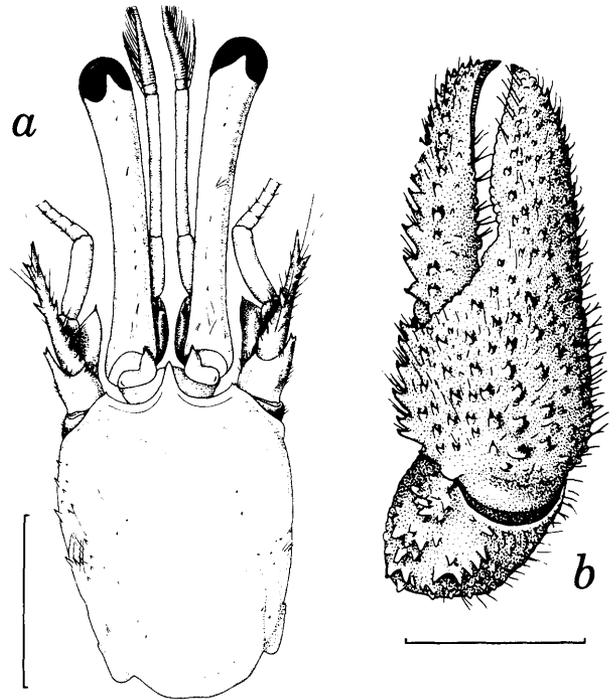


Fig. 143. *Paguristes spinipes* A. Milne Edwards. *a*, Anterior part of body in dorsal view; *b*, right chela and carpus, external view; *a*, 5 mm; *b*, 3 mm indicated (from Williams 1965).

teeth. Walking legs (legs 2 and 3) extending a little beyond chelipeds, ornamented with tufts of setae most numerous and rigid on dactyls; dactyls regularly curved and half again as long as propodi; crest of spines on carpus and propodus extending along part of dactyl of first walking legs, but reduced, and present on carpus only of second walking legs.

Measurements in mm.—Anterior shield: males, length 11.9, width 7.8; female, length 9.5, width 6.6.

Variation.—The eystalks are somewhat shorter than the front in young individuals but much longer in adults; they are frequently unequal in length. The cardiac region is calcified but the areas lateral to it are variably calcified (Milne Edwards and Bouvier 1893). The antennular peduncles may be shorter than the eystalks, and the antennal peduncle only half as long as the eystalks.

Color.—A spot of orange-red on external and internal faces of first walking legs, less definite on 2 following pairs; occasionally, traces of red coloration on anterior part of cephalothorax (Milne Edwards and Bouvier 1893). In alcohol, nearly white, each cheliped with conspicuous orange-yellow band across merus and faint trace of similar band on each walking leg (Hay and Shore 1918).

Habitat.—This deep-water hermit has been taken from shells of *Cassis* and *Xenophora*; 72 to 640 m (Wenner and Read 1982).

Type-locality.—Grenada, 168 m.

Known range.—Gulf Stream south of Cape Lookout, N. C.; off Cape Canaveral to Florida Straits, Sarasota, Fla.; Barbados to Pernambuco, Brazil.

Remarks.—Hazlett (1966a), listing *P. spinipes* as one of the more common deep-water hermits in the Straits of Florida, noted that it was not active at any time in temperatures of 15° or 25°C.

From ovigerous females captured in September off Yucatan in 240–320 m depths, Provenzano (1978) reared larvae and described development of three, rarely four, zoeal stages and a glaucothoe at 20°C. Duration of larval life at this temperature was at least six weeks, far in excess of the planktonic duration known for other members of the genus. He noted that there is evidence of widespread abbreviated development in the genus.

Paguristes tortugae Schmitt

Fig. 144

Paguristes tortugae Schmitt 1933:7, fig. 4.—Provenzano 1959:388, fig. 11A-B, 12D.—Williams 1965:119, fig. 96.—McLaughlin and Provenzano 1974:171, figs. 3; 4a; 5a-c; 6a,b,e,f; 7a-c; 8a-c; 11a; 12a-c; 13a,b,e,f; 14a-d,i.

Recognition characters.—Anterior shield of carapace noticeably longer than broad, dorsolateral surface and margins with numerous small spines or spiniform tubercles; rostrum triangular, in advance of lateral projections, each surmounted by spinule. Eyestalks slender, straight, as long as greatest width of anterior shield, with distinct, often irregular, dark bands distally; eye scales separated by rostrum, anterior process armed with 3 or 4 spines (occasionally 2) decreasing in size from median spine outward. Antennular peduncles reaching to base of cornea or slightly beyond. Antennal peduncles reaching to $\frac{3}{4}$ length of eyestalks; flagella not reaching to tips of chelipeds, setae sparse and moderately short; acicles obscured by hairs, armed with 1 spine on inner edge and at least 3 on outer edge.

Chelipeds equal, thickly covered with hairs, mesial margins of chelae and carpi straight, fitting closely together when retracted; hands with forwardly directed, hooked spines on mesial upper surface (4 or 5); inner margin, outer half, and outer margin of fixed finger; hairs arising along anterior part of base of tubercles giving squamose appearance; palms with dorsal surface flat or slightly convex, margins not appreciably elevated; dactyl with 7 more or less distinct, transverse rows of small,

horny-tipped tubercles, largest on upper margin; fingers with tips corneous, more or less spooned; lower surface of chela smooth except for some tufts of hairs. Walking legs (legs 2 and 3) with heavy fringes of hairs along upper and lower margins and some tufts on lateral surfaces, outer surface smooth; dactyls somewhat longer than propodi, tips dark, corneous, row of similar colored spinules on ventral border; inner surface of dactyls and propodi with squamiform tubercles near upper and lower margins, more pronounced where bases of hairs coincide with squamous tubercles. First walking legs with upper surface of propodus serrate, and few denticles at base of dactyl; 2 rows of spines on carpus, 1 on upper margin and 1 on upper part of inner surface, shallow groove on upper part of inner surface extending distad from carpus. Second walking legs with single row of spines on carpus; merus with 1 or 2 rows of small spines or spinulose protuberances and an anteroventral spine.

Measurements in mm.—Anterior shield: male,

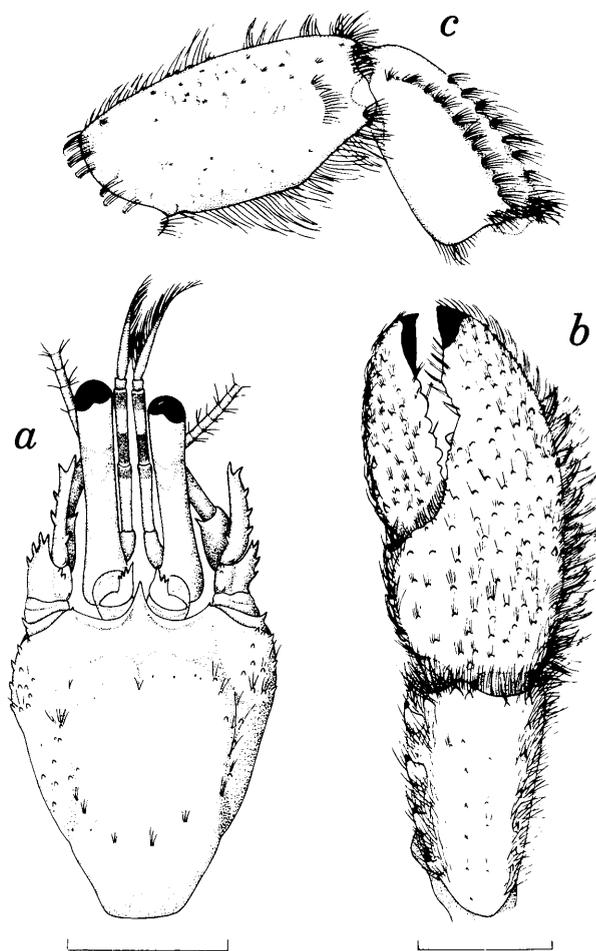


Fig. 144. *Paguristes tortugae* Schmitt. Male: a, anterior part of body in dorsal view; b, chela and carpus, external view; c, right second walking leg, merus and carpus, lateral view; a, 3 mm; b-c, 1 mm indicated (USNM 151492).

length 7.0, width 5.3; ovigerous female, length 5.0, width 3.7.

Color.—"In life: General body color varying from white to red or reddish-orange; ocular peduncles white, circumscribed with 1 or 2, often irregular or interrupted, bands of black near base of cornea; segments of antennular and antennal peduncles each circumscribed with band of black distally. Chelipeds white, pink or reddish, spines usually dark red or reddish-orange. In preservative: Color fading to uniform straw color; ocular peduncles often retaining traces of banding at bases of cornea" (McLaughlin and Provenzano 1974).

Habitat.—The holotype was taken among *Porites*, and part of the type-series in shells of *Astraea* and *Calliostoma*. Usually found on hard or shelly bottom (Tabb and Manning 1961) or in vicinity of corals; intertidal to 91 m (McLaughlin and Provenzano 1974).

Type-locality.—Off Fort Jefferson Dock, Garden Key, Dry Tortugas, Fla.

Known range.—Reefs off Beaufort, N. C., to southern and southeastern Florida; through West Indies to northern Brazil; (?) northern Gulf of Mexico.

Remarks.—McLaughlin and Provenzano (1974) revised the *P. tortugae* complex, treating seven very similar species. Identification of *P. tortugae* in the Atlantic part of the Carolinian Province is simplified because it is the only species of the group known to occur north of southern Florida.

Ovigerous females have been reported from February to October in Florida (Provenzano 1959), in June in North Carolina and August in South Carolina (Holthuis 1959). Behavior of glaucothoes is erratic when first entering shells, few animals being successful on first trial. Even early crab stages are subject to considerable error, suggesting that functional behavior patterns are a result of experience as well as inherited factors (Hazlett and Provenzano 1965).

***Paguristes triangulatus* A. Milne Edwards and Bouvier**

Fig. 145

Paguristes triangulatus A. Milne Edwards and Bouvier 1893:40, figs. 6–12.—Williams 1965:118, fig. 94.

Recognition characters.—Carapace somewhat hairy toward sides, and with scattered hairs on anterior shield; shield little longer than broad; front with thickened margin and pointed rostrum reaching

well beyond broadly angular, sometimes slightly spined, lateral projections. Eystalks long, slightly dilated but obliquely compressed at tips, line of hairs along dorsal side; eye scales acuminate, somewhat rugose on internal border. Antennular peduncles with about $\frac{1}{4}$ – $\frac{1}{2}$ of terminal article extending beyond eystalks. Antennal peduncles extending to base of cornea or as little as $\frac{3}{4}$ length of eystalks; acicles reaching about to middle of eystalks, spinose on internal and external borders, tip often bifurcate.

Chelipeds subequal, similar, upper surfaces tuberculate and hairy; inner margin of hands, carpi, and bases of dactyls with strong spines corneous at tips; upper surfaces of carpi and meri with few spines and spiniform tubercles corneous at tips. First walking legs (leg 2) with spiny crest on carpi, propodi, and base of dactyls; crest obsolescent on second pair; both pairs setose dorsally, dactyls curved, about as long as 2 preceding articles together. Dactyls of right side a little weaker than left and laterally compressed; proximal end of first left dactyl with cross section in form of curvilinear triangle, broadly rounded internal face forming base and obtusely pointed external face serving as apex; second left dactyl somewhat strong.

Measurements in mm.—Anterior shield: male, length 10, width 9.4; ovigerous female, length 7.5, width 7.0.

Color.—Legs and anterior part of cephalothorax tinted pink (Milne Edwards and Bouvier 1893); eystalks pink (Benedict 1901b); eystalks white or

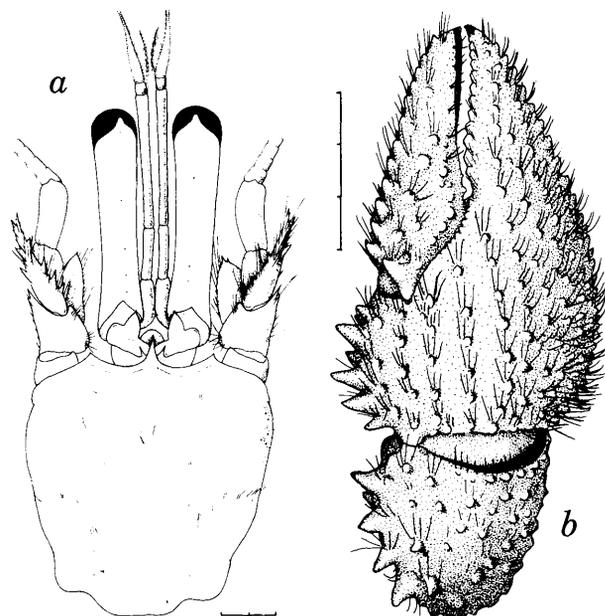


Fig. 145. *Paguristes triangulatus* A. Milne Edwards. *a*, Anterior part of body in dorsal view; *b*, right chela and carpus, external view; *a*, 2 mm; *b*, 3 mm indicated (from Williams 1965).

scarlet, antennal peduncle white, body and legs mottled white (specimens from Georgia).

Habitat.—The species has been observed in *Murex* (see Milne Edwards and Bouvier 1893), *Distorsio*, and *Phalium* shells; 12 to 150 m.

Type-locality.—Barbados, 136 m.

Known range.—Off Oregon Inlet, N. C. (12 m), to Tortugas, Fla.; Barbados; Trinidad.

Remarks.—Cerame-Vivas and Gray (1966) listed *P. triangulatus* as a tropical species in the Carolinian Province. Ovigerous females are known from Florida in August and October.

Superfamily Paguroidea

Family Paguridae

Key to Genera and Some Species

(In part from McLaughlin 1981)

1. Ischium of third maxilliped with mesioventral accessory spine near anterior end of mesial dentate crest; vas deferens of male not protruding . . . 2
 Ischium of third maxilliped without mesioventral accessory spine near anterior end of mesial dentate crest; left vas deferens of male protruding and spirally coiled *Iridopagurus caribbensis*
2. Hands more or less extended, not operculiform; fingers opening and closing horizontally; females without paired pleopods on first abdominal segment 3
 Hands operculiform, often flexed at nearly right angle to carpus, fingers opening and closing obliquely or at right angle to long axis of limb; females with paired pleopods on first abdominal segment, "Pylopagurid-like" genera 4
3. No paired appendages on first abdominal segment of either sex *Pagurus*
 Paired, short, slender pleopods on first abdominal segment of male (next 4 segments have unequally biramous appendage on left side) *Tomopaguropsis problematica*
4. Propodus of fourth legs with 1 row of scales 5
 Propodus of fourth legs with 2 or more rows of scales 7
5. Uropods symmetrical or nearly so *Pylopagurus discoidalis*
 Uropods markedly asymmetrical 6
6. Spines of chelae with basal rosettes *Rhodochirus rosaceus*
 Spines of chelae without basal rosettes *Phimochirus holthuisi*
7. Left chela triangular in cross section, dactyl and fixed finger not dorsoventrally flattened *Anisopagurus pygmaeus*
 Left chela not triangular in cross section, dactyl and fixed finger dorsoventrally flattened *Manucomplanus corallinus*

Genus *Iridopagurus* de Saint Laurent-Dechancé 1966

de Saint Laurent-Dechancé 1966:152.

Iridopagurus caribbensis (A. Milne Edwards and Bouvier)

Fig. 146

Spiropagurus caribbensis A. Milne Edwards and Bouvier 1893: 116, pl. 8, figs. 26–30.

Spiropagurus dispar.—Williams 1965:133, fig. 108.
Iridopagurus caribbensis.—de Saint Laurent-Dechancé 1966:167, figs. 14, 27, 32, 37.

Recognition characters.—Carapace smooth but with hairy tracts on anterior shield and especially on anterior portion of membranous branchial areas; anterior margin with broadly rounded rostrum and equally advanced acute lateral projections. Eye-stalks with cornea dilated, width slightly more than half length of stalk; stalk slightly exceeding proxi-

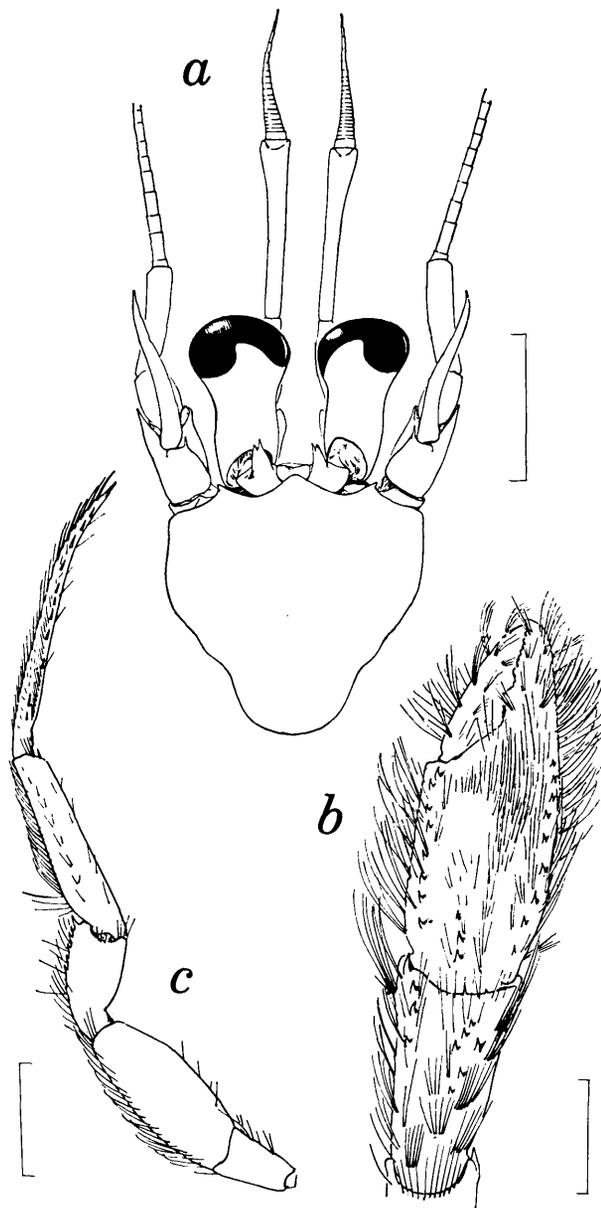


Fig. 146. *Iridopagurus caribbensis* (A. Milne Edwards and Bouvier). *a*, Anterior part of body in dorsal view; *b*, right chela and carpus, external view; *c*, left first walking leg, internal view; *a*, 5 mm; *b*, 2 mm; *c*, 10 mm indicated (from de Saint Laurent-Dechancé 1966).

mal end of terminal article of antennular peduncle and reaching about midlength of terminal article of antennal peduncle; eye scales somewhat triangular, with abruptly narrowed acute tip directed slightly laterad, and slightly exceeded by strong subterminal spine. Acicles slender, longer than eyestalks, reaching end of terminal article of antennal peduncle. Third maxillipeds lacking accessory spine near anterior end of mesial dentate crest.

Chelipeds elongate, setiferous, right chela larger than left. Major cheliped with fingers $\frac{1}{3}$ – $\frac{1}{2}$ length

of palm, cutting edges of fingers toothed; palm ornamented with dorsal submarginal row of distinct spines on each side and short central row proximally; carpus shorter than palm, with scattered spines dorsally. Minor cheliped similar but narrower; palm less spiny, and fingers with row of fine denticles on opposed edges. Two pairs of walking legs (legs 2 and 3) elongate, slender distally, somewhat less pubescent than chelipeds, propodi lacking ventral row of setae distally, carpi with low crest of spines.

Left vas deferens of male extended and prominent.

Measurements in mm.—Anterior shield: male, length 3.18, width 3.31.

Habitat.—This rare species has been found in depths of 15 to 50 m (de Saint Laurent-Dechancé 1966), 10 to 180 m (Young 1978).

Known range.—ESE of Charleston, S. C. (32°34'N, 79°05'W); WSW of Panama City, Fla. (30°19'N, 86°15.5'W); southern Florida, Virgin Islands, and Guadeloupe.

Remarks.—De Saint Laurent-Dechancé (1966) erected the genus *Iridopagurus* for reception of western Atlantic and eastern Pacific pagurids having an external, extended left vas deferens, triangular eye scales, and third maxillipeds lacking an accessory spine next to the mesial dentate crest on the ischium. She restricted *Spiropagurus* to the Indopacific and eastern Atlantic. She also pointed out distinctions between *I. dispar* and *I. caribbensis* which were synonymized by Williams (1965) following Provenzano (1961). The color notes given by Williams (1965) apply to *I. dispar*.

Small ovigerous females are known from Georgia in June. These specimens and others even smaller (shield length 1.3 mm) show the broad cornea described by de Saint Laurent-Dechancé (1966) but have acicles not reaching the distal edge of the eye. Relative length of the acicle may lengthen with increasing age.

Genus *Pagurus* Fabricius 1775

McLaughlin 1974:37.

Diagnosis.—Anterior shield well calcified. Eye scales usually triangular. Chelipeds unequal, right considerably larger than left, both oriented in horizontal plane; fourth legs subchelate, propodal rasp usually well developed. Third maxillipeds widely separated at base by sternum. Males with coxae of fifth legs equal, gonopores paired, no protruding vas deferens; females with gonopores paired. No paired pleopods in either sex, abdomen well developed, uropods asymmetrical. (After McLaughlin 1974.)

Key to Species

1. Eye scales unarmed or with single (rarely 2) subterminal spine 2
 Eye scales armed with 2 or more spines (small species). *P. carolinensis*
2. Width of major chela less than $\frac{1}{2}$ length. 3
 Width of major chela at least $\frac{1}{2}$ length. 10
3. Palm of small (left) chela triangular in cross section, upper surface divided
 by longitudinal ridge into 2 obliquely sloping facets 7
 Palm of small (left) chela not triangular in cross section, either oval or flat-
 tened and spiny dorsally 4
4. Length of eyestalks not more than 3.5 times greatest width. 5
 Length of eyestalks more than 3.5 times greatest width *P. annulipes*
5. Eye scales triangular; rostrum obtuse but definitely exceeding obsolescent
 lateral projections; major chela 3 or more times longer than wide
 *P. piercei*
 Eye scales rounded distally; rostrum obtuse but about equaling lateral pro-
 jections; major chela 2.5 (or less) times longer than wide 6
6. Chelipeds subcylindrical, relatively smooth on outer surface; eye scales
 somewhat rounded distally, dorsal surface shallowly excavated
 *P. longicarpus*
 Chelipeds not subcylindrical, relatively spiny on outer surface and setose;
 eye scales rounded distally but not excavated on dorsal surface.
 *P. defensus*
7. Palm of small (left) chela with conspicuous longitudinal ridge crested bear-
 ing single row of elevated sharp principal spines slanted inward; anterior
 part of sternite between third legs somewhat rectangular (almost twice as
 wide as long), its setae usually few and short. *P. pubescens*
 Palm of small (left) chela with broad longitudinal ridge crested bearing sharp
 or blunt spines (tending to form double row) not slanted inward 8
8. Eyestalks moderately to noticeably stout with definitely dilated cornea;
 moderate to large species in cold temperate or deeper offshore water. . 9
 Eyestalks slender, curved slightly outward, cornea only very slightly dilated;
 tiny Carolinian species. *P. hendersoni*
9. Chelipeds both sharply spined and setose on upper surfaces; anterior part
 of sternite between third legs almost semicircular, its setae usually many
 and long *P. arcuatus*
 Chelipeds bluntly spined (occasionally sharply) but not setose on upper sur-
 faces *P. politus*
10. Dactyl of major chela with sharply produced angle on mesial margin
 *P. pollicaris*
 Dactyl of major chela without sharply produced angle on mesial margin. . 11
11. Impressed spot (or spots) dorsally on chelae at base of fixed fingers
 *P. impressus*
 No impressed spots dorsally on chelae, hands normally inflated and often
 with broad longitudinal red-orange stripe persistent in alcohol
 *P. acadianus*

***Pagurus acadianus* Benedict**

Fig. 147

Pagurus acadianus Benedict 1901a:454, unnum-
 bered fig.—Rathbun 1929:26, fig. 34.—Wil-
 liams 1974c:19, fig. 53.

Recognition characters.—Anterior shield of cara-
 pace usually as wide as long, truncate posteriorly.

Rostrum pointed but broader than long, well ad-
 vanced beyond lateral projections each sur-
 mounted by small spine. Eyestalks constricted at
 midlength, dilated distally and obliquely deeper
 than broad, only half as long as width of shield;
 eye scales broadly concave on upper surface, each
 armed with subterminal spine. Antennular pe-
 duncles exceeding eyestalks by about length of ter-
 minal article. Antennal peduncles exceeding eye-

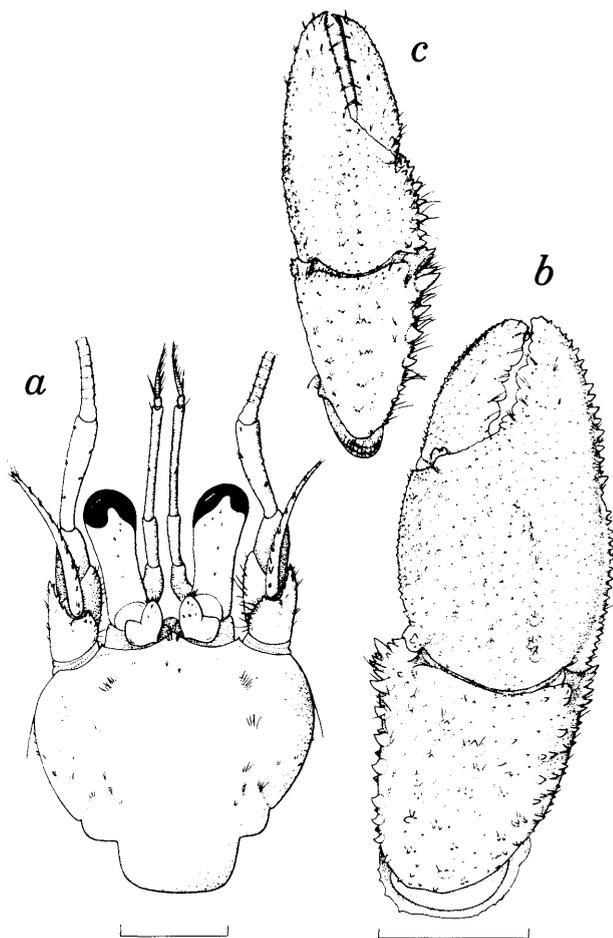


Fig. 147. *Pagurus acadianus* Benedict. Male: *a*, anterior part of body in dorsal view; *b-c*, right and left chelae and carpi in external view; *a*, 5 mm; *b-c*, 10 mm indicated (USNM 171680).

stalks by $\frac{2}{3}$ length of terminal article; acicles slender, curved outward and unarmed, nearly reaching terminus of peduncle.

Right cheliped much larger than left; hand sharply granulate above, granules a bit appressed below, row of short strong spines on lateral border and mesial border of dactyl, fingers with heavy calcareous teeth on opposed edges; carpus less granulate but more sharply spined. Minor cheliped much smaller, somewhat similarly ornamented, but compound row of prominent spines on mesial border of palm, tips of fingers corneous, and fewer spines on carpus. First and second walking legs (legs 2 and 3) with dactyls longer than propodi; dactyls smooth and convex laterally, concave mesially and with row of small corneous spines on upper and lower mesial borders and tufts of sparse setae in rows on upper border.

Measurements in mm.—Anterior shield: male, length 16.9, width 16.9; male, length 17.9, width 17.4; female, length 10.0, width 10.0; female, length 13.6, width 13.1.

Variation.—The anterior shield is slightly longer than wide in some individuals.

Color.—Upper surface of both chelae with broad longitudinal red-orange stripe often persistent in alcohol.

Habitat.—Low-water mark to 485 m (Williams 1974c).

Known range.—Grand Banks of Newfoundland and Gulf of St. Lawrence to mouth of Chesapeake Bay.

Remarks.—Details on distribution of this prominent member of the shelf fauna have been outlined by Bousfield (1958), Brunel (1970), and Squires (1966). Grant (1963), in a survey of a population in Salisbury Cove, Me., during two summer months, found about 20 individuals inhabiting a 147 m² area of rocky bottom. Low recapture after marking and release indicated transiency. Order of shell preference in laboratory tests, confirmed by field observation, descended from *Buccinum* through *Thais* to *Littorina*. It was suggested that shells such as *Buccinum* which have a higher internal volume/weight index are definitely preferred. Behavioral studies in the laboratory indicated that although the crabs had no visual orientation to shells they had been occupying, they were able to recognize these upon contact.

From eggs hatched and reared in the laboratory, Roberts (1973) described and figured four zoeal stages and a glaucothoe. Specific differences between *P. acadianus* and *P. bernhardus* based on adult morphology are borne out by differences in eggs and larval stages, though the species are closely related. Eggs of *P. acadianus* are slightly smaller than those of *P. bernhardus*, dark green rather than very dark purple, and larvae of the latter (from plankton) are markedly larger. There is similarity also to the larvae of *P. pubescens*, and probably as well to those of *P. arcuatus* which remain to be described. Ovigerous females have been collected from Cape Cod Bay in January and March.

Pagurus annulipes (Stimpson)

Fig. 148

Eupagurus annulipes Stimpson 1860a:243.

Pagurus annulipes.—Provenzano 1959:407 (part, not fig. 18).—Williams 1965:130 (part, not fig. 105).

Recognition characters.—Anterior shield of carapace as wide as or wider than long, truncate posteriorly. Rostrum rounded, about as long as rounded lateral projections of front. Eystalks nearly straight, shorter than front, slightly constricted in middle, cornea not dilated; eye scales flat, broad and

rounded, but with 1 or 2 spines on anterior border. Antennular peduncles exceeding eyestalks by about $\frac{1}{3}$ of distal article. Antennal peduncles nearly reaching or exceeding tip of eyestalks; acicles slender, curving outward, reaching about middle of last article of antennal peduncle; flagella exceeding major cheliped, adorned with long setae.

Chelipeds unequal, right much larger than left. Major cheliped long, subcylindrical, moderately and evenly granulate, except subspinose in some individuals, and variably hairy above, granules tending to be arranged in rows on palm; dactyl less than $\frac{1}{2}$ length of hand; carpus nearly twice as long as broad, spinulose along inner margin. Minor cheliped much shorter, compressed, thickly ciliate and somewhat spinulose in rows above; hand slightly shorter than carpus; fingers gaping and shorter than palm, cutting edges very finely and evenly spined distally, comblike spines of dactyl and hooked tips of both fingers corneous. First and second walking legs (legs 2 and 3) slender, compressed, with dactyls longer than propodi; carpus of left leg with distal spine on dorsal margin with or without spines on dorsal margin; carpus of right leg with several spines on dorsal margin.

Measurements in mm.—Anterior shield: male, length 2.25, width 2.56.

Variation.—Males have a tendency to attain larger sizes than females, and proportionately larger che-

lipeds (Provenzano 1959). There is considerable variation in sharpness of granules on the chelipeds as well as in length and density of hairs.

Habitat.—Fairly common on a variety of bottom types in Massachusetts, and on shelly bottom in the Beaufort Harbor, N. C., area. Offshore in North Carolina the species is found in dredge and grab samples on sand and broken shell bottom. Kellogg (1971) found it abundant in the Newport River, N. C., where tidal currents sweep the bottom, usually in *Anachis avara* shells, but mature males also in *Nassaricus vibex* shells which are larger. It occurs from near low tide mark to 26 m (Musick and McEachren, 1972) and has been taken along with numerous juvenile *Cancer irroratus* from stomachs of flounders (*Paralichthyes dentatus*) caught 15 mi. ESE of Oregon Inlet, N. C., in 37-m water.

Type-locality.—Beaufort Harbor, N. C.

Known range.—Vineyard Sound, Mass., to at least northern Florida (McLaughlin 1975).

Remarks.—Three similar species have been confused under the name *P. annulipes* (McLaughlin 1975). The southern limits for distribution of *P. annulipes* now seem established; Rouse (1970) reported it absent from the warm waters of southern Florida. *Pagurus bonairensis* Schmitt, having short setae on the antennal flagella rather than long ones as does *P. annulipes*, ranges from the northern Gulf of Mexico southward along the Florida coast and through the Caribbean (Rouse 1970; McLaughlin 1975). *Pagurus stimpsoni* (A. Milne Edwards and Bouvier, 1893) apparently is the Gulf of Mexico counterpart of *P. annulipes*, ranging from west Florida to Texas, but its exact status remains to be worked out (McLaughlin 1975).

Ovigerous females of true *P. annulipes* are known from about May to September in Massachusetts (Nyblade 1970) and almost year round in the Newport River, N. C. (Kellogg 1971). Nyblade (1970) described four zoeal stages and a glaucothoe for *P. annulipes* larval development and showed that Thompson's (1903b) early work erroneously attributed *P. longicarpus* larvae to *P. annulipes* and vice versa. At room temperature ($24^{\circ} \pm 2^{\circ}\text{C}$) in undiluted sea water at Woods Hole, four zoeal stages were passed in 14.8 days. Duration of the glaucothoe stage was not determined.

W. B. and F. J. Vernberg (1970) found that individuals of this species from the Cape Hatteras region exhibit some ability to adjust metabolic rate seasonally. In February, 30°C was an upper lethal limit, but not in June.

A bopyrid isopod, *Pseudasymmetrione markhami*, has been reported from the gill chambers of *P. annulipes* taken near Beaufort, N. C. (Adkison and Heard 1978).

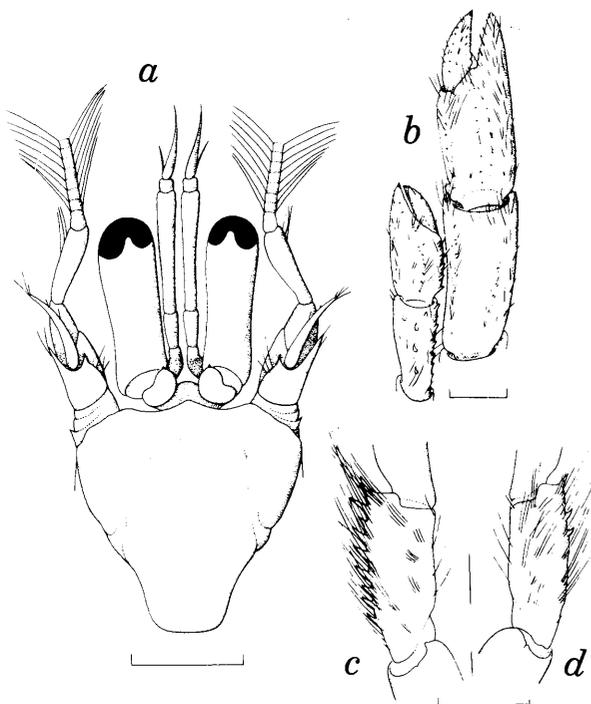


Fig. 148. *Pagurus annulipes* (Stimpson). Male: a, anterior part of body in dorsal view; b, chelae and carpi in external view; c, carpus of right first walking leg; d, same, left; a-d, 1 mm indicated (USNM 34076).

Pagurus arcuatus Squires

Fig. 149

Eupagurus pubescens.—Stimpson 1859:89 (not *kroyeri*).—Smith 1879:47.—Benedict 1896:99, fig. A.—Rathbun 1929:28, fig. 37.

Pagurus arcuatus Squires 1964: 361, figs. 1C, 2C, 5.
Pagurus banksensis Nesis 1964:667, fig. 4 part 2.

Recognition characters.—Anterior shield of carapace about as broad as long, lightly sculptured, few scattered setae, frontal margin inflated. Rostrum rounded, broader than long but tipped with small spine, well advanced beyond reduced lateral projections, each surmounted by small submarginal spine. Eystalks slightly constricted at middle, obliquely deeper than broad, length a bit more than half width of shield; eye scales narrow, concave, each tapering to strong subterminal spine. Antennular peduncles exceeding eystalks by about $\frac{1}{4}$ length of terminal article; acicles moderately stout, curved outward and reaching to near tip of eystalks.

Right cheliped much larger than left but upper surface of both moderately to sharply spinose and hairy; longitudinal, erect spiny ridge running full

length of minor hand, becoming double row of spines on palm, giving it curvilinear triangular shape in cross section. Major carpus with scattered spines or tubercles tending to form rows, row of spines on mesial margin becoming clustered near articulation with hand; minor carpus smoother. Walking legs (legs 2 and 3) with dactyls longer than propodi, nearly smooth, few scattered setae.

Sternite between third legs with anterior portion almost semicircular (nearly as long as broad), setae many and long.

Measurements in mm.—Anterior shield: male, length 14.9, width 13.9; ovigerous female, length 8.0, width 8.3.

Variation.—The semicircular sternal plate may be asymmetrical, but it always bears numerous long setae.

Habitat.—Often abundant on a variety of bottoms such as mud, sand, gravel, sandy-shell, sponges, rocks (Smith 1879), sometimes in association with *Epizoanthus*; low water mark to 270 m (Williams 1974c).

Type-locality.—Grand bank (Southeast Shoal) 43°30'15"N, 49°55'30"W, 55 m.

Known range.—Greenland to off Virginia Capes.

Remarks.—Squires (1964) untangled the misidentifications applied to this species and its close relative, *P. pubescens*, and McLaughlin (1973) elaborated on separation of the two. Both species are boreal or cold temperate forms whose latitudinal ranges overlap in the western Atlantic (Van Engel and Sandifer 1972, as *P. bernhardus*).

Ovigerous females are known from the Cape Cod–Grand Bank region in summer, and off Virginia in May.

Pagurus carolinensis McLaughlin

Fig. 150

Pagurus near *bonairensis*.—Pearse and Williams 1951:143.

Pagurus brevidactylus.—Provenzano 1959:413, fig. 20.—Williams 1965:132, fig. 107.—Forest and de Saint Laurent 1967:116, 120.—McLaughlin 1974:41.

Pagurus carolinensis McLaughlin 1975:365, figs. 4–6.

Recognition characters.—Anterior shield of carapace slightly longer than broad. Rostrum short, usually broadly rounded and about on line with triangular lateral projections. Eystalks swollen at base, tapering toward cornea; eye scales armed along anterior border with 3 to 6 spines. Antennular peduncles reaching at least to tips of eye-

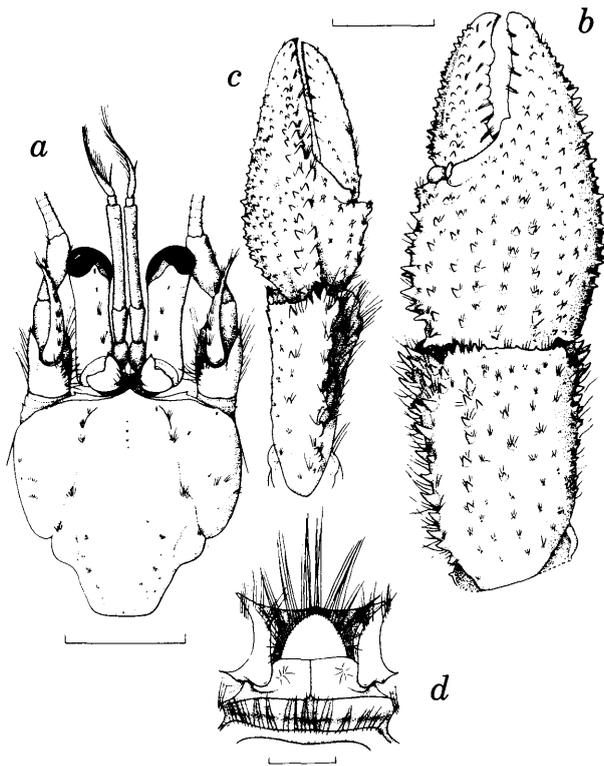


Fig. 149. *Pagurus arcuatus* Squires. Male: a, anterior part of body in dorsal view; b-c, right and left chelae and carpi, external view; d, sternite between third legs; a-c, 5 mm; d, 2 mm indicated (USNM 77444).

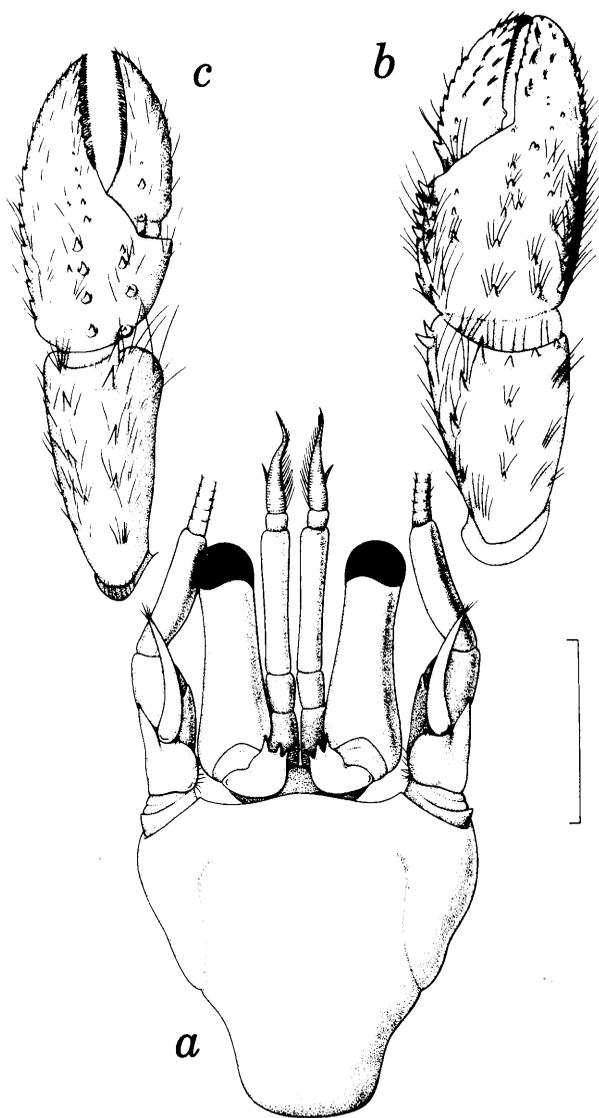


Fig. 150. *Pagurus carolinensis* McLaughlin. Male: *a*, anterior part of body in dorsal view; *b-c*, right and left chelae and carpi, external view; 1 mm indicated (USNM 90074).

stalks. Antennal peduncles slightly exceeding eyestalks; acicles reaching to base of cornea or slightly beyond.

Chelipeds unequal in males, right larger than left, equal or subequal in females; finger tips corneous, spooned. Hands covered with fine hairs, outer margin edged with very short spines, upper surface with small spines or tubercles; carpi with strong spines above. Walking legs (legs 2 and 3) with long, fine, inconspicuous hairs; dactyls shorter than propodi and with 5 to 8 conspicuous spines along inferior margin; propodi with only 1 or 2 inconspicuous spinules along inner margin.

Measurements in mm.—Anterior shield: ovigerous females, length 2.0, width 1.81; length 1.66, width 1.66.

Color.—Walking legs each characteristically colored with 6 rust-red, or maroon stripes on propodus, carpus, and merus, fewer on dactyl; stripes longitudinal and interrupted at ends of each article; ground color of walking legs yellow; hands brown with almost white fingers, not striped; carapace with scattering of red and white pigment in fresh specimens (Provenzano 1959).

Habitat.—The species seems to prefer hard bottoms in areas where water circulation is fairly good (Provenzano 1959); 2 to 53 m.

Type-locality.—Black Rocks, off New River, North Carolina.

Known range.—Newport River (Kellogg 1971) and Cape Lookout, N. C., to southern Florida.

Remarks.—This species for many years was confused with *P. brevidactylus* (Stimpson) sensu stricto which is distributed in Bermuda and from northeastern Florida to northern South America. *Pagurus brevidactylus* has spinier hands than *P. carolinensis*. Provenzano (1959) called attention to sexual dimorphism in *P. carolinensis*. In females the hands are nearly the same size and the right hand is spooned and serrate along the inside margin of the fingers, whereas in males the right hand is not only the larger but the finger tips appear more acuminate and the opposing margins of the fingers each bear a tooth. Many small specimens from Georgia have rather stout eyestalks, and lengths of dactyls and propodi of the walking legs are equal.

Ovigerous females have been collected from June to August and November in North Carolina, March to August in Florida, and July to October in Georgia.

Pagurus defensus (Benedict)

Fig. 151

Eupagurus defensus Benedict 1892:7.

Pagurus defensus.—Williams 1965:127, fig. 102.

Recognition characters.—Anterior shield of carapace broader than long, subcordate. Rostral projection broadly rounded, lateral processes triangular, armed at apex with short spine. Eyestalks stout, much dilated and flattened distally; eye scales broad, rounded, anterior margin forming semicircle, armed with subterminal spine. Antennular peduncles extending beyond eyestalks by $\frac{2}{3}$ or more length of terminal article. Antennal peduncle extending beyond eyestalks by about $\frac{1}{2}$ length of terminal article; acicle curving outward and extending somewhat beyond eyestalk.

Chelipeds unequal, right larger than left. Major chela little wider than carpus, fingers slightly agape,

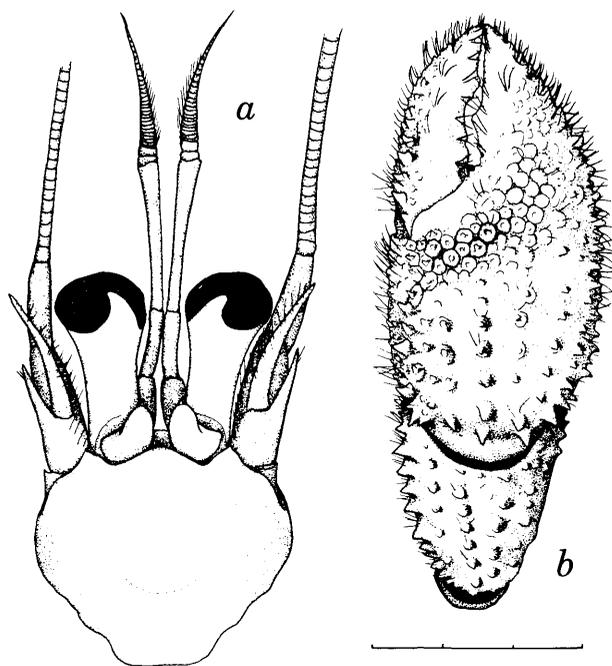


Fig. 151. *Pagurus defensus* (Benedict). Female: *a*, anterior part of body in dorsal view; *b*, right chela and carpus, external view; 3 mm indicated (from Williams 1965).

margins set with comb of long slender spines; upper surface with more or less diagonal rows of spines on palm; irregularly but closely set plates near base of fixed finger and occasionally on dactyl, spine or tubercle usually arising from center of each plate; carpus with 3 rows of sharp spines, 1 on outer margin, 1 on upper surface and 1 on inner surface. Minor chela extending to base of major dactyl; hand armed with spines as in opposite member but hairier and no spine-bearing plates present; fingers agape; carpus with double crest of spines, outer margin convex, inner margin straight and flat; merus compressed. Walking legs (legs 2 and 3) long and slender, dactyls lightly setose, longer than preceding 2 articles together; propodus and carpus with crest of spines.

Measurements in mm.—Anterior shield: male, length 5.9, width 6.5; female, length 3.1, width 3.7.

Variation.—There is considerable variation in length of spines on the chela and amount of hair on the major chela; fingers of the chelae do not gape in small individuals.

Habitat.—Twenty-five to 90 m.

Type-locality.—Gulf of Mexico between Delta of Mississippi River and Cedar Keys, Fla., 55 m.

Known range.—Cape Hatteras, N. C., to Georgia; Tortugas, Fla., to Alabama.

Remarks.—Cerame-Vivas and Gray (1966) listed this species from tropical Caribbean waters along the North Carolina shelf.

Ovigerous females have been taken south of Ocracoke Inlet, N. C., in July, and a mature female from 25 m about 25 mi. SE of New River Inlet, N. C.

Pagurus hendersoni Wass

Fig. 152

Pagurus hendersoni Wass 1963:144, figs. 5a-f.

Recognition characters.—Anterior shield of carapace a little longer than wide, smooth, rounded laterally, few scattered setae. Rostrum broadly rounded, slightly exceeding more sharply tipped broad lateral projections. Eyestalks shorter than shield but slender, slightly curved outward, and with slightly dilated cornea; eye scales oval, slightly concave, with prominent subterminal spine. Antennular peduncles equaling eyestalks when extended, those of antennae nearly as long. Acicle unarmed, reaching about $\frac{2}{3}$ length of eye.

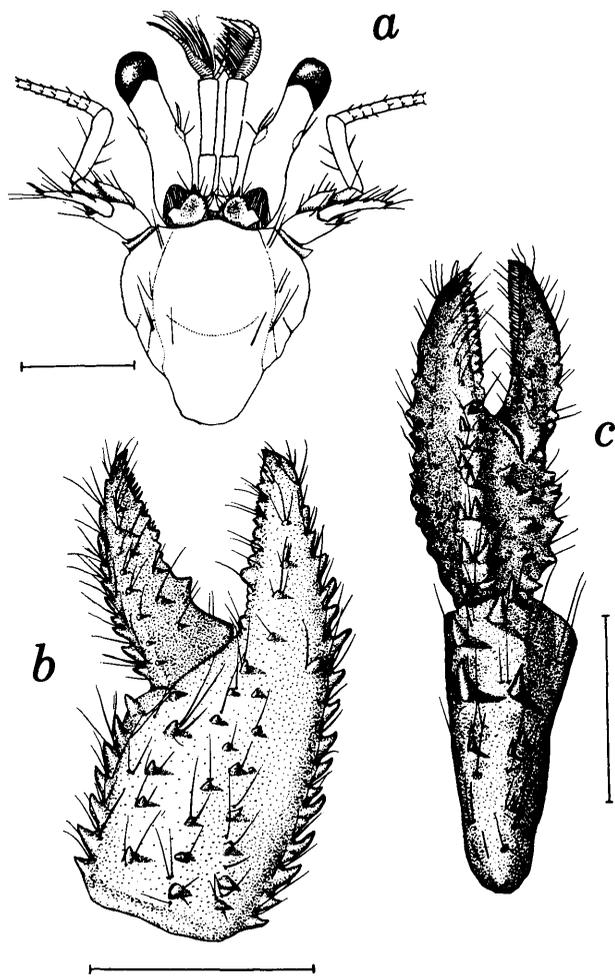


Fig. 152. *Pagurus hendersoni* Wass. Female: *a*, anterior part of body in dorsal view; *b*, right chela; *c*, left chela and carpus, external views; 1 mm indicated (from Wass 1963).

Right cheliped larger than left, strong, short and stout; chela rounded above and armed with obtuse spines in irregular rows except for 2 rows on dactyl, outer margin with strong teeth; carpus with strong mesiodorsal spines forming 2 rows distally; usually a row of slender spines laterally flanked by denticles on margin; merus with stout spine on inner ventral angle, few low denticles on opposite angle and distodorsal spine directed forward from margin. Minor chela with prominent dorsal ridge on palm bearing generally double row of spines extending on propodal finger where it bears a few denticles, row of widely spaced denticles between ridge and bluntly serrate outer margin, blunt spines along mesial margin and others parallel on upper surface; finger spooned, cutting edge of dactyl corneous, fixed finger with calcareous teeth; carpus with spinules proximally and strong spines distally on upper surface; merus with 1 or 2 spines ventrally on inner margin and irregular row of spinules on outer margin. Walking legs (legs 2 and 3) with dactyls longer than propodi.

Measurements in mm.—Anterior shield: female, length 1.8, width 1.7.

Variation.—Spination of the chelae varies; one mature female has a nearly smooth major chela.

Type-locality.—Pourtales Plateau, 10 mi. S Key West, Fla., 229 m “rocky (coral).”

Known range.—Off Georgia, 31°26'30"N, 79°42'15"W, 89–77 m; Florida Straits and Dry Tortugas.

Remarks.—Only the type-series and four specimens from Georgia are known; all are ovigerous females (in August) except one juvenile. This is a tiny species notable for the longitudinal ridge on the minor chela, slender eyes, and usually well-armed chelipeds.

Pagurus impressus (Benedict)

Fig. 153

Eupagurus impressus Benedict 1892:5.

Pagurus impressus.—Provenzano 1959:399, fig. 15.—Williams 1965:129, fig. 104.

Recognition characters.—Anterior shield of carapace about as broad as long, flattened; narrow longitudinal notch at anterolateral corners. Rostrum much rounded, in line with somewhat more angular lateral projections of front. Eyestalks shorter than width of shield, cornea dilated and flattened; eye scales with moderately slender, acuminate, slightly excavated anterior lobe, subterminal spine large. Antennular peduncles exceeding eyestalks by about $\frac{3}{4}$ length of terminal article. Antennal pe-

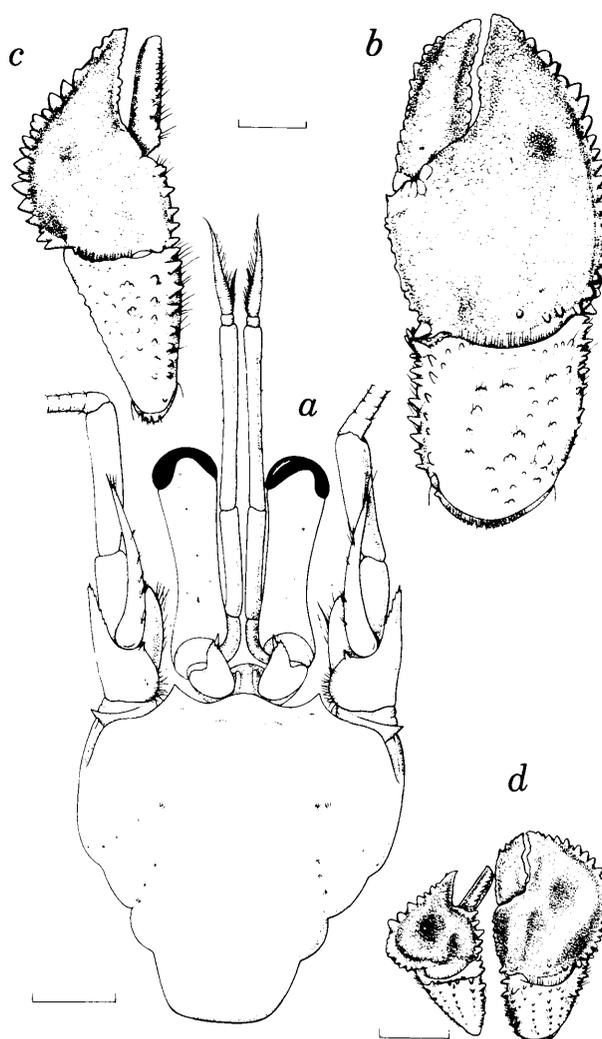


Fig. 153. *Pagurus impressus* (Benedict). Ovigerous female: *a*, anterior part of body in dorsal view; *b-c*, right and left chelae and carpi, external view; *d*, same, smaller female. USNM 102669, *a*, 3 mm, *b-c*, 5 mm indicated; USNM 122725, *d*, 5mm indicated.

duncles slightly exceeding cornea; acicles curving outward, reaching to base of cornea, hairy on mesial edge.

Chelipeds unequal, right much larger than left, upper surfaces of palms dented; both covered with small, closely crowded granules, outer margins bearing enlarged granules or small spines. Dactyl of major cheliped with rounded angle on mesial border near tip followed by marginal spines or granules, tips of fingers calcareous and hooked; carpus with longitudinal rows of small spines often obscured by irregularly arranged additional spines, row of well-developed spines along inner edge. Minor cheliped reaching to angle of major dactyl; row of spines along inner margin of hand and carpus; fingers somewhat spooned behind hooked, corneous tips, cutting edges well defined, dactyls with mesial border tuberculate; carpus with sev-

eral rows of small spines. First and second walking legs (legs 2 and 3) with dactyls much longer than propodi; first pair with row of small, well-defined spines along upper margin of propodus and carpus; second pair with spines reduced.

Measurements in mm.—Anterior shield: male, length 12.9, width 13.0; ovigerous females, length 10.8, width 10.9; length 3.9, width 3.9.

Variation.—There is considerable variation in the depth of dents on upper surfaces of the palms. Older individuals tend to have uniformly shallower dents than juveniles or small adults in which palms vary from nearly smooth to deeply pitted. Specimens from the Gulf of Mexico population seem to have somewhat smoother hands than many from the Atlantic shelf.

Color.—Hands solid rust to chocolate brown, other appendages brownish with alternating thin bands of light color; antennae, antennules, and peduncles yellow; eyestalks brown above, bright blue below with bright scarlet at base of eyestalks (Provenzano 1959).

Habitat.—On sandy bottom, grassy flats or pilings; occasionally found in sponges (Wass 1955), often in a species of *Ficulina* in North Carolina; 1 to 33 m. Kellogg (pers. comm.) found young *P. impressus* in the Newport River, N. C., estuary.

Type-locality.—Boca Ciega Bay, inner shore of Pine Key [mouth of Tampa Bay], Florida (from holotype jar label).

Known range.—Off Diamond Shoals, N. C., to near Cape Canaveral, Fla.; Florida Bay, near Flamingo, north to vicinity of Pensacola, Fla. (Cooley 1978); Port Aransas, Tex.

Remarks.—Ovigerous females have been taken in January and February in Georgia and the Carolinas, and February and April in Florida. The species is rare in southern Florida (Rouse 1970; Tabb and Manning 1961).

Türkay (1968) recognized a subspecies, *P. i. zilchi*, from Isla de Margarita, Venezuela, that is very close to typical *P. impressus*.

Pagurus longicarpus Say

Fig. 154

Pagurus longicarpus Say 1817:163.—Provenzano 1959:394, fig. 13.—Williams 1965:125, fig. 101.

Recognition characters.—Anterior shield of carapace subcordate, truncate posteriorly, about as long as broad. Rostrum obsolete, hardly as advanced as lateral projections of front. Eyestalks stout, 2 to 3 times longer than broad, much shorter than width of anterior shield, cornea dilated; eye scales with

concave, oval anterior lobe armed with subterminal spine. Antennular peduncles exceeding eyes by $\frac{1}{2}$ – $\frac{3}{4}$ length of terminal article. Antennal peduncles exceeding eyes by about $\frac{1}{3}$ length of terminal article; acicles slender, curved sinuously outward, reaching to tip of cornea; flagella exceeding tip of major cheliped.

Right cheliped much larger and longer than left, subcylindrical, devoid of hairs except for few short setae along inner edges of fingers; width of hand less than $\frac{1}{2}$ total length, palm lightly crested and minutely dentate along outer margin, upper surface minutely granulate and with 2 incomplete rows of subspinous tubercles and scattered smaller ones. Left cheliped smaller, hairier, similarly formed but relatively broader; fingers with cutting edges distally, gaping at base. First and second walking legs (legs 2 and 3) with dactyls longer than propodi, extending about as far as chelipeds.

Measurements in mm.—Anterior shield: male, length 7.25, width 7.5; ovigerous female, length 4.5, width 5.0.

Color.—Color varies with locality; specimens from west Florida lighter than those of east coast; upper surface of chelipeds and all walking legs iridescent; posterior carapace light green; hand white with median diffused pigment stripe, carpus with dorsal stripe and on each side; walking legs with dactyl unstriped, propodus with lateral stripe, merus with single lateral muddy brown stripe and transverse stripe from lower margin to broad pigmented area on upper surface; antennae with dark

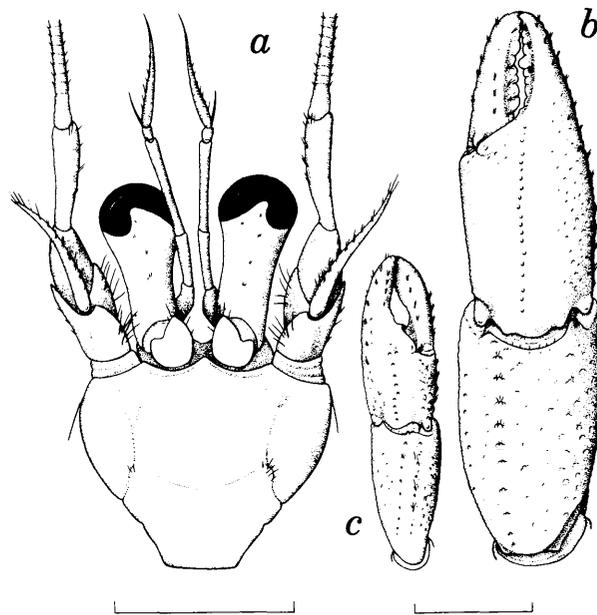


Fig. 154. *Pagurus longicarpus* Say. Male: a, anterior part of body in dorsal view; b-c, right and left chelae and carpi, external view; 5 mm indicated.

bands alternating with shorter white bands. Young may have transverse band on each article of walking legs rather than stripe; lateral stripes of major cheliped with V-shaped appearance in dorsal view (Provenzano 1959, from west Florida specimens).

Habitat.—Common on harbor beaches, in harbor channels and along shallow littoral on a variety of bottoms, but usually soft substrate (Kellogg 1971); to 200 m (Wenner and Boesch 1979).

Type-locality.—"Inhabits bay shore" [east coast of United States].

Known range.—Minas Basin and Chignecto Bay (Bousfield and Leim 1960; E. L. Bousfield, personal communication) to Hutchinson Island, Fla. (Camp, et al. 1977); southwestern Florida to coast of Texas (Provenzano 1959; Rouse 1970; Whitten, et al. 1950).

Remarks.—*Pagurus longicarpus* is one of the commonest decapod crustaceans in shallow water along the coast of the eastern United States. Like other easily collected crustaceans, it has been the subject of a number of ecological, physiological, and behavioral studies. Provenzano (1959) suggested that the Atlantic coast and Gulf of Mexico forms, with a hiatus between their ranges, may be subspecifically distinct.

The general habitat of *P. longicarpus*, summarized above, has been commented upon by other authors (Pearse, et al. 1942; Allee 1923). Allee concluded that the ubiquity of this hermit crab prevents it from being of aid in distinguishing shallow-water communities. Functional morphology of the mouthparts (Roberts 1968a) is related to a diet of diatoms, detritus and algae (Sanders, et al. 1962) as well as occasional infaunal invertebrates. Caine (1975) found that the diet is 45% scavenged material, 10% algae, and 40% detritus and sand. Scully (1978) described utilization of surface foam as food in very shallow water and reviewed food studies on hermits.

In Narragansett Bay, Rebach (1974) showed by experiment and field observation that the species has seasonal migratory and burrowing responses, burrowing preferably in sand as temperatures lower in fall to around 10°C and at the same time moving to deeper water, finally coming to occupy grounds greater than 5 m deep at 1.3°–1.7°C in winter where no hermits at all occur in summer. During spring, the hermits return to water along the strand. Kinne, et al. (1963) found that *P. longicarpus* has no osmoregulatory capacity.

The breeding season varies with latitude. In Massachusetts it extends mainly from early May to mid-September (Bumpus in Sumner, et al. 1913b), but an ovigerous female has been collected on April 23 from Cape Cod Bay. Farther south breeding ex-

tends into winter: February in North Carolina; March through July in Georgia; September to April in Florida (Dragovich and Kelly 1964; Wass 1955, in part); winter in Texas (Fotheringham 1975).

Roberts (1970; 1971a, b, c) reared four zoeal stages and a glaucothoe from females taken at Gloucester Point, Va. In finger bowls of unfiltered sea water (19–22‰) no prezoal stages were observed except when culture conditions were sub-optimal. In conjunction with Nyblade (1970) he showed that Thompson's (1901, 1903b) *P. longicarpus* larvae were really *P. annulipes*. In an array of salinities (18–30.5‰), development through the glaucothoe extended 21.6–24.4 days and in lower salinities a few days longer, indicating broad adaptation to estuarine salinities. Larvae can detect a salinity reduction of 2.5‰ and probably less. Mortality of isolated glaucothoes is unaffected by shell presence or absence, but in mass culture unprotected animals are cannibalized. Among available shells, 50% of the glaucothoes entered a shell after 24 hr, up to 93% after 48 hr, and a few which failed to enter a shell did so immediately after molt to the first juvenile instar. Intermolt duration was not significantly affected by shell presence or absence.

Shell selection in hermit crabs has been studied by a host of workers. Reese (1962), basing experiments largely on *P. longicarpus*, showed that natural occurrence of hermit crabs in certain species of shells is explicable by at least two factors: an actual preference for certain species of shells, and relative abundance of shells of different species in different habitats. The two factors may operate singly or together. Hermits tested were able to discriminate among at least three species of shells, regardless of whether or not they had previous experience with the shells. The crabs were also able to discriminate among conspecific shells of different weights, and they selected shells of a specific weight relative to their own. Inception of shell-entering behavior occurs in the glaucothoe stage, appears to be composed of innate components, and is fully expressed when the glaucothoe enters its first shell except that the glaucothoe shows little visual orientation to shells.

Fotheringham (1976; 1976a) observed that *Clibanarius vittatus*, *Pagurus pollicaris* and *P. longicarpus* have broadly overlapping shell utilization patterns along the Texas coast. Wright (1973) showed that species of *Pagurus* (*longicarpus* and *pollicaris*) offered clean shells or shells bearing colonial hydroids, *Podocoryne carnea* or *Hydractinia echinata*, chose the hydroid-covered shells, whereas *Clibanarius vittatus* avoided the latter. *Pagurus* species were not stung by the hydroid zooids, and indeed were occasionally seen eating hydroids from a neigh-

bor's shell. Wright thought that they may thus gradually gain immunity to stings.

Pagurus longicarpus may mature four months after settling from the plankton and reach its asymptotic size within the next eight months. This rapid growth may enable it to preempt shells which are required for the successful brooding of a large clutch of eggs. Growth rates of crabs in preferred shells are greater than those of crabs in small shells (Fotheringham 1976, 1976a), but observed molting rate was the same in either case. Ovigerous females bore 260–4,054 eggs.

In another vein, conditioned and natural behavior of *P. longicarpus* have been studied. Spaulding (1904) found the crab able to profit by experience in vision and taste experiments, and able to learn faster than *P. pollicaris*. Fink (1941) claimed deconditioning of fear-reflex activity over a period of 18 days; older crabs responded more slowly than young ones. Hazlett (1966b) showed the results of work with shell-less crabs, as that of Allee and Douglas (1945), to be atypical because shell-less crabs do not occur in nature. Evacuation of the shell is not a matter of force. Actions of an attacking crab which result in eviction of the loser are at a signal level. Rapping and shaking are negative situations which the defender would avoid if possible; an evacuation is one means of avoiding them. The loser of a shell fight is not physically damaged in any way. First reactions of an attacker are to attain an opposed position directly or to turn the other crab over and over with its ambulatories. Weight of shell is an important factor in selection. The attacker is visually and, in a recently molted defender's case, chemically oriented to shells of approximately the right size. "Rolling" allows more judgment of size. "Signals" reduce physical damage. Hazlett (1972) also showed that in *P. longicarpus* intensity of display is inversely proportional to distance from an intruder (another crab or a mirror).

Autotomy and regeneration in this species received attention from Morgan (1900, 1901) and Haseman (1907), though investigations on this subject with other species now supersede the early studies. The first three pairs of legs have a fracture joint near their bases, hence can be autotomized, but the last two pairs lack these and cannot be autotomized. Injuries distal to the fracture plane result in autotomy and regeneration; those proximal to the plane do not result in autotomy. Injured abdominal appendages are readily regenerated. Hazeman carried this work farther showing that when the chelipeds were removed at their breaking joint they differentiated from the tip proximally, but the first two pairs of clawed (walking?) legs differentiated from the base toward the tip.

Direction of differentiation in the cheliped can be reversed by injuring the developing bud.

Kropp and Perkins (1933) showed that in *P. longicarpus*, and other remotely related decapods, the chromatophore activity substance in the eyestalk will induce contraction of chromatophores in other species, and postulated that the substance is genetically similar throughout the group.

Fraenkel (1960) emphasized the importance of exposure duration in determining an upper temperature tolerance limit of 36°C for *P. longicarpus*.

Finally, Reinhard (1944, 1945) and Reinhard and Buckeridge (1950) discussed parasitism in *P. longicarpus*. An examination of 8,000 crabs showed a 1% infestation with a larval acanthocephalid belonging to the genus *Polymorphus*. The worm was found in the abdominal cavity (?) usually attached to the hind gut or sometimes among tubules of the hepatopancreas. The usual number of cysts per host was one, though as many as three occurred. Reinhard also described an entoniscid isopod, *Paguritherium alatum*, from this species. Entering the crab's body through the dorsal side of the eyestalk, and remaining in contact with this point of entry, the parasite elongates with but little damage to thoracic organs, but becomes greatly distended in the abdominal region. There it restricts the hepatopancreas and nearly obliterates the gonads as it grows. Infestation does not externally modify the male host. In females, the parasite reduces size of the first three pleopods, especially length of the endopod, and causes partial or complete loss of ovigerous hairs on the external surface of the endopod and protopod. Thus, secondary sexual characters of the female crab are altered. One percent of the crabs investigated were infested with this parasite.

Pagurus piercei Wass

Fig. 155

Pagurus piercei Wass 1963:147, figs. 7a-g.

Recognition characters.—Anterior shield of carapace as broad as long, combs of stiff setae arranged serially to either side of gastric region. Frontal margin with broadly obtuse rostrum advanced beyond obsolescent lateral projections. Eyestalks shorter than width of shield, equally swollen at base and cornea, with combs of setae dorsally and laterally; eye scales triangular, each terminating in spinule. Antennular peduncles when extended exceeding eyestalks by nearly full length of terminal segment, those of antennae by 1/3 of terminal segment. Acicles unarmed, exceeding eyestalks.

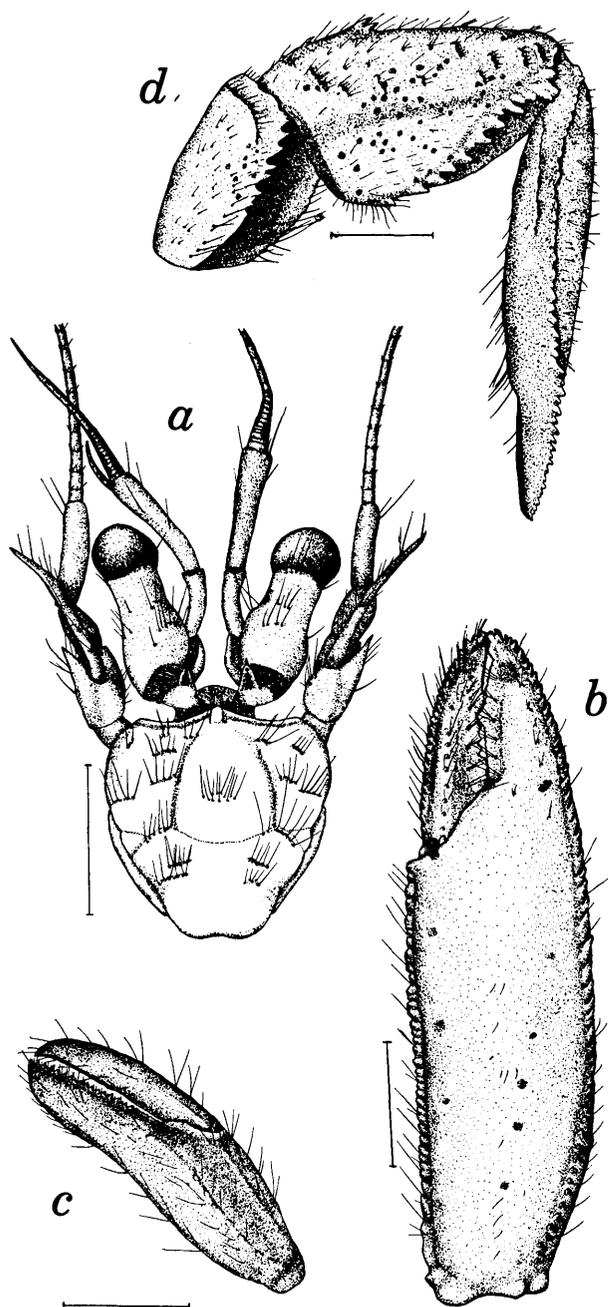


Fig. 155. *Pagurus piercei* Wass. Male: a, anterior part of body in dorsal view; b-c, right and left chelae, external view; d, right cheliped, lateral view. USNM 106599, holotype, 1 mm indicated (from Wass 1963).

Right cheliped much larger than left, elongate; chela over 3.5 times as long as wide, margins finely serrate, upper surface smooth and with fine setae; carpus and merus excessively swollen; carpus twice as broad as propodus, armed with row of strong teeth on mesial margin, series of smaller teeth on ventromesial and ventrolateral margins, and a few dorsal spines; merus with row of teeth on ventrolateral margin. Minor chela over 3 times as long as

wide, fingers elongate and spooned, fine setae most noticeable ventrally; merus and carpus each with 3 short spines on lateral anteroventral margin; carpus with few denticles and numerous setae dorsally. Walking legs (legs 2 and 3) slender, minute distodorsal tooth on carpus and row of ventral spinules on dactyls; rasp of fourth leg with single row of scales.

Measurements in mm.—Anterior shield: holotype male, length and width 1.6.

Color.—"Specimen in alcohol two months. A faint red persists in narrow longitudinal stripes on walking legs and in a few spots on major chela" (Wass 1963).

Habitat.—The holotype was taken from a piece of coral hooked from the bottom by a fisherman (Wass 1963); 73–260 m (Wenner and Boesch 1979).

Type-locality.—39 mi. SE Port Aransas, Tex., 73 m.

Known range.—Type-locality and 30°51'30"N, 79°58'W off Georgia.

Remarks.—Wass (1963) noted that this species is probably associated mainly with reefs and not taken by usual methods of collecting. The specimen from Georgia is a juvenile male in which the carpus and merus of the large cheliped are not relatively so swollen as in the holotype.

Pagurus politus (Smith)

Fig. 156

Eupagurus sp. Smith 1881:428.

Eupagurus politus Smith 1882:12, pl. 2, fig. 5.—1883:27, pl. 4, fig. 4.—Fowler 1912:579.

Pagurus politus.—Rathbun 1905:16.

Recognition characters.—Anterior shield of carapace broader than long, smooth. Rostrum broadly rounded and not reaching level of acute lateral projections, each armed with short spine. Eyestalks about 1.25 times longer than distance between lateral projections of front, cornea distinctly dilated, stalk depressed; eye scales small, concave dorsally, narrow, each armed with small submarginal spine at tip. Antennular peduncles exceeding eyestalks by about $\frac{2}{3}$ length of terminal article. Antennal peduncles reaching slightly beyond eyestalks; acicles slender, sinuously curved, reaching tip of terminal article.

Right cheliped larger than left; both chelae similarly ornamented dorsally with numerous rounded, slightly appressed to spiniform tubercles; minor chela with low, central longitudinal ridge dorsally giving hand curvilinearly triangular shape in cross section, dactyl smooth dorsally; tubercles somewhat more widely spaced on carpi, minor carpus

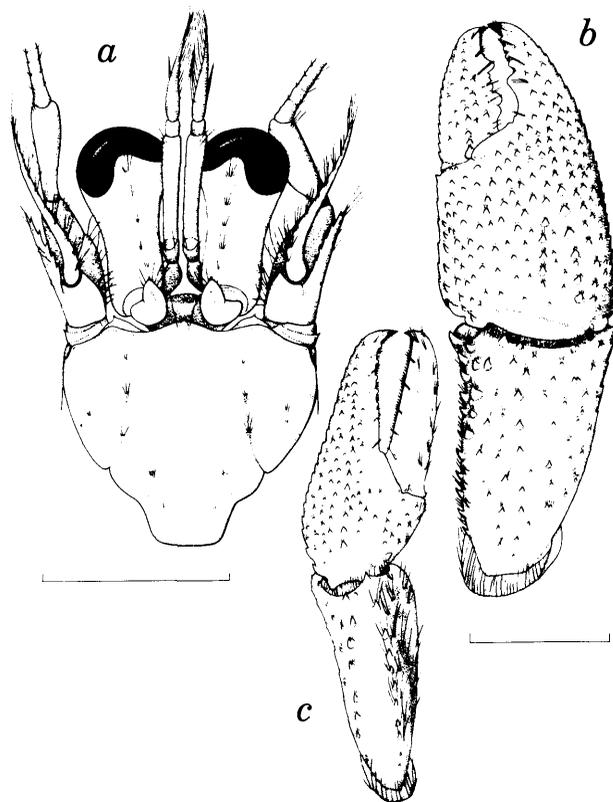


Fig. 156. *Pagurus politus* Smith. Male: *a*, anterior part of body in dorsal view; *b-c*, right and left chelae and carpi, external view; 5 mm indicated (USNM 5899).

with smooth longitudinal tract between mesial marginal row of sharp tubercles and median dorsal row; both chelae nearly devoid of hairs, those of females slightly more hirsute. Walking legs (legs 2 and 3) with curved dactyls much longer and more slender than propodi, each dactyl with ventral row of fine corneous spines distally.

Measurements in mm.—Anterior shield: male, length 12.9, width 14.1; ovigerous female, length 6.4, width 7.1.

Color.—Generally pale orange, tips of chelae and walking legs white, eyes black (Smith 1882).

Habitat.—Essentially an offshore form recorded mostly near edge of continental shelf and on continental slope; (20?) 30 to 1170 m.

Type-localities.—Not designated in original description, but syntypes from four localities off New Jersey to Massachusetts were indicated by Smith (1882). The male he illustrated, is in the type collection of USNM (21452), from off Martha's Vineyard, Mass., 40°03'48"N, 70°45'54"W, 130 m, *Fish Hawk* Stn. 922; others in the collection of MCZ, Harvard University, are from U. S. Fish Commission Stn. 309, 40°11'40"N, 68°22'10"W, 556 m, and Stn. 310, 39°59'16"N, 70°18'30"W, 475.5 m.

Known range.—Georges Bank to off Dry Tortugas, Fla. (Williams 1974c).

Remarks.—Though *P. politus* is a species abundantly represented in the USNM collection, there are few references to it in the literature. Pilsbry (1907) referred to occurrence of the barnacle *Poecilasma kaempferi novaengliae* on the carapace of a specimen taken off Martha's Vineyard. The species is occasionally associated with carcinoecia of *Epi-zoanthus*.

Many records of ovigerous females indicate a long, if not year round, breeding season throughout the length of the range.

Hazlett (1966a) listed *P. politus* as strongest in a ranking of *Pagurus* species on the basis of pagurid behavior expression. He characterized it as a large crab, very active at 15°C, which holds the shell off the substrate, avoids conspecifics in the light, less in red light, and has three kinds of cheliped display.

Pagurus pollicaris Say

Fig. 157

Pagurus pollicaris Say 1817:162.—Provenzano 1959:401, fig. 16.—Williams 1965:128, fig. 103.

Recognition characters.—Anterior shield of carapace subcordate, slightly longer than broad, truncate posteriorly. Rostrum slightly less advanced than lateral projections of front, lateral projections rounded but with inferior anterolateral spinule. Eystalks moderately stout, not so long as width of anterior carapace, nearly straight, cornea dilated; eye scales with round tipped, slightly concave anterior lobe armed with inferior subterminal spine. Antennular peduncles exceeding eystalks; acicles slender, curved outward, reaching to or beyond base of cornea, hairy mesially.

Chelipeds unequal, right much larger than left, both covered with small, closely spaced, often elevated and sharpened granules, outer margins with enlarged granules or small spines. Major chela stout, hand flattened; dactyl with prominent, projecting angle on mesial border; carpus with tubercles tending to be larger and more widely spaced than on hand, subspinose and ciliated on upper surface; merus with few squamiform tubercles. Minor chela with inner border dentate, dactyl without projecting angle, dentation of inner border continued on inner dorsal border of carpus. First and second walking legs (legs 2 and 3) with dactyls much longer than propodi; first pair with small, well-defined spines along upper margin of propodus and carpus; second pair with spines reduced.

Measurements in mm.—Anterior shield: males, length 21.3, width 19.2; length 20.7, width 19.9; ovigerous females, length 17.8, width 18.7; length 14.7, width 13.9.

Color.—Color varies with locality, individuals from west Florida being lighter than those of northeastern states. Chelipeds basically white with gray margins mesially, tips of dactyls, and with dark area in center of upper surface; remainder of body light gray-tan; eyestalks brown below cornea; hairs on antennules rusty brown (Provenzano 1959, for west Florida form). Massachusetts form reddish brown.

Habitat.—Deep channels of harbors and littoral waters; also found in shallow estuaries near ocean; near low-tide mark to 112 m (Wenner and Boesch 1979).

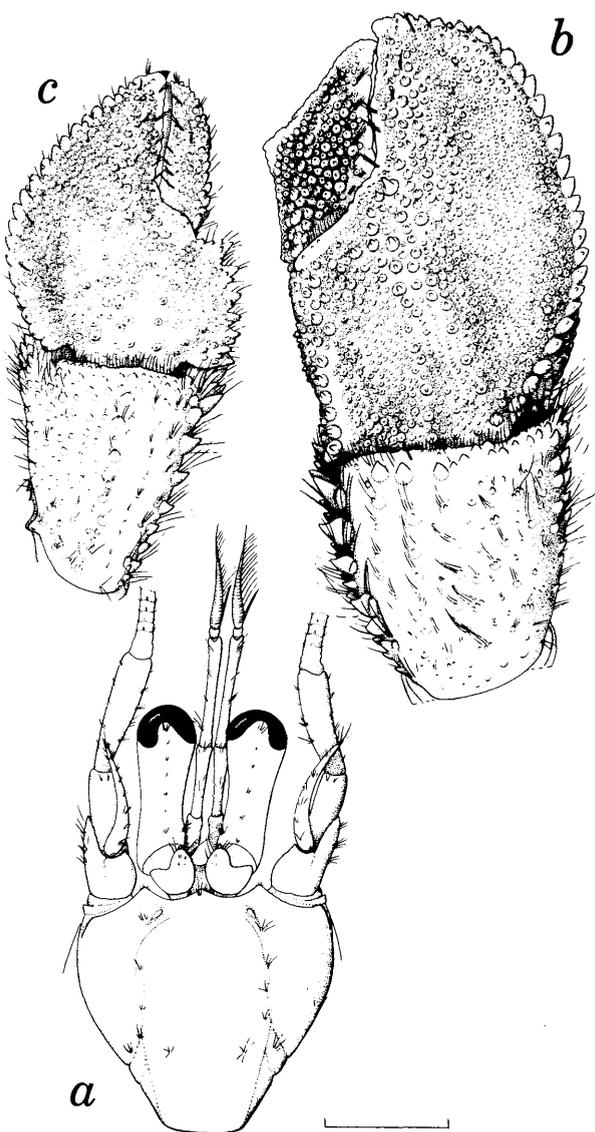


Fig. 157. *Pagurus pollicaris* Say. Female: a, anterior part of body in dorsal view; b-c, right and left chelae and carpi, external view; 5 mm indicated (USNM 173576).

Type-locality.—[East] "coast of the United States."

Known range.—Grand Manan, New Brunswick, to northeastern Florida; Key West, Fla., to Texas (Provenzano 1959, in part).

Remarks.—Differences in color between Atlantic and Gulf populations as well as the disjunct distribution suggest existence of two subspecies (Provenzano 1959).

Blake (1953) reported *P. pollicaris* from the Pleistocene of Maryland.

Ovigerous females have been reported in March, November, and December in Florida (Provenzano 1959; Dragovich and Kelly 1964), January and February in North Carolina, winter in Texas (Fotheringham 1975), April in Chesapeake Bay, and from early spring to the end of June in Massachusetts by Nyblade (1970) who also described four larval stages and a glaucothoe from laboratory rearings. In these experiments the larvae were maintained at $24^{\circ} \pm 2^{\circ}\text{C}$ and $16^{\circ} \pm 0.5^{\circ}\text{C}$ in constant light. In the first regime the four zoeal stages were passed in 15.2 days, 56.7 days in the second. Duration of the post-larval stage was not determined. Johnson (1964) gave details on the male reproductive system.

Chapple (1969a, b, c), by dissection, sectioning of tissues, experiments and substitution of a transparent plastic facsimile of a *Polynices* shell, demonstrated that *P. pollicaris* carries the shell by the columella in the crook of the abdomen, and also described components in the abdomen (including musculature and its innervation) responding to calculated forces bearing on it. Fotheringham (1976; 1976a) observed that *Clibanarius vittatus*, *Pagurus longicarpus*, and *P. pollicaris* have broadly overlapping shell utilization patterns along the Texas coast. The latter may mature four months after leaving the plankton but does not reach its asymptotic size for approximately three years. *Pagurus pollicaris* grew significantly faster in shells of preferred size than in small shells, but molted at the same rate in each. Shell weight and internal volume affect egg clutch size in this species. Females were observed with 514–10,961 eggs. Meiss and Norman (1977a, b) compared the stomatogastric ossicles and musculature to that in penaeideans, astacideans and brachyurans, finding the structure to reflect generally accepted concepts of the phylogenetic position of the anomurans. Caine (1976) found spacing of the longitudinal bars in the gland filter of the gastric mill to be directly related to particle size in diet among six species of hermit crabs. Among these, *P. pollicaris* had a finer filter than progressively coarser *P. longicarpus*, *Clibanarius vittatus*, and *Petrochirus diogenes*. Stomach contents of *P. pollicaris* were 50% flocculent detritus, 35% scavenged material

and 15% sand grains (Caine 1975).

Kellogg (1971) found small individuals in *Nassarius obsoletus* and *Terebra dislocata* shells, but larger individuals in *Polynices* and *Busycon*. The species is prone to cloaking the shells with anemones, *Calliactis tricolor*, whenever possible, and individuals can be seen stealing the anemones from each other in aquaria (Anonymous 1975). The polyclad turbellarian *Stylochus zebra* is a commensal with *P. pollicaris* from Massachusetts to North Carolina, but there and south of this region the turbellarian lives in association with other hermits, feeding mainly on the shell encrusting *Crepidula plana* (see Lytwyn and McDermott 1976).

Sikora, et al. (1972) found *P. pollicaris* in stomachs of two species of hake, *Urophycis regius* and *U. floridanus*, in Georgia estuaries. In aquaria, *P. pollicaris* will eat the jellyfishes *Cyanea capillata* or *Stomolophus meleagris* in absence of other food (Phillips, et al. 1969).

***Pagurus pubescens* Kröyer**

Fig. 158

Pagurus pubescens Kröyer 1838:314 [86].—Squires 1964:359, figs. 1A, 2A, 6.—McLaughlin 1973:564, figs. 1B, 2B, 3B.

Eupagurus kroyeri Stimpson 1859:89 [43].—Smith 1879:48.—Benedict 1896:99, fig. B.

Pagurus kroyeri.—Rathbun 1929:27, fig. 36.

Recognition characters.—Anterior shield of carapace a little longer than broad, lightly sculptured, few scattered setae, frontal margin inflated. Rostrum with rectangular to obtuse tip slightly dilated distally, length about half width of shield; eye scales ovate, each tipped by strong submarginal spine. Antennular peduncles exceeding eyestalks by nearly full length of terminal article. Antennal peduncles exceeding eyestalks by about half length of terminal article; acicles unarmed, slender and curved sinuously outward, exceeding eyestalks.

Right cheliped much larger than left; hand and carpus armed with small to medium-sized spines most prominent on margins of hand and mesial margin of carpus where they become clustered near articulation with hand; few strong single and smaller compound spines on anterior margin of carpus. Minor chela with distinctive, central, longitudinal ridge of single-file spines on palm tending somewhat mesad along its crest to form abrupt slight overhang, but gradually sloping laterally and anteriorly to margin of hand and propodal finger; dactyl and part of palm mesial to ridge rather

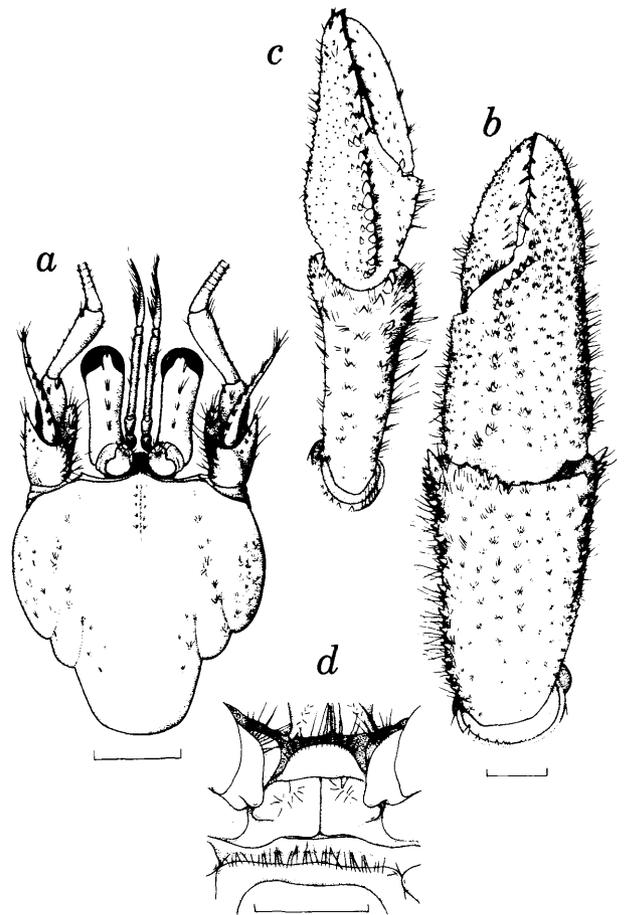


Fig. 158. *Pagurus pubescens* Kröyer. Male: a, anterior part of body in dorsal view; b-c, right and left chelae and carpi, external view; d, sternite between third legs; 5 mm indicated (USNM 98058).

smooth; lateral margin of hand with row of moderate spines, carpus laterally expanded anteriorly and armed with clustered spines; scattered hairs on both chelipeds, longest on carpi and ventral surface of hands. Walking legs (legs 2 and 3) with dactyls longer than propodi, smooth laterally but spined mesially, both articles with scattered tufts of setae.

Anterior part of sternite between third legs somewhat rectangular (almost twice as wide as long), its distal edge bearing short, sparse setae.

Measurements in mm.—Anterior shield: male, length 17.6, width 16.6; ovigerous females, length 11.6, width 11.0; length 8.3, width 7.8.

Variation.—The anterior portion of the sternite between the third legs is basically rectangular but varies somewhat in shape, and the setae on its distal edge are usually sparse but may be either short or long. The eye scales vary in width and some have supernumerary spines on tubercles on the mesial margin. The rostrum varies in acuteness at the tip.

Habitat.—This species has been reported from a wide variety of bottoms in arctic, subarctic, and boreal waters (Smith 1879; Squires 1957), tending to occur in deeper water in the southern parts of its range. Squires (1966) reported it occurring from 4 to 550 m, but mostly from 10 to 110 m, and in temperatures of -1.6° to 4.6°C in the northerly parts of its range.

Type-locality.—W. Greenland (Squires 1964).

Known range.—West Greenland, Foxe Basin, and Hudson Bay to off Cape Hatteras; Spitzbergen, Novaya Zemlya, and Barents Sea to Faeroes, Hebrides, England (except south coast), and south-western Ireland (partly summarized in Williams 1974c).

Remarks.—Bousfield and Laubitz (1972), and Brunel (1970), gave further details on distribution in southeastern Canada. McLaughlin (1973) elaborated further distinctions between *P. pubescens* and the seemingly related *P. bernhardus* of Europe, showing morphological differences in both larvae and adults and at the same time questioning the possibility of hybridization between the two as was proposed by Jennings (1972).

Breeding season has not been reported in detail from the broad area of distribution. Squires (1962) recorded spawning in Frobisher Bay, Baffin Island, in autumn, and there are ovigerous females in the USNM collection from the northeastern Grand Banks in June, upper St. Lawrence estuary in July, and off Virginia in March.

Genera of the *Pylopagurus* Group

The genus *Pylopagurus* sensu lato has been split into a number of new genera (McLaughlin 1981). This somewhat heterogeneous assemblage has the following main characters, but the reader should see McLaughlin's revision for ample diagnoses of the new taxa: Right chela enlarged in form of operculum more or less exactly closing orifice of crab's protective housing, flexing at right angle on limb and prevented from complete extension by anterior edge of carpus, lower surface regularly convex; left chela more or less reduced; fingers of both flexed chelae moving in plane perpendicular to axis of body, those of minor chela ending in corneous tips. Frontal margin with 3 acuminate to obtuse projections. Fourth legs subchelate to nearly chelate; fifth chelate with well-developed rasp on fingers. Female with pair of pleopods behind last thoracic sternum followed by 4 unpaired pleopods along left side; male lacking first pair and with only 3 along left side. (Modified after A. Milne Edwards and Bouvier 1893.)

Genus *Anisopagurus* McLaughlin 1981

McLaughlin 1981:6.

Anisopagurus pygmaeus (Bouvier)

Fig. 159

Eupagurus pygmaeus Bouvier 1918:11, fig. 4.

Pagurus pygmaeus.—Provenzano 1959:410, fig. 19.

Anisopagurus pygmaeus.—McLaughlin 1981:6.

Recognition characters.—Anterior shield of carapace longer than wide and relatively smooth. Rostrum obtuse and slightly in advance of each lateral projection surmounted by slightly subterminal spine. Eyestalks shorter than width of anterior shield, wide at base, constricted in middle; eye scales with elongate anterior lobe armed along anteromesial margin with 3 to 5 spines. Antennular peduncles extending beyond eyestalks by about half length of terminal article. Antennal peduncle also

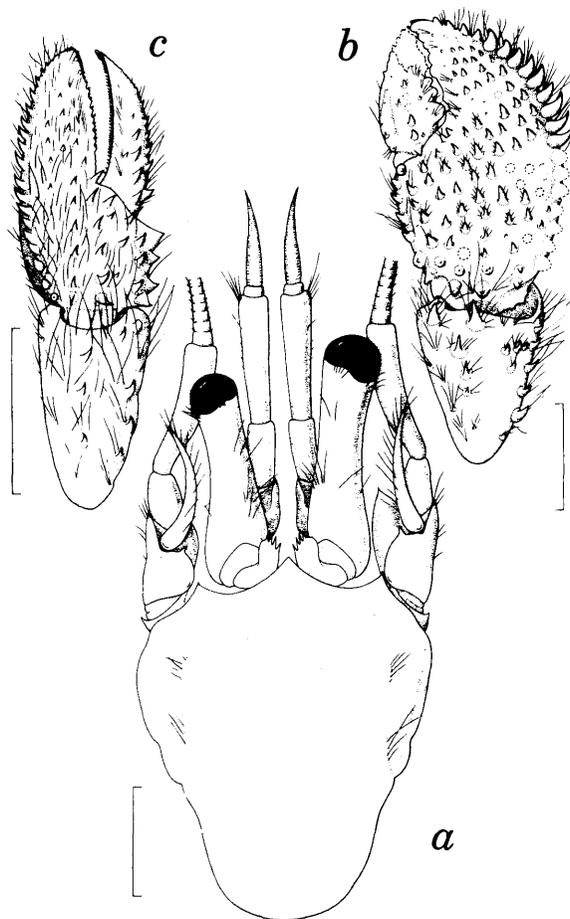


Fig. 159. *Anisopagurus pygmaeus* (Bouvier). a, Anterior part of body in dorsal view; b-c, right and left chelae and carpi. USNM 122457, a-b, male; USNM 48763, c, female; 1 mm indicated.

exceeding eyestalks; unarmed acicle curving outward, with tip reaching to or beyond base of cornea.

Chelipeds unequal, right much larger than left, both with some long, fine setae. Major chela sub-oval, more or less rimmed with row of strong, forward projecting spines; upper surface covered with smaller, nearly blunt, forward trending spines; carpus with 3 or more strong spines on upper anteromesial surface and 2 or more located laterally near short row of spines along lateral margin. Minor chela twice as long as broad; fingers spooned, with comb of fine corneous teeth on opposed edge distally; upper surface with many blunt spines (occasionally sharp), some formed into 2 central longitudinal rows; carpus with double row of strong forward-projecting spines on upper surface. First and second walking legs (legs 2 and 3) with dactyls shorter than propodi, variable number of spines on both articles.

Measurements in mm.—Anterior shield: male, length 2.5, width 2.9; ovigerous females, length 1.76, width 1.76; length 1.88, width 1.63.

Variation.—The lateral projections are obsolescent in some mature females and juveniles, their position being indicated only by the submarginal spine.

Color.—“. . . 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 (no. 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-light 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. The eggs are yellow-orange.” (Hazlett 1966b.)

Habitat.—Hazlett (1966b) working in Curaçao found this small species limited to waters with open circulation and on a substrate of medium to large rocks with space between them and covered with a heavy, encrusting, red-scarlet algal growth (instead of the usual brown or green algae or detritus). Crabs were found in a meter or less of water, and during day always hidden beneath rocks and stones. *Pagurus brevidactylus* sensu stricto and *Phymochirus* (= *Pylopagurus*) *operculatus* were present in the same microenvironment; mostly this was in rock piles constructed by fishermen for breakwaters. To 82 m.

Type-locality.—Bahia de Socapa (= Zocappa) near Santiago de Cuba.

Known range.—Off Little River Inlet, S. C.;

southern Florida, including Tortugas, to Puerto Rico; Curaçao; to 82 m.

Remarks.—Ovigerous females are recorded in May from Cuba, July from Tortugas, August from South Carolina, and Hazlett (1966b) observed them in Curaçao.

Glaucothoes of *A. pygmaeus* oriented poorly in their first contact with shells (Hazlett and Provenzano 1965), some individuals making several attempts over periods of days before entering shells. Young crabs interact little with each other, but the older crabs do. In other studies, Hazlett (1966a, b) placed *A. pygmaeus* low in a ranking of *Pagurus* species expressing pagurid behavior. Shell fighting involves rapping and shell shaking; raps may be as many as 113/min, most of the motions being equal to the length of the eyestalks but some are half the length of the cephalothorax. Activity is mainly nocturnal. Mating behavior was observed in some detail.

Genus *Manucomplanus* McLaughlin 1981

McLaughlin 1981:6.

Manucomplanus corallinus (Benedict)

Fig. 160

Eupagurus corallinus Benedict 1892:23.

Pagurus corallinus.—Hay and Shore 1918:412, pl. 30, fig. 4.

Pylopagurus corallinus.—Williams 1965:134, fig. 110.

Manucomplanus corallinus.—McLaughlin 1981:6.

Recognition characters.—Anterior shield of carapace subcordate, smooth, truncate posteriorly. Rostrum obtuse, produced beyond rounded, unarmed lateral projection of front. Eyestalks stout, falling far short of tip of antennular peduncle, largest distally, cornea dilated; eye scales sharply pointed and with prominent subterminal spine. Antennal peduncle nearly as long as that of antennule; acicle reaching nearly to tip of cornea.

Chelipeds unequal, right larger than left and operculiform. Upper surface of major chela flattened or slightly excavated, covered with small, slender spines becoming flattened and mushroom-shaped on fixed finger as well as a few on dactyl; hand fringed with spines, often alternately large and small, becoming longer near tips of fingers, inner surface with spinose tubercles between base of dactyl and recess receiving carpus, recess bounded by crest; carpus approximately as long as palm, upper surface thickly set with sharp, spiny

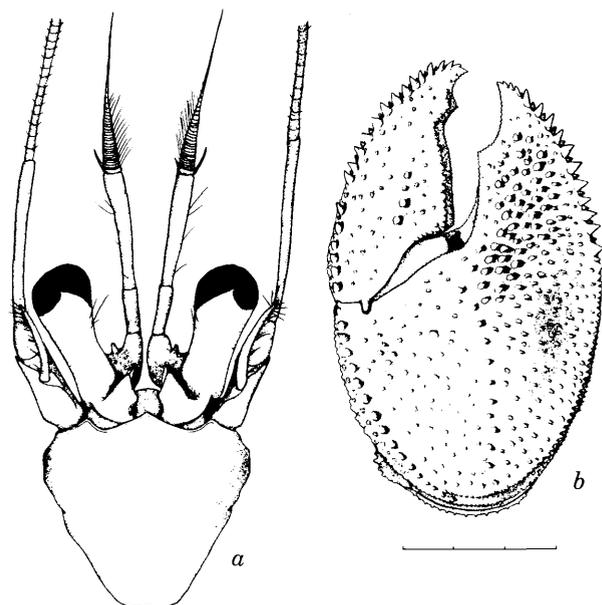


Fig. 160. *Manucomplanus corallinus* (Benedict). a, Anterior part of body in dorsal view; b, right chela, external view; (from two specimens) 3 mm indicated (from Williams 1965).

granules, margin with rows of small spines; merus compressed, quadrilateral when viewed laterally. Minor chela with hand broad, flattened; fingers broad, gaping at base; carpus compressed, surmounted by inner row of small and outer row of larger spines; merus compressed. Carpus and propodus of first walking leg and carpus of second crested with acute spines; dactyls setose, row of movable, distally pointing spines on ventral margin.

Measurements in mm.—Anterior shield: male, length 3.5, width 4.1; ovigerous female, length 2.4, width 2.6.

Color.—Large cheliped with merus and carpus blotched red and white; small cheliped and walking legs banded with same color (Benedict 1892).

Habitat.—In tunicates, sponges, stony corals, and bryozoans; 38 to 91 m (Wenner and Read 1982).

Type-locality.—Off Key West, Florida.

Known range.—Off Cape Lookout, N. C., to Gulf of Mexico between Cedar Keys, Fla., and Mississippi Delta; off Cape Catoche, Yucatan; a mutilated ovigerous female, probably of this species, off French Guiana (USNM 119889).

Remarks.—Ovigerous females have been taken off South Carolina in March, southern and western Florida in March and June, Georgia in June, and French Guiana (?) in September.

A specimen from Georgia was housed in a bryozoan "Texas longhorn shell."

Metabolically as well as geographically, this spe-

cies is tropical in affinities (W. B. and F. J. Vernberg 1970).

Genus *Phimochirus* McLaughlin 1981

McLaughlin 1981:4.

Phimochirus holthuisi (Provenzano)

Fig. 161

Pylopagurus operculatus.—Holthuis 1959:157, fig. 31.

Pylopagurus holthuisi Provenzano 1961:162, fig. 3.

Phimochirus holthuisi.—McLaughlin 1981:4.

Recognition characters.—Anterior shield of carapace about as long as wide, subcordate. Rostrum obsolete, hardly in advance of semi-acute lateral projections; anterolateral angles sloping posterolaterally without shoulders. Eyestalks about 3 times longer than wide, cornea dilated; eye scales slender, grooved dorsally, each ending in acute tooth or spine. Antennular peduncles extending slightly beyond cornea. Antennal peduncles not exceeding cornea; acicles simple, unarmed, reaching past posterior margin of cornea.

Chelipeds unequal, right larger than left and operculiform. Major chela slightly longer than greatest width, upper surface inflated, margins thin, slightly upturned and serrated; mesial margin of palm ending in prominent acute projection at base of dactyl, low rounded granules distributed over distal surface of palm and on fixed finger; dactyl with shallow groove on dorsal surface between 2 rows of round granules; carpus with 4 low appressed teeth on mesiodorsal margin, prominent mesiodistal tooth, and low ridge on distolateral margin; merus rounded dorsally in lateral view, ventral spine at anterolateral corner, anteromesial margin irregularly serrated and pair of small spines on dorsal anterior margin. Minor chela narrow, fingers spooned, tufts of heavy setae between fingers and on ventral surface; carpus with spine on anterodorsal-lateral-mesial margins and row of spines behind latter. Dactyls of walking legs longer than propodi, strong row of spines ventrally and weaker mesiodorsally; propodus with 1 or more weak ventral spines; merus with anterior dorsal tooth.

Measurements in mm.—Anterior shield: male, length 4.4, width 4.4; ovigerous (?) female, length 3.9, width 3.6.

Color.—"Anterior carapace with symmetrically placed pairs of short, longitudinal dark stripes. Posterior carapace markings blue. Blue spots on

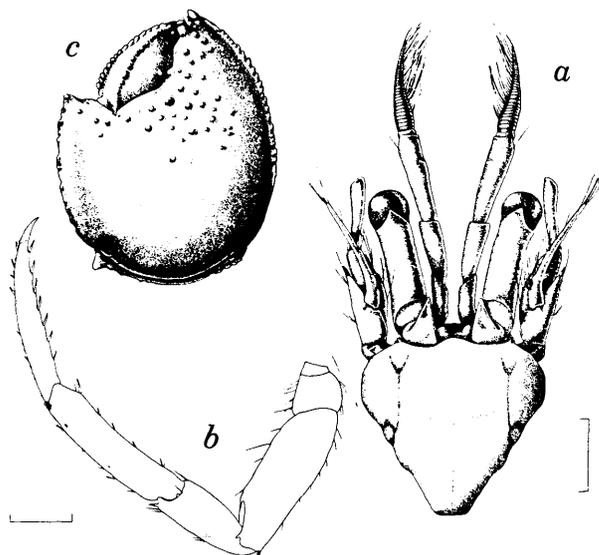


Fig. 161. *Phimochirus holthuisi* (Provenzano). a, Anterior part of body in dorsal view; b, first walking leg; c, right chela, external view; a, 5 mm; b-c, 2 mm indicated (from Holthuis 1959).

dorsal surface of abdominal somites. Eyestalks with thin ring of brownish pigment on proximal third. Antennules with brownish-yellow pigment band around ultimate and penultimate segments. Antennal scale and peduncle with spots of similar color. Major manus white distally, on dorsal surface very diffusely colored proximally with faint reddish-purple. (Paratype, with a few small scattered orange spots on dorsal face of merus.) Major carpus irregularly but diffusely colored with purple, anterodorsal margin with alternating white and dark spots. Merus blotched with purple. Minor manus colored similarly to walking legs which have on the dactylus a brownish longitudinal stripe on each side, another on the dorsal margin and one ventrally. Propodus with two stripes on each side, a fifth on dorsal margin, ventral stripe very diffuse. Stripes otherwise imposed on a diffuse yellow background which forms a band around each segment" (Provenzano 1961, from holotype).

Habitat.—Shell, sand, mud and coral bottoms; 15 to 104 m.

Type-locality.—Sand patch on coral rock bottom, 4½ mi. SE Ram's Head, St. John, Virgin Islands, 15–18 m.

Known range.—Off Oregon Inlet, N. C. (Herbst, et al. 1978), to Alabama (?); through West Indies to Surinam.

Remarks.—The species is closely related to *Phimochirus* (= *Pylopagurus*) *operculatus*. An ovigerous female taken off Alabama in March (USNM 102504) is questionably referred to this species; it has relatively longer eyestalks and eye scales than the holotype male and an acute rostrum exceeding each

lateral projection surmounted by an outwardly directed spinule. The major chela is missing from this specimen.

The deepest recorded occurrence is off Georgia, 30°51'30"N, 79°58'W. Specimens are recorded from stomachs of large adult hogfish, *Lachnolaimus maximus*, at St. John (Provenzano 1961).

Genus *Pylopagurus* A. Milne Edwards and Bouvier 1893

McLaughlin 1981:2.

Pylopagurus discoidalis (A. Milne Edwards)

Fig. 162

Eupagurus discoidalis A. Milne Edwards 1880:41.

Pylopagurus discoidalis.—A. Milne Edwards and Bouvier 1893:76, pl. 6, figs. 7–14.—Williams 1965:134, fig. 109.—McLaughlin 1981:2.

Recognition characters.—Anterior shield of carapace strongly calcified, subcordate, smooth, truncate posteriorly; anterior margin with large, sharp-pointed rostrum extending beyond middle of eye scales; lateral projections rudimentary, low and rounded, borders lateral to them very oblique. Eyestalks short, thick, widest distally, shorter than length of frontal border, not reaching middle of terminal article of antennular and antennal peduncles, cornea large; eye scales narrow, lanceolate. Acicles without spine and deflected a little outward, varying from shorter than to slightly exceeding eyestalks.

Chelipeds unequal, right larger than left. Major chela in form of operculum adapted to close openings in *Dentalium* shells or similar tubes; chela flexing at right angle on carpus and incapable of complete extension, upper surface smooth, flattened or slightly excavated, nearly discoidal in outline, surrounded by raised border with finely crenulate edge, lower surface slightly wrinkled with lines; fingers compressed, internal border of dactylus with rounded tubercles; carpus short, dilated in front, external surface ornamented with granulations following feebly squamose irregular lines (occurring also on hand back of edge forming operculiform portion), and with few denticles on anterior border. Minor cheliped shorter, chela oval, very fine denticles on lateral border; fingers agape at base and terminating in corneous tips; carpus with some spines on crest. Walking legs reaching tip of major chela, dactyls setose and with lanceolate, corneous terminal claw well developed.

Measurements in mm.—Anterior shield: male,

length 5.5, width 4.4; ovigerous female, length 3.9, width 3.5.

Variation.—The large chela may be elongate, but becomes more discoidal with advancing age (Milne Edwards and Bouvier 1893).

Color.—Whitish but with large areas of reddish on hands, on each article of legs, and ring of same color near base of eyes; reddish color may extend over anterior part of cephalothorax (Milne Edwards and Bouvier 1893).

Habitat.—The species has been taken from *Dentalium* shells and from annelid tubes of similar shape; 55 to 930 m.

Type-locality.—Montserrat, 220 m.

Known range.—ENE Oregon Inlet, N. C. (Provenzano 1963a), through eastern Gulf of Mexico and West Indies to mouth of Amazon River, Brazil.

Remarks.—Ovigerous females are known from the northern Gulf of Mexico in March, and are recorded in November from southern Florida and Brazil.

Hazlett (1966a) stated that living only in scaphopod shells [?] seems to have affected behavior patterns in this species; the crab can move quickly but not backward because the housing digs into sand, therefore the crabs tend to withdraw into their shells during aggressive interactions. As they walk, feed, etc., the major hand is at an oblique angle to the carpus, thus always in a "presentation" position; cheliped extension is from this position when two

come together. Other movements of the small chelae were also discussed.

Genus *Rhodochirus* McLaughlin 1981

McLaughlin 1981:3.

Rhodochirus rosaceus (A. Milne Edwards and Bouvier)

Fig. 163

Pylopagurus rosaceus A. Milne Edwards and Bouvier 1893:97, pl. 7, figs. 10–17.—Hay and Shore 1918:413, pl. 30, fig. 5.—Williams 1965:135, fig. 111.

Pylopagurus acutus Forest and de Saint Laurent 1967:148, figs. 114, 120–123.

Rhodochirus rosaceus.—McLaughlin 1981:3.

Recognition characters.—Anterior shield of carapace subcordate, truncate posteriorly; anterior margin with 3 projections, rostrum obtuse and falling short of strong lateral projections, each terminating in minute spine; sides of dorsal surface and anterior surface with few tufts of setae. Eye stalks stout, shorter than anterior shield, distinctly dilated distally and with 3 or 4 tufts of setae in line along upper surface; eye scales subacute anteriorly, each ending in slender subterminal spine. Antennal peduncle extending beyond eye, flagellum slender and longer than body; acicle strongly curved, reaching almost to distal edge of cornea.

Chelipeds unequal, right much larger than left. Both chelae capable of being bent down at right angle to carpus to form, either singly or together, an operculum closing orifice of cavity inhabited by crab. Both margins of major chela, and outer margin of minor chela, armed with row of close-set, conical teeth; upper surface of both hairy and covered with closely crowded, rosettelike tubercles each consisting of central larger tubercle surrounded by smaller ones; major chela with longitudinal ridge on each finger, ridge on minor propodus much weaker, concavity on propodi of each between central ridge and lateral margin; inner surface of major hand slightly rugose between base of dactyl and recess receiving carpus. Carpus of major cheliped with scattered sharp spines and hairs dorsally, strongest along mesial margin; merus with cross striae on upper surfaces, its anterior edges serrated with teeth in single row. Minor cheliped similar but hairier and with crest of spines on carpus. Walking legs of medium length, first and second of left side, and second of right side exceeding large

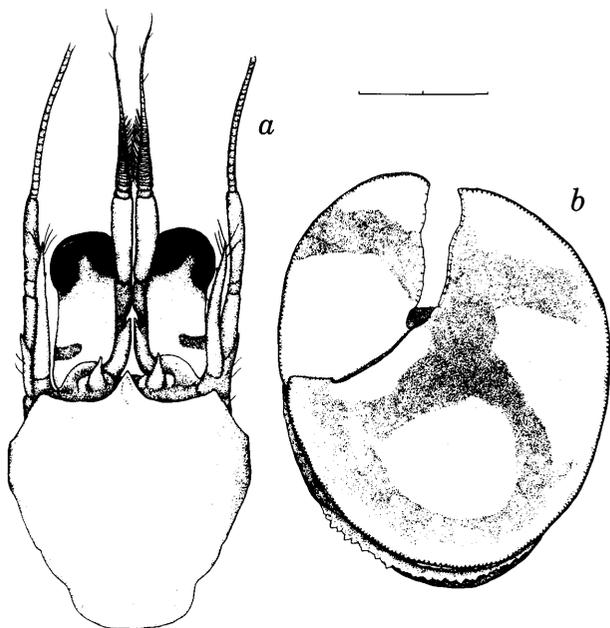


Fig. 162. *Pylopagurus discoidalis* (A. Milne Edwards). Ovigerous female: *a*, anterior part of body in dorsal view, eyestalks showing color pattern; *b*, right chela, external surface showing color pattern; 2 mm indicated (from Williams 1965).

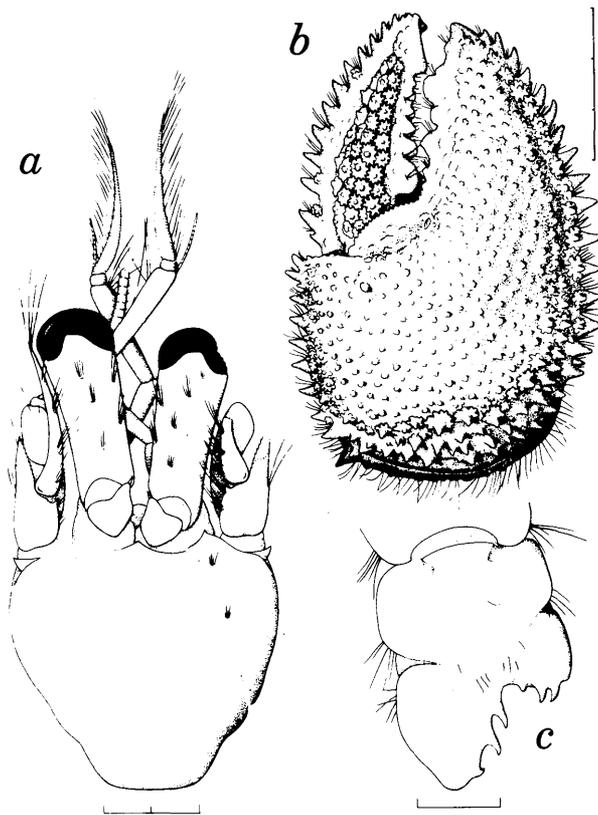


Fig. 163. *Rhodochirus rosaceus* (A. Milne Edwards and Bouvier). a, Anterior part of body in dorsal view; b, right chela, external view (from Williams 1965); c, telson. a, MCZ, holotype female, 2 mm; b, 3 mm; c, holotype female, 1 mm indicated.

chela, articles setose on dorsal margin, dactyls with row of ventral spines.

Measurements in mm.—Anterior shield: male, length 5.3, width 5.6; ovigerous female, length 3.7, width 3.9; holotype female, length 5.5, width 5.6.

Color.—Some specimens faded in alcohol retain alternate, longitudinal, light and orange to reddish stripes on dorsal and lateral surfaces of the walking legs, and tints of reddish on the chelipeds and eyestalks.

Habitat.—The holotype was taken from an unknown species of the molluscan genus *Antillophos* (= *Phos*); 119 to 168 m; (70–90 m, Cain 1972).

Type-locality.—Grenada, 168 m.

Known range.—South of Cape Lookout, N. C.; Grenada, and Surinam.

Remarks.—An ovigerous female is known from Surinam in September. The record listed from off Western Dry Rocks, Key West, Fla. (Williams 1965), is an incorrect identification.

Forest and de Saint Laurent (1967) compared their new species, *Rhodochirus* (= *Pylopagurus*) *acutus*, to *P. rosaceus* saying that it seemed closer to the form described by Hay and Shore (1918) and Williams (1965) from North Carolina than to *Rhodo-*

chirus (= *Pylopagurus*) *rosaceus* but that comparison of the type of *P. rosaceus* with specimens of Williams and the type of *P. acutus* would be necessary to verify this hypothesis. I have not seen the type of *P. acutus*, but reliance on good illustrations (Forest and de Saint Laurent 1967), the holotype of *P. rosaceus*, and specimens from the Western Atlantic yields the following information.

The type of *P. rosaceus* is a damaged, partly decalcified female specimen which was imperfectly illustrated by Milne Edwards and Bouvier (1893). Their illustration shows the eyestalks and eye scales too close together and lateral projections of the shield devoid of spines. The left side of the shield is now fractured and the right side broken and folded over, but, when laid in position, the right lateral projection exceeds the level of the obtuse rostrum and is tipped by a tiny spine directed laterad. From the type and comparative material, it seems evident that there is considerable variation in the rostrum. In material from North Carolina (USNM 51046, 102719) the rostrum is obtuse, but in a lot of 12 specimens from French Guiana (USNM 103481) the rostrum is obtuse in 6, intermediate in 2, and acute in 4. None of the above are exactly like the holotype; all except 102719 have tiny spines on the lateral projections, but though rostrums vary in length, none are as advanced as shown by *P. acutus* (Forest and de Saint Laurent 1967). Telson spines are bluntest in the type of *P. rosaceus*, but acute in most of the other material except a male from 51406. On balance it seems that all of these are probably one species, more acutely spinose in southern parts of their range, becoming less so with age.

Genus *Tomopaguropsis* Alcock 1905

Alcock 1905:136.

Tomopaguropsis problematica (A. Milne Edwards and Bouvier)

Figs. 164–165

Eupagurus? *problematicus* A. Milne Edwards and Bouvier 1893:151, pl. 11, figs. 1–10.

Tomopaguropsis problematica.—Alcock 1905:137.

Recognition characters.—Anterior shield of carapace fairly smooth but grooved at sides, slightly wider than long, truncate posteriorly. Rostrum acute, extending between eye scales and well advanced beyond acute, divergent, spiniform tips of lateral projections. Eyestalks somewhat dilated at cornea, a bit longer than distance between lateral

projection of front; anterior projection of eye scales formed as a bent triangle directed outward distally and tipped by tiny spine, dorsal surface convex. Antennular peduncles exceeding eyestalks by about $\frac{3}{4}$ length of terminal article. Antennal peduncle about length of eyestalk; acicles rather stout, curved outward and extending to tip of peduncle.

Chelipeds superficially similar in shape but right larger than left. Major chela with irregular short setae dorsally, surface a bit uneven but essentially smooth except for few tubercles or low spines along mesial margin; dactyl of female less than half length of hand, with 2 or more sometimes conspicuous teeth proximal to conspicuous tooth at midlength of propodal finger; carpus rather smooth dorsally but row of low, well-separated spines on mesial margin and 1 or 2 near anterior border. Minor hand shorter, narrower, more uneven, and with finger proportionately thicker in lateral view; carpus a bit

spinier and hairier than opposite member. Walking legs (legs 2 and 3) little longer than chelipeds, rather stout, conspicuously setose dorsally, dactyls longer than propodi.

Measurements in mm.—Anterior shield: male, length 3.5, width 3.88; female, length 5.0, width 5.25.

Habitat.—13.7 to 528 m.

Type-locality.—Near Sand Key [SSW Key West, Fla.], 228.6 m.

Known range.— $1\frac{3}{4}$ mi. NE Cape Lookout, N. C.; southern Florida and Bahamas; Barbados; off Honduras ($16^{\circ}39'N$, $82^{\circ}29'W$).

Remarks.—I left this species out of the Carolinian fauna in 1965 because the single specimen known from near Cape Lookout, N. C., had a question mark on the jar label after the vessel name

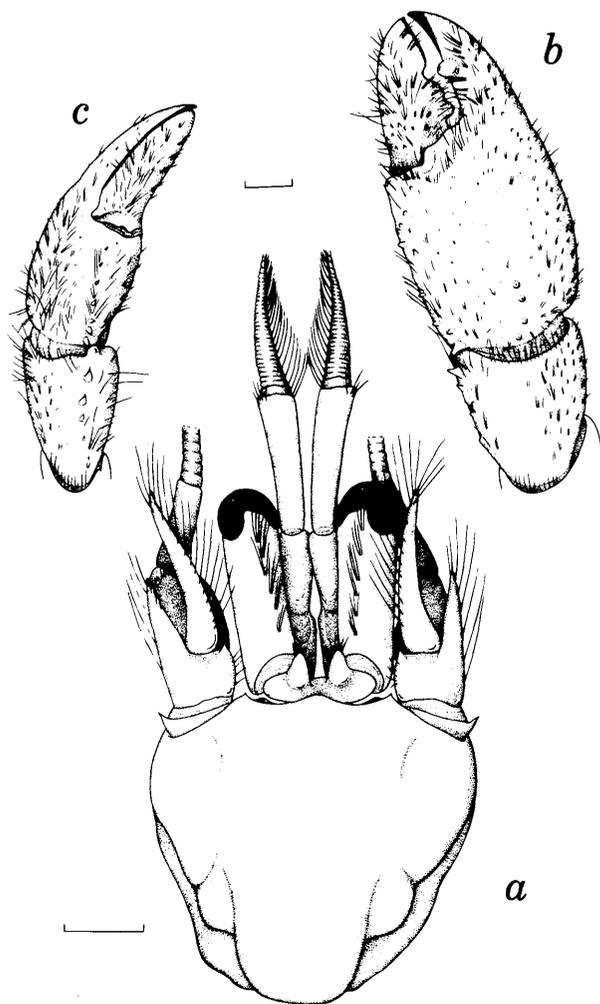


Fig. 164. *Tomopaguropsis problematica* (A. Milne Edwards and Bouvier). Male: *a*, anterior part of body in dorsal view; *b-c*, right and left chelae and carpi, external view; 1 mm indicated (MCZ, holotype).

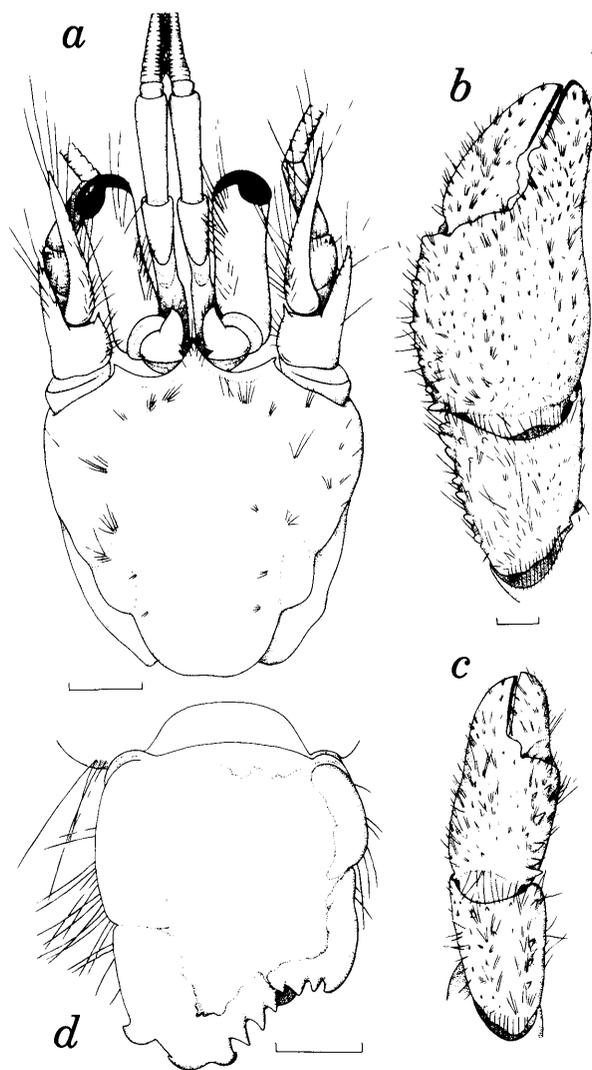


Fig. 165. *Tomopaguropsis problematica* (A. Milne Edwards and Bouvier). Female: *a*, anterior part of body in dorsal view; *b-c*, right and left chela and carpi, external view; *d*, telson; 1 mm indicated (USNM 102720).

(made out in 1958). I now consider this record valid. The specimen was collected by the *Fish Hawk* in 1902 in sample 7302, the first sample taken in that cruise off North Carolina. There is no question concerning the locality marked in either the *Fish Hawk* records or the USNM (102720) catalog entry.

Family Lithodidae

Crablike; abdomen more or less firm, often segmented, bent under thorax. Tail fan not developed, uropods absent. First pair of legs chelate; fourth pair like third; fifth pair very small, folded under carapace to give superficial appearance of only 4 pairs of legs (Rathbun 1929).

Genus *Lithodes* Latreille 1806

Latreille 1806:39.—Rathbun 1929:29.—Balss 1957:1592.—Hemming 1958b:175.

Lithodes maja (Linnaeus)

Fig. 166

Cancer maja Linnaeus 1758:629.

Lithodes Maia.—Bell 1853:165, fig.

Lithodes maia.—Bouvier 1896:10, 24.—Selbie 1921:56, pl. 9, figs. 1–4.—Rathbun 1929:29, fig. 39.

Lithodes maja.—Stephensen 1935:8.—Holthuis 1950:141, figs. 51, 52, 53.—Balss 1957:1592, fig. 1170.—Squires 1965a:110.

Recognition characters.—Carapace pyriform in outline, about as long as broad, exclusive of rostrum and marginal spines; margin somewhat reflexed and armed with numerous long, strong spines, anterolateral ones strongest; dorsal surface ornamented with numerous spines and tubercles, regions distinct and elevated except sunken hepatic area. Rostrum prominent, elongate, bifurcated at tip, armed on basal $\frac{1}{3}$ with 2 divergent spines and near base with 2 or more divergent dorsal-dorsolateral spines; prominent, forwardly curved, median ventral spine between divergent eyestalks.

Chelipeds unequal, shorter than adjacent walking legs; merus and carpus armed with strong, sharp spines on mesial and dorsal surfaces; hands with scattered moderate spines on mesial margin and sharp tubercles dorsally; fingers spooned at tips, about as long as palm and finely serrate on opposed cutting edges of smaller chela, shorter than palm and with broad calcareous teeth on opposed cutting edges of larger chela, tufts of stiff setae on

fingers of both hands. Second to fourth legs similar, elongate, cylindrical proximally to compressed distally and strongly spined on merus, carpus and propodus; each dactyl somewhat compressed, curved, terminating in slender corneous tip, and armed proximally with prominent lateral and mesial spine, usually smaller pair of dorsal spines, and 2 or more still smaller appressed spines on external (dorsal) surface, sparse row of very slender spines ventrally. Fifth legs reduced and folded beneath carapace in gill chamber, each ending in tiny, spatulate, hairy chela.

Abdomen greatly modified, permanently folded beneath cephalothorax; first and second segment fused in broad, calcified, tuberculate and spiny, nearly vertical curved plate; remaining segments more or less molded into flattened, tuberculate, plastronlike structure composed of tuberculate leathery central portion bounded by radiating, calcified, paired plates of third, fourth and fifth segments and unpaired sixth, in turn bounded by narrow calcified marginal plates (in males) and telson; third to fifth segments symmetrical in males, but strongly asymmetrical in females with plates of third, fourth and fifth segments much enlarged on left side and narrow marginal plates lacking on left.

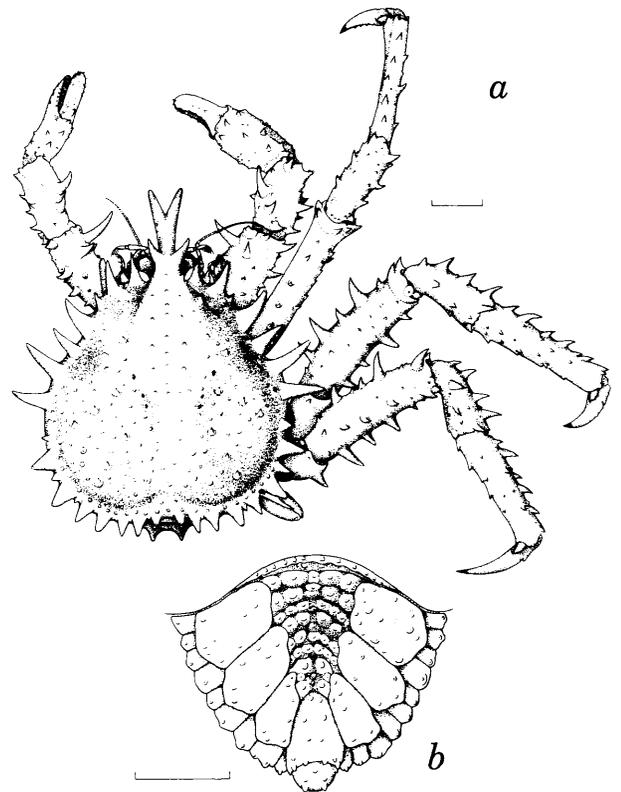


Fig. 166. *Lithodes maja* Linnaeus. Male: a, dorsal view, walking legs of left side not shown; b, abdomen; 10 mm indicated (USNM 2015).

Measurements in mm.—Extreme length of carapace including spines at least 145 in large specimens, sex unknown (Selbie 1921), but usually smaller. Kampf and Kittel (1952/53) pictured specimen with leg span of about 40 cm.

Variation.—Spinination varies individually and the rostrum is not always provided with dorsal spines on the basal third.

Color.—“Madder brown, tubercles and spines tipped with vinaceous cinnamon; legs obscurely banded with two shades of the brown” (Rathbun 1929); yellowish red, spines darker, under surface paler (Bell 1853); bright red with dull spines (Holthuis 1950).

Habitat.—Essentially a boreal species from moderate depths but not found in waters below 0°C and rare below 2.5°C (Blacker 1957); 65–790 m (Rathbun 1929; Selbie 1921; Squires 1965a, 1966; Stephensen 1935).

Type-locality.—*Habitat in Oceano Europaeo.*

Known range.—East and west Greenland to Sandy Hook, N. J.; Iceland; Spitsbergen; Barents Sea and North Sea to Netherlands and Belgium, Western Scotland to Isle of Man, and western Ireland to County Cork (Christiansen and Christiansen 1962; Hillis 1966; O’Riordan 1968; Rae and Lamont 1963; Selbie 1921; Squires 1966).

Remarks.—In European waters, ovigerous females are known from December to March (Holthuis 1950) and in December and April from Bear

Island south of Spitsbergen (Blacker 1957); in the northwestern Atlantic, about 60% of females are ovigerous in autumn (Squires 1970). MacDonald, et al. (1957) summarized knowledge of larval development and described the eggs; two zoeal stages and a glaucothoe are known from laboratory hatchings and plankton.

Old individuals may be greatly overgrown with fouling organisms such as calcareous worm tubes (Sivertsen 1953).

Section Galatheidea

Superfamily Galatheoidea

Family Galatheidae

Carapace longer than wide, often ornamented with transverse, ciliated lines. Rostrum distinct and strongly pointed, projecting beyond eyes. Antennular peduncle elongate. Antennae with 4-jointed peduncle. Chelipeds greatly elongated, slender. First, second, and third walking legs well developed; last leg feeble, reduced in size. Abdomen bent upon itself but not folded under thorax; males with pair of sexually modified pleopods on segments 3, 4 and 5; females with rudimentary pleopods on second segment, fully developed pleopods on 3, 4 and 5.

Key to Genera and Species

(Adapted from Chace 1942)

1. Rostrum rather broad, concave or flattened above, margins toothed *Galathea rostrata*
Rostrum slender, occasionally very finely serrate but toothless; supraocular teeth at base [*Munida*] 2
2. Posterior margin of carapace unarmed, no median spines on cardiac region 3
Ridge along posterior margin of carapace armed with spines, 1 or more spines on cardiac region, rostral spine slightly shorter than supraocular spines *M. longipes*
3. Basal segment of antennular peduncle with distolateral spine longer than distomesial spine; a large species *M. valida*
Basal segment of antennular peduncle with distomesial spine longer than distolateral spine 4
4. Merus of third maxillipeds with single spine on lower margin 5
Merus of third maxillipeds with 3 or 4 spines on lower margin. *M. irrasa*
5. Supraocular spines reaching to distal edge of or beyond cornea; a medium-sized to large species *M. iris iris*
Supraocular spine not reaching to distal edge of cornea; a small species. *M. pusilla*

Genus *Galathea* Fabricius 1793

Fabricius 1793:471.—Hemming 1958b:143.—Baba 1969:9.

***Galathea rostrata* A. Milne Edwards**

Fig. 167

Galathea rostrata A. Milne Edwards 1880:47.—Hay and Shore 1918:402, pl. 29, fig. 4.—Chace 1942:30.—Haig 1956:2.—Williams 1965:105, fig. 81.

Recognition characters.—Carapace somewhat flattened; transverse ciliated ridges prominent, at least 4 continuous for entire width; lateral margins with number of acute spines, each spine at end of ridge.

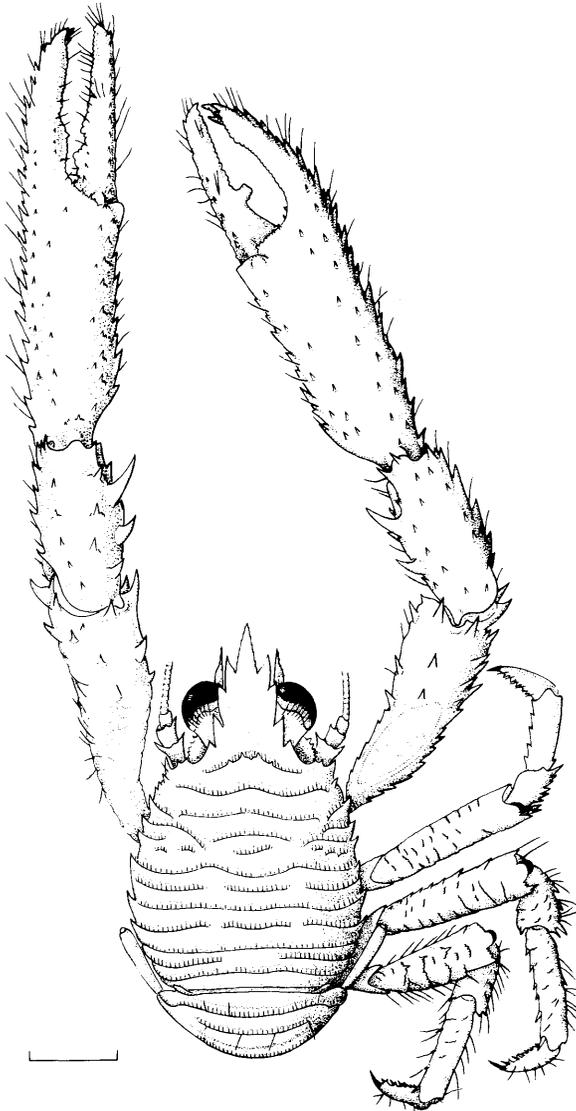


Fig. 167. *Galathea rostrata* A. Milne Edwards. Male in dorsal view, walking legs of left side not shown; 2 mm indicated (USNM 9604).

Front prolonged into broad, shallowly excavated rostrum armed with usually 4 strong, anteriorly pointing spines on each side, and prominent, narrowly triangular tip. Merus of third maxillipeds with 3 or 4 spines on lower margin.

Chelipeds nearly twice as long as body, comparatively heavy; with rows of spines or spiniform granules along margins and appressed, squamiform, ciliated granules on surfaces; a few larger spines on carpus and distal end of merus. Hand little shorter than body; opposed edges of fingers finely serrate, nearly straight in juveniles but increasingly uneven in adults; chelipeds often asymmetrical in males with fingers of larger hand gaping.

Abdomen with transverse striae similar to those on carapace but lacking lateral spines.

Measurements in mm.—Length of carapace including rostrum: male 10.6, ovigerous female 9.6.

Color.—Ground color off-white, cream, and light yellow; mottled with orange and reddish orange especially on legs, less evident on body; spines red or tipped with red; a single small circular reddish spot in center of each branchial region; a white band on propodi of walking legs; distal half of fingers white (from specimen recently preserved in formalin).

Habitat.—Has been taken from the coral, *Oculina diffusa*, in the northeastern Gulf of Mexico (S. Alexander, personal communication), and ivory tree coral (see below); 18 to 92 m.

Type-locality.—16 miles north of Jolbos Islands [Yucatan Peninsula] at 26 m.

Known range.—Off Cape Hatteras, N. C., to southern Florida, northwestern Florida to Mississippi Delta, and off Cape Catoche, Yucatan, Mexico (Gore 1979). A Block Island, Rhode Is., record (2155 m) is either an error or an accidental occurrence.

Remarks.—Ovigerous females are known from Yucatan in January and February, off western Florida from January to April, off northeastern Florida in March and April, and North Carolina in March (Milne Edwards and Bouvier 1897; Gore 1979; USNM, and UNC-IMS records).

Gore (1979) described larvae of *G. rostrata* reared under laboratory conditions. Ovigerous females taken with a clump of ivory tree coral in a cloth bag by a lock-out diver on 15 April 1977 in 80 m, 12°C water off eastern Florida were returned to the laboratory and maintained until eggs hatched. Variation in duration and number of zoeal stages appeared to be temperature-dependent; larvae reared at 15°C developed through five zoeal stages and attained megalopa stage in 52 days, whereas larvae cultured at 20°C passed through four of five zoeal stages, reaching megalopa in 18 or 23 days

respectively. Some variation in morphology of stages was noted and compared to that in other larval galatheids.

Genus *Munida* Leach 1820

Leach 1820:52.—Milne Edwards and Bouvier 1897:20.—China 1966:256.—Zariquiey Alvarez 1968:281.

Munida iris iris A. Milne Edwards

Fig. 168

Munida iris A. Milne Edwards 1880:49.—Milne Edwards and Bouvier 1894:256.—1897:21, pl. 2, figs. 2–7.—Benedict 1902:310.—Pequegnat and Pequegnat 1970:131.

Munida caribaea.—Smith 1881:428.—1883:40, pl. 3, fig. 11.—1884:355.—1886:643 (not *Munida caribaea* Stimpson 1860a:246 or *Munida caribaea*.—Milne Edwards 1880:49).

Munida sp. indet.—Smith 1882:22.

Recognition characters.—Carapace narrowed both anteriorly and posteriorly, sides arcuate, adorned with transverse lines of iridescent pubescence, spiny. Rostral spine much longer than supraocular spines; latter not extending to distal edge of cornea. Gastric area with pair of spines behind supraocular spines and 2 or (usually) more spinules more or less transversely in line with these on each side, spine close to each hepatic region; 1 or more spines on each triangular area near cephalic groove; 1 to 4 spines (plus occasional tubercles) on each branchial region behind cervical groove; long anterolateral spine followed by 6 (occasionally 5) lateral spines. Basal article of antennular peduncle with mesial spine longer than distal lateral spine, slender spine dorsal to latter somewhat variable in length. Merus of third maxillipeds with single strong spine on lower margin, distal spinule may be absent or present.

Chelipeds very long and slender, usually subcylindrical; covered with ciliated, squamose rugosities becoming progressively finer and more widely spaced distally; merus with longitudinal rows of spines. Fingers straight except occasionally gaping near base in one or both hands of large individuals, varying from as long as to $\frac{3}{4}$ length of palm, prehensile edges with single row of closely spaced, fine serrations interrupted by few larger teeth; tips hooked and crossing. Walking legs with mesiodorsal distal spine on carpus, merus with prominent distal spines and mesiodorsal row of spines.

Second segment of abdomen (apparent first)

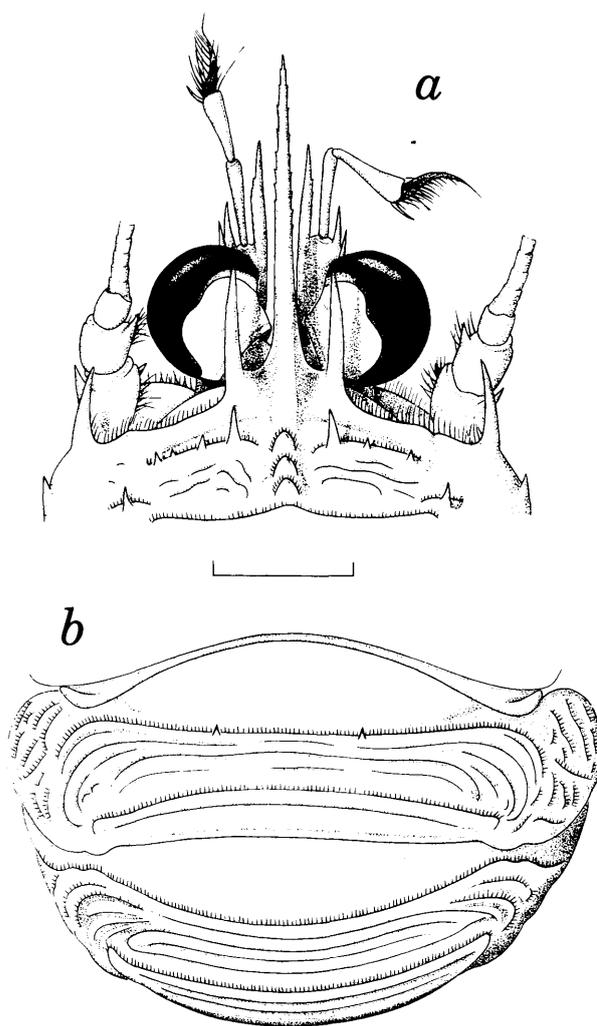


Fig. 168. *Munida iris iris* A. Milne Edwards. Female: a, frontal region and appendages in dorsal view; b, second, third, and part of fourth abdominal segments, dorsal view; 5 mm indicated (USNM 48811).

armed with pair of spinules on anterior margin, occasionally a second or third small pair.

Measurements in mm.—Length of carapace including rostrum: male 47, female 45, ovigerous females 12.6 to 44. Length of unusually large disarticulated left chela with gaping fingers 228.

Habitat.—43 to 613 m (Wenner and Boesch 1979; Wenner and Read 1982).

Type-locality.—Off Barbados, 382 m, Blake Stn. 274.

Known range.—SSE of Martha's Vineyard, Mass., through southeastern Gulf of Mexico to near Cozumel Island, Yucatan, and through Caribbean islands to off mouth of Amazon River.

Remarks.—This species is the most abundantly represented *Munida* from the western Atlantic in the USNM collection, some lots containing hundreds of specimens. The eastern Atlantic form, recognized as *M. iris* by Milne Edwards and Bou-

vier (1897), was regarded as a subspecies (*M. iris rutlanti*) by Zariquey (1952a, 1952b).

Musick and McEachran (1972) found *M. i. iris* associated mainly with *Homarus americanus* and *Cancer borealis* which together probably form a stable "nucleus of a shelf-edge upper slope decapod fauna which also includes *Nephropsis aculeata*, *Bathynectes superba* [= *longispina*], and *Rochinia crassa*," along the Chesapeake Bight.

The breeding season as shown by ovigerous females is long, perhaps year round in parts of the range. Present records are as follows: southern Florida, February to August; Georgia, May; North Carolina, June and October; southern New England, August and September; Delaware capes to off Chesapeake Bay, October; off Amazon River, November.

Williams and Brown (1972) analyzed age and reproductive condition of a sample of 251 *M. iris* taken at a depth of 275 m off North Carolina in June (Eastward Stn. 9888). The sample contained 63.7% females, representing a statistically significant departure from a 1:1 male-female ratio, including both parasitized and non-parasitized individuals. Of 160 females, 135 were ovigerous, bearing an estimated average of 7,900 eggs each. There was a highly significant statistical difference between the mean size of large males and females in this sample, but both comparisons with other species and measurements given above indicate that the two sexes reach comparable carapace lengths. Sizes of males in the sample apparently fitted into 3 groups: (1) small, 19 mm or less in length of carapace; (2) intermediate, 20-22 mm (including the mean size, 21.3 mm); and (3) large, 23-26 mm. All males in the latter group had markedly enlarged chelipeds, much larger than females of comparable size, and a few males in the intermediate group showed this development. Such allometry in this and other species of *Munida* is correlated with attainment of sexual maturity.

Two males in the sample harbored attached barnacles, *Trilasmis (Poecilasma) inaequilaterale* (Pilsbry) on the chelipeds. Two ovigerous females possessed long, thin, white colored unidentified worms coiled within the egg masses on the underside of the abdomen. Twenty-five specimens were parasitized by bopyrid isopods later identified as *Anuropodione carolinensis* (see Markham 1973). Of non-ovigerous females, 56% were infested with the bopyrid, but overall incidence of parasites in the sample was 10%.

Munida irrasa A. Milne Edwards

Fig. 169

Munida irrasa A. Milne Edwards 1880:49.—Hay and Shore 1918:402, pl. 28, fig. 8.—Chace 1942:46.—

Haig 1956:3.—Williams 1965:105, fig. 82.—Pequegnat and Pequegnat 1970:132.—Scelzo 1973:163.

Munida caribea.—Young 1900:403.—Türkay 1968:249.

Recognition characters.—Carapace narrowed anteriorly, adorned with transverse lines of iridescent pubescence, spiny. Rostral spine much longer than supraocular spine, latter not extending to distal edge of cornea. Row of 6-10 spines across gastric region (pair behind supraocular spines largest) in addition to 1 or 2 on each hepatic region, 2 to 5 on each triangular area and 1 to 4 on either side behind cervical groove on mesial portion of each branchial region; anterolateral spine long, followed by 6 distinct lateral spines. Basal article of antennular peduncle with distomesial spine longer than distal lateral spine, slender spine dorsal to latter somewhat variable in length, occasionally diverging anterolaterad. Merus of third maxillipeds with 3 or 4 spines on lower margin.

Chelipeds 3 or 4 times as long as carapace, subcylindrical except for somewhat flattened and broadened hand of large, mature males; covered with ciliated, squamose to tuberculiform rugosities becoming progressively finer distally; merus with rows of spines continued but reduced on carpus and hands. Fingers usually straight; prehensile

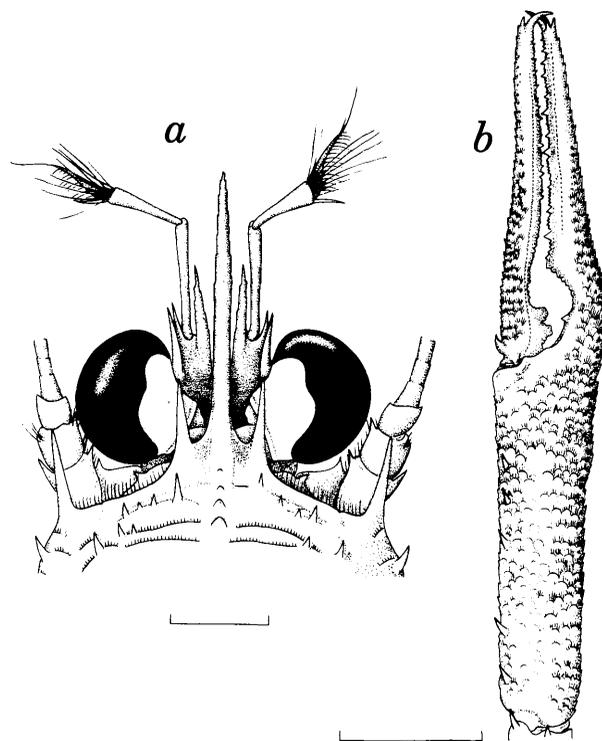


Fig. 169. *Munida irrasa* A. Milne Edwards. Male: a, frontal region and appendages in dorsal view; b, right chela, external view; a, 2 mm; b, 5 mm indicated (USNM 136629).

edges with single row of fine serrations interrupted by few larger teeth, meeting throughout except gaping at base in large, mature males; tips hooked and crossing. Most prominent spines on walking legs at distal end of merus and carpus.

Abdomen without spines.

Measurements in mm.—Length of carapace including rostrum: male 18.8; ovigerous females 4 (Chace 1942) to 15.4.

Habitat.—14 to 475 m.

Type-locality.—Not designated with certainty; syntypes from 10 localities in the Gulf of Mexico and Caribbean (MCZ).

Known range.—Off Cape Lookout, N. C., through eastern Gulf of Mexico and Caribbean Sea to 34°14'S, 51°40'W off Uruguay; "600 mi. off St. Davids, Bermuda" (USNM).

Remarks.—The Uruguay record from R/V *Walter Herwig* was reported as 41°40'W longitude by Scelzo (1973) but is recorded as above in USNM.

The name *Munida caribaea* in its various spellings has caused confusion, but as Faxon (1895) pointed out, Stimpson's (1860a) *M. caribaea* "is absolutely indeterminable from his brief notice of it, and the types were burned in the great Chicago fire." Faxon recommended that the name be dropped, a practice followed by most authors thereafter, although Young (1900) and Türkay (1968) recognized forms under this name whose descriptions most closely fit that of *M. irrasa*.

Munida longipes A. Milne Edwards

Fig. 170

Munida longipes A. Milne Edwards 1880:50.—Hay and Shore 1918:402, pl. 28, fig. 9.—Schmitt 1935a:178.—Chace 1942:47.—Pequegnat and Pequegnat 1970:132, fig. 5–3.

Recognition characters.—Carapace narrowed both anteriorly and posteriorly, sides arcuate; depressed and somewhat unevenly arched dorsally; adorned with strong transverse lines of raised, lightly ciliated, close-set, fine tubercles; cervical groove fairly deep. Supraocular spine reaching about to distal edge of cornea, rostrum shorter except in some juveniles. Gastric area with pair of strong spines behind cervical groove on each branchial region and often behind each a smaller spine, sometimes even a third still smaller; median spine usually on raised cardiac region (rarely additional clustered spinules); pair of strong spines on posterior margin; strong anterolateral spine followed by irregular row of marginal spines, third and fourth superior in size and position to remainder. Basal article of antennular peduncle with distolat-

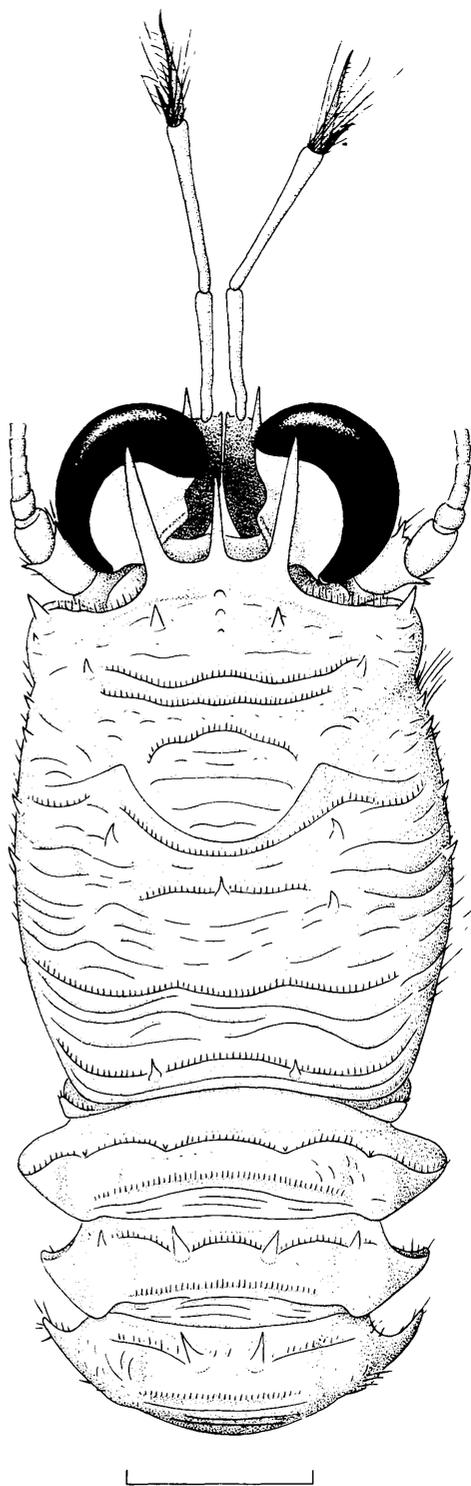


Fig. 170. *Munida longipes* A. Milne Edwards. Body of male in dorsal view; 5 mm indicated (USNM 92857).

eral spine much longer than distomesial spine. Merus of third maxillipeds with single spine on lower margin.

Chelipeds long and slender, usually subcylindrical but palms slightly expanded, covered with many ciliated rather sharply tuberculiform rugosities tending to form rows except on fingers. Fingers straight, smooth, about $\frac{1}{3}$ or less length of palm,

prismatic in cross section; prehensile edges meeting throughout length, each with single irregular row of small teeth; tips hooked and crossing, fixed finger with strong subterminal spine externally at base of hooked tip. Walking legs as long as chelipeds; rows of well-developed spines on meri and few similar spines on carpi.

Abdomen unevenly arched dorsally, 4 spines on anterior margin of second (apparent first) and third segments, and 2 spines on fourth.

Measurements in mm.—Length of carapace including rostrum: male 18, female 18, ovigerous female 22.

Habitat.—40 to 618 m (Wenner and Read 1982).

Type-locality.—Not designated with certainty; syntypes from 7 localities off Cuba and the Lesser Antilles (MCZ).

Known range.—SE Cape Lookout, N. C., through Gulf of Mexico to British Honduras, and through West Indies to Curaçao.

Remarks.—There is considerable variation in number of the smaller spines and spinules on the carapace. Not all setae are iridescent, but some are so along sides of the body and in tufts on the legs. This species tends to be very brittle in preservation.

Ovigerous females are known from: South Carolina and Mayaguez, P. R., harbor in January; east of Mississippi River Delta in February; northwest of St. Thomas, V. I., in March; off Tortugas, Cape Canaveral, and Alabama in April; Bahama Bank in May; off Mississippi River Delta to SE Florida in July; SE of Cape Lookout, N. C., and in western Gulf of Mexico in November.

Munida pusilla Benedict

Fig. 171

Munida pusilla Benedict 1902:268, fig. 16.—Haig 1956:2.

Recognition characters.—Carapace narrowed both anteriorly and posteriorly, sides arcuate, adorned with transverse lines of iridescent pubescence. Rostral spine much longer than supraocular spines; latter short, not half length of eyes. Gastric area with pair of spines behind supraocular spine and 2 or more spinules transversely in line with these, spine close to each hepatic region; 2 or 3 spinules on each triangular area near cervical groove, 1 on each branchial region behind cervical groove; long anterolateral spine followed by 5 or 6 lateral spines. Basal article of antennular peduncle with mesial spine longer than distal lateral spine, slender spine dorsal to latter somewhat variable in length. Merus

of third maxillipeds with single spine on lower margin.

Chelipeds of male long and slender, usually subcylindrical; covered with ciliated, squamose to tuberculiform rugosities becoming progressively finer distally; merus with rows of spines continued but reduced on carpus and hands. Fingers usually straight, prehensile edges with single row of closely spaced, fine serrations interrupted by few larger teeth, meeting throughout length except occasionally gaping near base in one or both hands; tips hooked and crossing. Cheliped of female shorter and spinier. Most prominent spines on walking legs at distal end of merus and carpus.

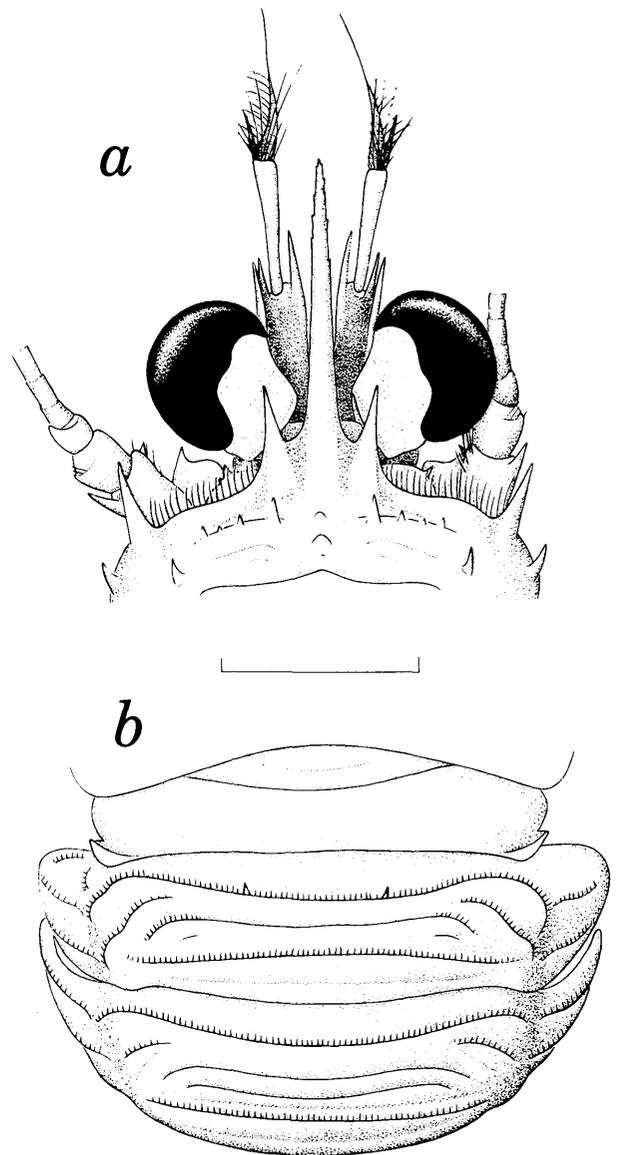


Fig. 171. *Munida pusilla* Benedict. Ovigerous female: a, frontal region and appendages in dorsal view; b, first, second and third abdominal segments, dorsal view; 2 mm indicated (UNC-IMS 2608).

Second segment of abdomen (apparent first) sometimes armed with pair of tiny spinules on anterior margin.

Measurements in mm.—Length of carapace including rostrum: male 12.6; ovigerous female 4.8 to 10.3.

Habitat.—33 to 133 m.

Type-locality.—Albatross Stn. 2405, Gulf of Mexico [south of Cape San Blas, Fla., 28°45'N, 85°02'W, 55 m].

Known range.—Off Cape Lookout, N. C., to Straits of Florida and through eastern Gulf of Mexico to Yucatan; Colombia and Trinidad.

Remarks.—*Munida pusilla* is a small species similar to *M. iris* and *M. irrasa*. There is variation in spination on the carapace and abdomen; spinules may or may not be present on the anterior margin of the second abdominal segment and, if present, seem more pronounced in larger individuals.

Ovigerous females are known from Yucatan in January, Florida from February to April and in September, and North Carolina in June.

Munida valida Smith

Figs. 172–173

Munida valida Smith 1883:42, pl. 1.—Milne Edwards and Bouvier 1894:256.—Pequegnat and Pequegnat 1970:137.

Recognition characters.—Carapace with sides almost parallel, curved mesad posteriorly, narrowed slightly anterior to cervical groove; rather evenly arched dorsally; adorned with transverse line of raised, ciliated, close-set, fine tubercles. Rostrum and supraocular spine stout; rostrum usually more than twice mesial length of supraocular spines which in turn extend to or beyond distal edge of cornea (somewhat shorter in juveniles); supraocular spines divergent and directed somewhat dorsally, rostrum broadly upturned distally. Gastric area with pair of strong spines behind supraocular spines; much smaller spine of spinule usually behind each of these; spine behind cervical groove on each branchial region; strong spine on rounded (more oblique in young) anterolateral margin and 5 or 6 marginal spines behind it. Basal article of antennule with distolateral spine longer than distomesial spine, prominent, ascending, slender spine dorsal to former sometimes obscuring it. Merus of third maxillipeds with prominent central spine and blunter distal one on lower margin.

Chelipeds elongate, subcylindrical (flattened in adults) and spiny; most of surface, sometimes including fingers, covered with short, dense pilosity. Fingers about as long as palm (variable); prehen-

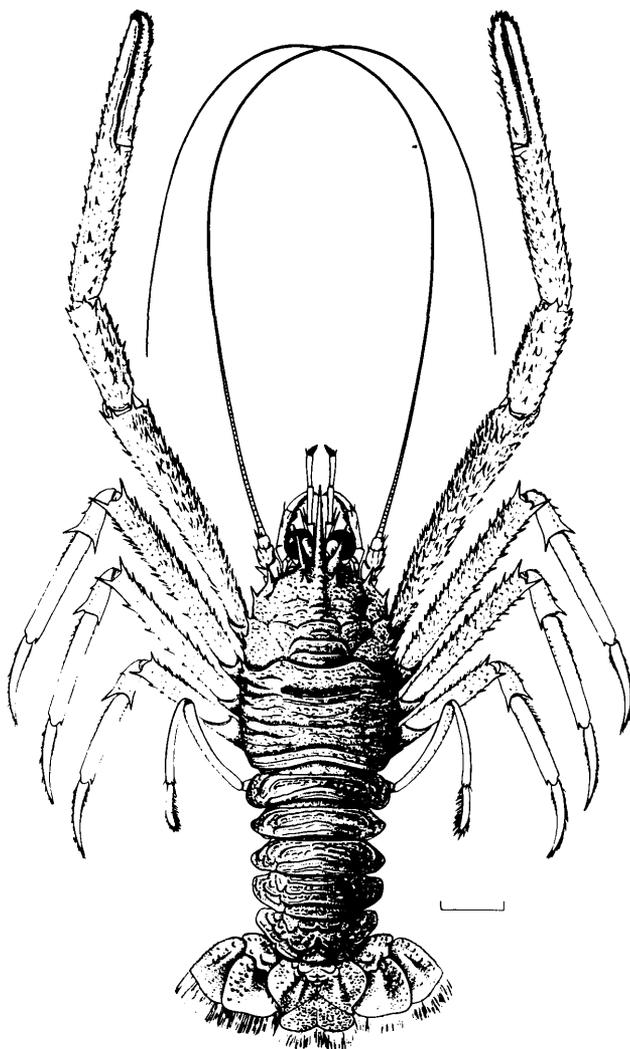


Fig. 172. *Munida valida* Smith. Male in dorsal view, 20 mm indicated (from Smith 1883).

sile edges straight, each with single row of fine teeth and hooked, crossing tips; chelae in few males noticeably broadened with fingers gaping proximally, dactyl with raised proximal tooth row or enlarged single tooth, tips occasionally spooned and finely toothed. Walking legs shorter than chelipeds, prominent acute spine on meri and carpi, propodi much smoother but with ventral row of fine acute spines.

Abdomen evenly arched dorsally, second (apparent first) and third segments with spinules on anterior margin.

Measurements in mm.—Length of carapace including rostrum: male 54, female 48, ovigerous female 49.

Habitat.—90 to 1823 m (Wenner and Boesch 1979), but shallower occurrences are known. A sample from Gerda Stn. 490, Straits of Florida, 26°37'N, 78°57'W, taken in 1- and 2-m 00-mesh plankton nets at a depth of 0–9 m between 0505

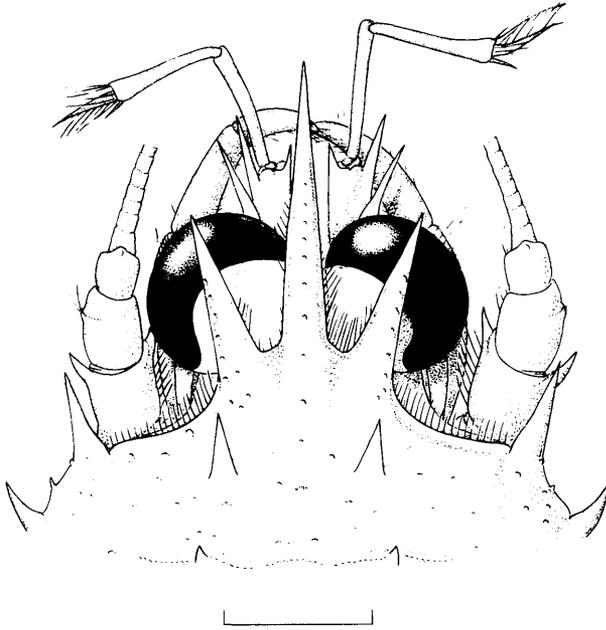


Fig. 173. *Mumida valida* Smith. Male frontal region and appendages in dorsal view; 5 mm indicated (USNM 136673).

and 0605 hr over a bottom depth of 384–402 m on 3 February 1965 (USNM 136673) contains many large adults including ovigerous females.

Type-locality.—Off southern New England, *Fish Hawk* Stn. 1112, 39°56'N, 70°35'W, 448 m; Stn. 1124, 40°01'N, 68°54'W, 1171 m.

Known range.—Off southern New England through Gulf of Mexico to Golfo de Morrosquillo, Colombia, and Curaçao.

Remarks.—The original drawing by J. H. Emerton of the male specimen Smith (1883) described from *Fish Hawk* Stn. 1112 (USNM 7313) is reproduced here. Whereabouts of the female from Stn. 1124 is unknown.

Milne Edwards and Bouvier (1894) and Benedict (1902) cleared up possible confusion of this species with *M. miles*. The two species are distinct, *M. miles* having much shorter supraocular spines than *M. valida*.

Menzies, et al. (1973) listed *M. valida* as a dweller in the archibenthal zone (450–950 m) that occasionally rises to the continental shelf. They, and Rowe and Menzies (1968), showed photographs of *M. valida* oriented to bottom currents on the continental slope off North Carolina (302–800 m). These photographs suggested that some of the individuals faced north away from the Gulf Stream current (in June when the photos were taken), and still others seemed to face south in the deep counter current. An alternate suggestion was that some water may be recirculated, carried along by the Gulf Stream at low velocity, and that the crabs face away from water of “high” velocity into “low” velocity.

Ovigerous females have been recorded nearly the year round: off North Carolina in January and November; eastern and southeastern Florida in February, April and June; southern New England in August; east of Mississippi River Delta in September; western Gulf of Mexico in November.

Some specimens from Florida in the USNM collection bear sacculinid parasites. Others, especially large males, bear the barnacle, *Trilasmis* (*Poecilasma*) *kaempferi* (Darwin).

Family Porcellanidae

General form crablike. Carapace well calcified, depressed, regions usually not well defined; front often prominent but never with rostrum greatly projecting beyond eyes. Antennae inserted external to eyes, with 3 movable articles and a flagellum. Basal articles of antennules broad. Outer maxillipeds too large to be contained in buccal cavity. Chelipeds moderately elongate, usually broad, symmetrical, composed of 7 segments, bent under and held closely against thorax; males with pair of pleopods on segment 2, sometimes rudimentary or absent; females with pair of pleopods on segments 3, 4, and 5, those on 3 sometimes reduced or absent. Telson composed of 5 or 7 well-calcified pieces (Haig 1960).

Key to Genera and Species

(Modified after Chace 1942)

1. Form elongate, “hippalike”; telson much longer than broad
 *Euceramus praelongus*
 Form less elongate; telson usually broader than long, never much longer than broad 2
2. Lateral wall of carapace broken up into 2 or more pieces separated by membranous interspaces; front triangular or transverse in dorsal view, never with projecting teeth; carapace subquadrate 3

- Lateral wall of carapace nearly always entire; if not, front distinctly tridentate in dorsal view; carapace not subquadrate 4
3. Carapace with numerous transverse tufts of setae; chelipeds and legs setose *Pachycheles pilosus*
Carapace relatively smooth, not setose; chelipeds deeply ridged and eroded, not setose *Pachycheles rugimanus*
4. Basal antennal article small, not joining margin of carapace, articles with free access to orbit *Petrolisthes galathinus*
Basal antennal article strongly produced forward and broadly in contact with margin of carapace, movable part far removed from orbit. 5
5. Dactyls of walking legs armed with strong, fixed spines; carapace distinctly broader than long *Polyonyx gibbesi*
Dactyls of walking legs ending in simple spine, usually with small, movable accessory spinules on lower margin 6
6. Front strongly tridentate in dorsal view; chelipeds not tuberculate 7
Front trilobate in anterior view; chelipeds tuberculate *Megalobrachium soriatum*
7. Cervical groove terminating anterolaterally in shallow indentation at edge of carapace *Porcellana sayana*
Cervical groove terminating anterolaterally in distinct, longitudinal, V-shaped cleft at edge of carapace. *Porcellana sigsbeiana*

Genus *Euceramus* Stimpson 1860

Stimpson 1860b:445.—Haig 1960:187.

Euceramus praelongus Stimpson

Fig. 174

Euceramus praelongus Stimpson 1860b:445.—Hay and Shore 1918:405, pl. 29, fig. 3.—Haig 1956:7.—Williams 1965:109, fig. 86.

Recognition characters.—Carapace subcylindrical, elongate, covered with minute, irregular, transverse rugae; sides slightly arcuate; anterolateral margins with 2 small spines (more or less obtuse) on each side behind antennae. Front tridentate, rostrum about twice length of lateral spines; broad, shallow V-shaped indentation at posterior edge of carapace. Eyes well developed. Antennules short. Antennae about $\frac{3}{4}$ length of body, flagella with sparse, fine setae; basal article short, not produced forward; movable articles not far removed from orbit. Third maxillipeds large, forming subquadrate shield extending laterally almost to edge of carapace.

Legs and underparts with ornamentation similar to carapace, ridges more pronounced and setate on distal articles. Chelipeds stout, subequal; somewhat stouter in males than in females; fingers about as long as palm, more gaping in males than in females. First pair of walking legs shorter than

second and third pairs.

Abdomen small, fringed with setae, distal segments narrow; uropods reduced. Telson longer than broad, composed of 7 elements.

Measurements in mm.—Length of carapace from tip of rostrum to center of posterior indentation: males 16; ovigerous females 15.4.

Color.—Background of carapace greenish gray to greenish tan with lighter and darker line of color delineating striae and marginal furrow; a light longitudinal stripe, broadest anteriorly, along mid-dorsal line; purplish marking along lines separating major regions of carapace; legs mottled with greenish gray or tan as on carapace; suggestion of iridescence on body and legs (from specimen collected by L. McCloskey, Morehead City Harbor, N. C., Aug. 7, 1962).

Habitat.—Sandy beaches below water line, and on both smooth and broken-shell bottoms; low-water mark to 38 m.

Type-locality.—Beaufort, N. C.

Known range.—Delaware Bay (USNM; Watling and Maurer, 1976) to Aransas area of Texas coast.

Remarks.—Haig (1960) placed *Euceramus* between the group of porcellanid "genera in which the basal antennal segment is short and not broadly in contact with the anterior margin of the carapace, and the group of genera in which the basal segment is strongly produced forward so that the movable segments are far removed from the orbit."

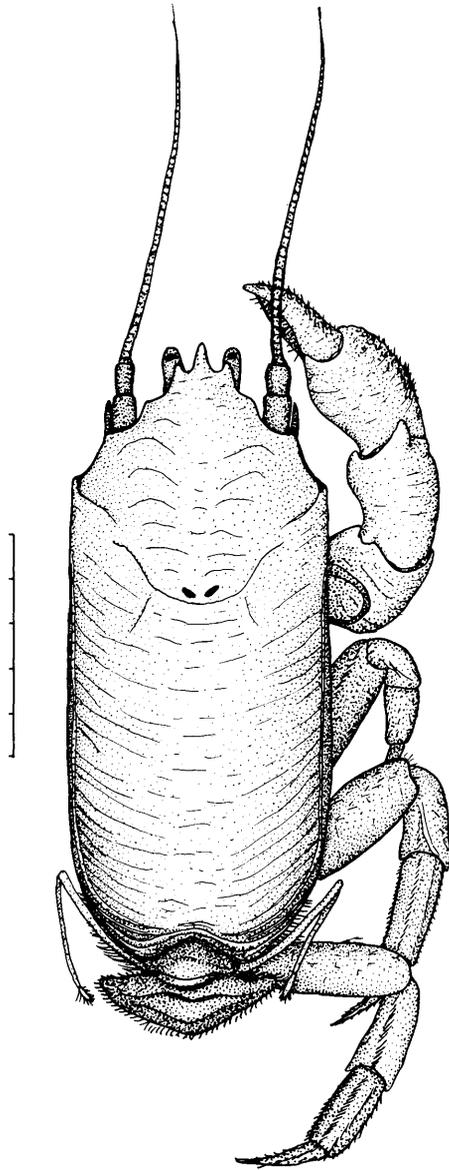


Fig. 174. *Euceramus praelongus* Stimpson. Animal in dorsal view, fifth leg only of left side shown, 5 mm indicated (from Williams 1965).

Hay and Shore (1918) and Haig (1956) remarked that *E. praelongus* is a rare species. Pearse, et al. (1942) helped to explain its apparent rarity by describing its adaptation to life in the substrate, drawing parallels to *Emerita*, *Lepidopa* and *Ogyrides*. They characterized it as a highly adapted burrower which burrows backward in subtidal sand along beaches, but it is also found on rubble-covered bottoms and the depth range indicates general adaptation to burrowing in shallow shelf waters. Rouse (1970) gave data on occurrence in southwestern Florida in temperatures of 16°–29°C over

a salinity range of 29 to 39‰. Juveniles have occasionally been taken in nocturnal surface plankton tows inside inlets in North Carolina. The animal scrapes entrapped food from the hairy antennae with setose mouthparts.

Ovigerous females are known from Florida in January (Camp, et al. 1977); Georgia in February, April and May; North Carolina in May and November; mouth of Chesapeake Bay in July; and York River, Va., in August (Roberts 1968b). Roberts (1968b) reared larvae in 21.5‰ salinity water at temperatures ranging from 25° to 28°C, finding two zoeal stages and a megalopa. He compared these to larvae of other porcellanids in a discussion and useful table. Sandifer (1973d) reported larvae in plankton from the mouth of Chesapeake Bay to some distance up York River, Va., from June to October in a temperature range of 19.3° to 37.9°C over a salinity range of 15.74 to 32.34‰, with greatest abundance in August and September. One larva in a January sample (4.9°C) may have resulted from error in sorting. Most were stage I larvae and most were in bottom samples.

Genus *Megalobrachium* Stimpson 1858

Stimpson 1858:228.—Haig 1960:212.

Megalobrachium soriatum (Say)

Fig. 175

Porcellana soriata Say 1818:456.—Hay and Shore 1918:404, pl. 29, fig. 6.

Porcellanopsis soriata.—Haig 1956:35.

Megalobrachium soriatum.—Haig 1960:229.—Williams 1965:112, fig. 89.—Felder 1973:32, pl. 4, fig. 12.—Gore and Abele 1976:17.

Recognition characters.—Carapace somewhat hexagonal, slightly wider than long; sides emarginate, unevenly and sharply tuberculate; lateral walls more or less hairy; areolations well marked, some tuberculate. Front irregularly rounded in dorsal view, median and lateral lobes produced downward in frontal view. Orbits well defined; eyes well developed. Antennae about as long as carapace; basal article strongly produced forward and broadly in contact with margin of carapace; movable article slender and removed from orbit.

Chelipeds long and heavy, roughly tuberculate; hand fringed with long hair along lower margin and with granulate tubercles in rather well-defined

rows; fingers with white, usually strongly hooked tips; carpus with 1 strong spine and some smaller spines on anterior border, dorsal aspect with tubercles irregularly arranged and appearing granulate under slight magnification; merus ornamented distally like carpus. First 3 pairs of walking legs stout, lightly setose and with sharp, curved dactyls.

Telson composed of 5 elements.

Measurements in mm.—Carapace: male, length 5, width 5.5; ovigerous female, length 4 to 5, width 4 to 5.5.

Color.—In life a dirty gray; in alcohol a rusty or grayish red.

Habitat.—Free living among corals, rocks, and sponges; in North Carolina found especially in canals of sponges taken from fishing banks offshore near Beaufort Inlet (Hay and Shore 1918; Pearse and Williams 1951). Wass (1955) found the species in sponges of the genus *Ircinia* in Florida, and Gore (USNM records) found it in *Oculina* coral off Vero Beach, Fla.; shore to 171 m.

Type-locality.—St. Catherines Island, Ga.

Known range.—Off Cape Hatteras, N. C., to Port Aransas, Tex.; West Indies to Barbados; Contoy, Mexico; Bahia Caledonia and Galeta Island, Panama.

Remarks.—This small porcellanid crab, very close to its Pacific congener, *M. tuberculipes* (Lockington), is rare in the southwestern Caribbean (Gore and Abele 1976).

Ovigerous females have been taken off the Carolinas in June, July, and August. Rouse (1970) found

them year round in southwestern Florida at temperatures of 19°–30°C in salinities of 24 to 45‰. Gore (1973) reared larval stages from an ovigerous female caught just off Vero Beach, Fla., in late June. Held in nonflowing but aerated 35‰ salinity seawater at room temperature of 25°C, the eggs hatched in nine days. A prezoal stage lasting only 10 min to 1 h molted through two subsequent zoal stages of about six days duration each before transforming to the megalopa which lived, at most, eight days but failed to transform to first crab stage. Larval stages were illustrated, described and compared to those of related species.

McCloskey (1970) discussed association of this crab with the scleractinian coral, *Oculina arbuscula*, community along the Carolinas.

Genus *Pachycheles* Stimpson

Stimpson 1858:22.—Haig 1960:131.

Pachycheles pilosus (H. Milne Edwards)

Fig. 176

Porcellana pilosa H. Milne Edwards 1837:255.

Pachycheles pilosus.—Haig 1956:11.—Williams 1965:108, fig. 84.

Recognition characters.—Carapace slightly broader than long, flattened but somewhat more convex from front to back than from side to side; lightly rugose along sides, with numerous short, transverse tufts of setae except scattered setae on frontal region. Frontal margin sinuous, slightly produced in middle, with submarginal row of setae. Anterolateral margins emarginate. Epimeral pieces of metabranchial regions separated by membranous interspaces, posterior part consisting of 1 or more pieces. Orbits deeply excavated, postorbital angle spiniform; eyes short, stout. Antenna with first movable article bearing buttressed spine on anterior margin; second article with spine near middle of anterior border; third article short, smooth.

Chelipeds unequal, stout, ornamented with numerous long, dark setae with shorter ones between; hands inflated, lateral margin of each spined and tuberculate below, obsolescent spines on inner edge of palm and dactyl; fingers short, major fixed fingers with single blunt tooth, opposed edges of minor fingers serrated; carpus with number of prominent white tubercles on proximal part, mesial border with about 3 spines; merus outlined dorsally with long setae, usually a stout spine and large white tubercle at inner distal angle. First 3 pairs of

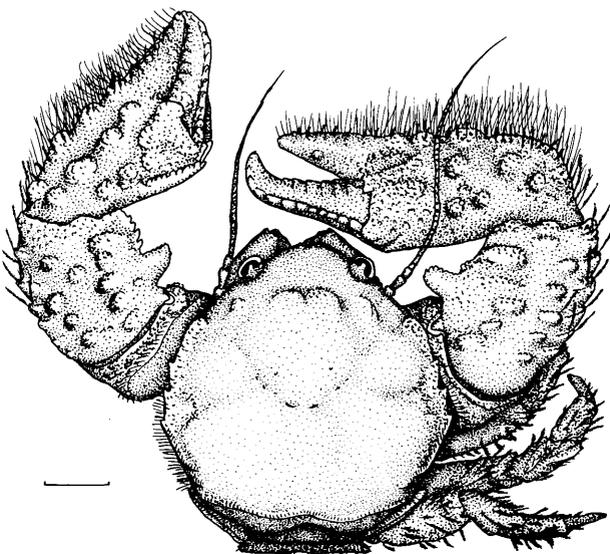


Fig. 175. *Megalobrachium soriatum* (Say). Animal in dorsal view; second, third, and fourth legs of left side not shown; 1 mm indicated (from Williams 1965).

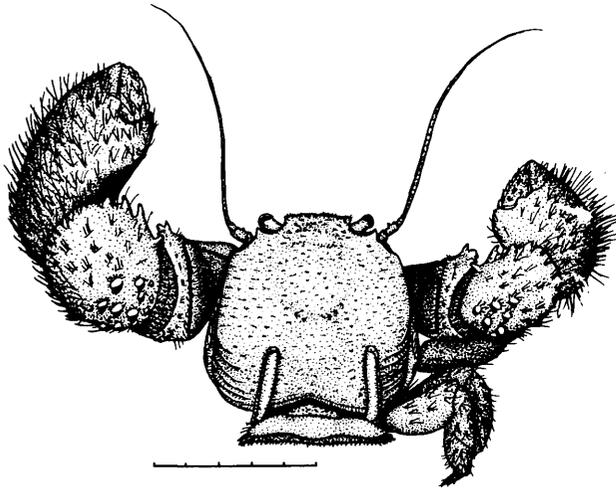


Fig. 176. *Pachycheles pilosus* (H. Milne Edwards). Animal in dorsal view; second, third, and fourth legs of left side not shown; 5 mm indicated (from Williams 1965).

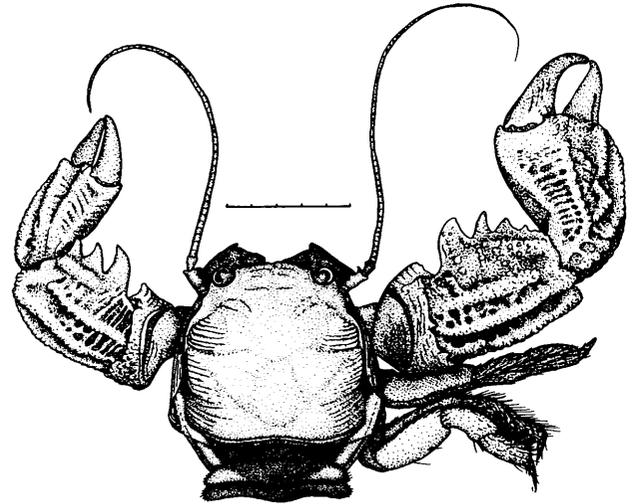


Fig. 177. *Pachycheles rugimanus* A. Milne Edwards. Animal in dorsal view; second, third, and fourth legs of left side not shown; 5 mm indicated (from Williams 1965).

walking legs with hairy covering similar to chelipeds, few spines below on dactyls and propodi.

Telson composed of 5 elements.

Measurements in mm.—Length of carapace: males 7; ovigerous females 5 to 7 (Haig 1956).

Habitat.—In corals; to 7 + m (Schmitt 1935a).

Type-locality.—Vicinity of Charleston, S. C.

Known range.—Charleston, S. C.; Key West to Sarasota Bay, Fla.; through West Indies to Tobago and Aruba.

Remarks.—Ovigerous females have been found in the West Indies from February to May (Haig 1956, in part). Rathbun (1926) reported a Pliocene species of *Pachycheles* from Central America.

Pachycheles rugimanus A. Milne Edwards

Fig. 177

Pachycheles rugimanus A. Milne Edwards 1880:36.—Hay and Shore 1918:404, pl. 29, fig. 2.—Haig 1956:12.—Williams 1965:108, fig. 85.

Recognition characters.—Carapace about as long as wide, flat from side to side, convex from front to back, slightly rugose along sides; anterolateral margins emarginate; epimeral pieces of metabranchial region separated by membranous interspaces, posterior portion consisting of 1 or more pieces. Front broad, slightly produced in middle, margin projecting downward, hardly visible from above. Orbits deeply excavated, margins slightly raised, postorbital angle spiniform; eyes short, stout, retractile. Antenna with first movable article bearing slightly serrate spine on anterior margin; sec-

ond article with row of unequal spines on anterior border; third article short, smooth.

Chelipeds subequal, stout; carpus with 4 anterior spines, graded in size, proximal one largest, upper surface with 4 prominent longitudinal, tuberculate ridges, deep channels between crossed by irregular septae forming rows of oblong pits; ridges and pitted channels continued onto hand but with less regularity in arrangement, fingers tuberculate almost to tips; merus crossed by few rugae distally, rugose and serrate spine at inner distal angle. First 3 pairs of walking legs stout and with distal articles setose.

Telson composed of 5 elements.

Measurements in mm.—Carapace: male, length 8, width 7; ovigerous female, length 8, width 9.

Color.—Brownish red, fingers vermilion.

Habitat.—To depth of 145 m (Schmitt 1935a).

Known range.—Off Cape Lookout, N. C., through Florida to St. Thomas, V. I., and Contoy Island, Mexico; Pernambuco, Brazil (Coelho 1964).

Remarks.—Only a few collections of this species have been recorded from widely scattered localities. Cain (1972) gave collection data for specimens from the *Lithothamnion* reef off Cape Lookout, N. C. Ovigerous females have been taken in February and March from the Carolinas and west Florida, and in September in North Carolina, Georgia and east Florida.

Genus *Petrolisthes* Stimpson 1858

Stimpson 1858:240.—Haig 1960:21.—China 1966:250.

Petrolisthes galathinus (Bosc)

Fig. 178

Porcellana galathina Bosc [1802]:233, pl. 6, fig. 2.

Petrolisthes galathinus.—Hay and Shore 1918:404, pl. 29, fig. 1.—Haig 1956:22.—1960:36.—Williams 1965:107, fig. 83.—Coelho 1966a:56.—Gore 1970:965.—Gore and Abele 1976:21.

Recognition characters.—Carapace covered with strong, transverse, ciliated rugae, scarcely interrupted at grooves separating well-marked regions; frontal region granulate, metabranchial regions plicate. Rostrum broad, triangular, sinuous sided, with broad median depression usually covered with short pubescence. Supraorbital spine present, not distinct in large specimens; postorbital angle produced into small spine-tipped tooth; epibranchial spine strong. Eyes well developed. Antenna with first movable article bearing anteromesial, spine-tipped, lamellar lobe; second and third articles lightly rugose.

Chelipeds large, covered with strong, ciliated rugae continuing obliquely and almost unbroken across carpus and hand, broken into series of shorter rugae on fingers; hand broad, flattened,

rugae on outer margin spiniform in smaller specimens, outer margin often fringed with plumose hairs; dactyl sinuous, fingers closing closely, thick tuft of pubescence below; carpus about twice as long as wide, anterior margin with 4 to 6 strong serrate spines, row of spines on posterior margin; merus with strong rugose lobe at inner distal angle. First 3 pairs of walking legs rugose; upper margin of meri with fringe of plumose hairs, anterior margin on first and second legs with 6 to 9 spines, on third with 5 to 7, merus of first and second with postero-distal spine; all articles covered with long, non-plumose setae.

Sternum, sternal plastron, abdomen, ventral surface of outer maxillipeds, chelipeds and walking legs covered with strong striations.

Telson composed of 7 elements.

Measurements in mm.—Length of carapace: males 7 to 17; non-ovigerous females 6 to 11 (15?); ovigerous females 7 to 14 (Haig 1960; Holthuis 1959).

Color.—Grayish brown without markings in life; in alcohol, light brown with purple or dark red line and dots on rugae (Hay and Shore 1918). Spaces between rugae yellow; lower surface, including abdomen, deep red (Faxon *in* Haig 1960). Blue gray to white with dark reddish purple striations (R. H. Gore, personal communication).

Habitat.—Under stones and associated with sponges, corals and anemones in littoral; from sand and sand-shell bottom in somewhat deeper water (Haig 1960; Dragovich and Kelly 1964); shell hash in tide pools and intertidal regions (Gore and Abele 1976), low water mark to 54 m.

Type-locality.—Unknown.

Known range.—Cape Hatteras, N. C., through Gulf of Mexico and Caribbean Sea to Rio de Janeiro, Brazil; Ilha Trinidad off Brazil; Pacific Ocean from Isla San Lucas, Costa Rica, to off La Libertad, Ecuador.

Remarks.—Haig (1956, 1960) gave a full review of this species and Gore (1970) added notes on morphology. Ovigerous females are known from the Caribbean area from January to August, and from North Carolina and the Gulf of Mexico from June to October (Gore 1974; Gore and Abele 1976; Haig 1956, 1960; Holthuis 1959, in part; Rickner 1975; Rouse 1970). Ovigerous females from North Carolina have been found with rhizocephalans (USNM 51050).

Rathbun (1926) described a fossil species, *P. avitus*, from the Pliocene of Central America which is similar to the recent *P. galathinus*.

Randall (1967) reported *P. galathinus* from stomach contents of the dusky squirrelfish, *Holocentrus vexillarius*, rock hind, *Epinephelus adscensionis*, Nas-

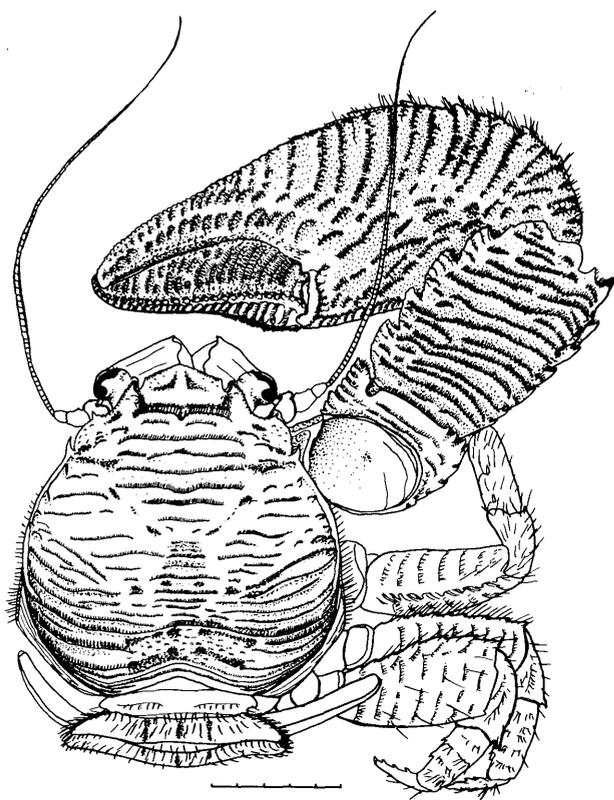


Fig. 178. *Petrolisthes galathinus* (Bosc). Animal in dorsal view, fifth leg only of left side shown, 5 mm indicated (from Williams 1965).

sau grouper, *E. striatus*, striped drum, *Equetus acuminatus*, Spanish hogfish, *Bodianus rufus*, and reef scorpionfish, *Scorpaenodes caribbaeus*.

Genus *Polyonyx* Stimpson 1858

Stimpson 1858:233.—Haig 1960:232.

Polyonyx gibbesi Haig

Fig. 179

Porcellana macrocheles Gibbes 1850:191.

Polyonyx macrocheles.—Hay and Shore 1918:405, pl. 29, fig. 8.

Polyonyx gibbesi Haig 1956:28.—Williams 1965:113, fig. 90.

Recognition characters.—Carapace smooth, finely plicate, transversely oval, about $\frac{1}{4}$ to $\frac{1}{3}$ wider than long; front hardly produced, margin slightly sinuous; posterolateral portions with scattered, feathered hairs; infolded lateral parts separated from rest of carapace by deep fissure. Orbits small; eyes small, cornea reduced. Antenna slender, about 1.5 times as long as body; basal article strongly produced forward; movable articles far removed from orbit.

Chelipeds unequal, long and distorted; inner margin of hands convex, very thinly fringed with plumose hairs, outer margin nearly straight, emarginate, densely fringed with long plumose hairs; major hand nearly twice as long as carapace; fingers short, hooked at tip, toothed on cutting edges, dactyl falciform with largest tooth in middle, fixed finger with largest tooth in proximal $\frac{1}{3}$; minor hand with straighter fingers; carpus as long as palm, thick, anterior margin produced into thin crest, subrec-

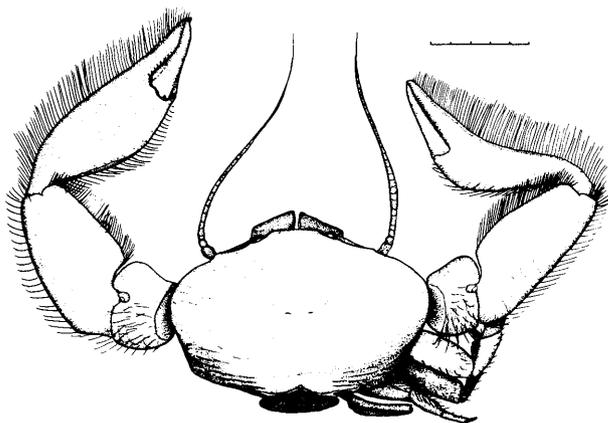


Fig. 179. *Polyonyx gibbesi* Haig. Female in dorsal view, second to fifth legs of left side not shown, 5 mm indicated (from Williams 1965).

tangular proximally, fringed with fine plumose hairs, thinner fringe of shorter hairs on outer margin; merus subcubical, finely rugose above, plumose-hairy dorsolaterally, inner distal angle produced. Three pairs of walking legs sparsely hairy, dactyls with 4 corneous spines on lower margin closing against weaker spines on distal part of propodus, merus of second and third walking legs minutely spinulose below. Last legs with long tufts of hairs on chela and distal end of carpus.

Telson composed of 7 elements.

Measurements in mm.—Carapace: male, width 11; female, length 10, width 14; ovigerous females, width 8.4 to 16.

Color.—Grayish white, sometimes stained with brown. Rickner (1975a) characterized the carapace and chelipeds of males as yellowish orange to moderate brown and females as yellowish to light brownish gray with occasionally moderate yellowish brown chelipeds.

Habitat.—A common commensal of the annelid *Chaetopterus variopedatus*, seldom found outside tubes of this worm; intertidal to 47 m (Gore 1974).

Type-locality.—Coast of South Carolina.

Known range.—Woods Hole, Mass., to Uruguay (Coelho and Ramos 1972).

Remarks.—Unlike other porcellanids occurring along the east coast of the United States, *Polyonyx gibbesi* has been the subject of ecological studies. Enders (1905), at Beaufort, N. C., and Pearse (1913), at Woods Hole, Mass., studied inhabitants of the tubes of *Chaetopterus variopedatus*, finding *P. gibbesi* to be common commensals in both areas. Both authors found usually a male and a female crab in the same tube, although Enders found 6 isolated ovigerous females in the course of a summer. Pearse found the species to be strongly thigmotactic; crabs seemingly too large to enter *Chaetopterus* tubes entered and left an artificial tube at will in the laboratory.

Observed crabs usually moved backward or sideways on open sand, using the chelipeds as an aid in walking, or at times swam clumsily upside down by flapping the abdomen. They showed little ability to burrow. The respiratory mechanism seemed well adapted to life in confinement, for the respiratory currents were strong and capable of being shifted with the change in direction of water flow in the worm tubes. Crabs in an experimental tube tolerated considerable fouling of the water.

Pearse gave an excellent figure of the chelate and tufted last legs which are used extensively in the meticulous preening characteristic of this species. The plumes of hairs on the appendages, especially those on the third maxillipeds, are used as nets for capturing food from water currents. Caine (1975)

summarized information on feeding, pointing out that the species not only "net-fishes" passively in water passing through the host worm's tube, usually near the exhalent opening, but also actively filters by alternate movements of the third maxillipeds. Stomach contents indicted a detritus-diatom mixture with some algal filaments present, and the author thought that *P. gibbesi* may gather additional food with the densely setose ventral margin of the chelipeds and probably also feeds on fecal matter of the host.

Gray (1961), reviewing the life history and ecology of the species, found the breeding season at Beaufort, N. C., to extend at least from April to December, and ovigerous females are otherwise known in January from Georgia, February and March from Florida, June to August in Texas (Rickner 1975), and July from Venezuela (Gore 1974). Usually when a pair of *P. gibbesi* was found in a tube, adult crabs of no other species were present. Gray concluded that the crabs enter worm tubes by chance, not in response to attractants.

In the years since Enders's and Pearse's studies, the proportion of *Polyonyx gibbesi* and *Pinnixa chaetoptera* at Woods Hole and Beaufort has changed. Woods Hole: 1913, 22% *Polyonyx*/78% *Pinnixa*; 1959, 66%/34%—Beaufort: 1905, 83%/17%; 1958–59, 39%/61%. Gray postulated that the more southerly species, *Polyonyx gibbesi*, has increased in the Woods Hole area because of warming climate. In the Beaufort area, decline may have resulted from hurricane damage (before the study) which destroyed many *Chaetopterus* tubes. Gray also found that *Polyonyx gibbesi* prefers less muddy bottoms than *Pinnixa chaetoptera*. He considered *Polyonyx gibbesi* an obligate commensal of *Chaetopterus*.

Craig (1974) concurred with much of Gray's analysis. He also found that the relative abundance of *Polyonyx gibbesi* in samples of intertidal *Chaetopterus* tubes steadily decreased northward, that the crabs could not withstand temperatures of 10°C for more than a few days, and that they are sensitive to desiccation. However, the zoeae and adults of *Polyonyx gibbesi* were less tolerant of high temperature than comparable stages of *Pinnixa chaetoptera*, as indicated by both lethal limit and metabolic studies.

Gore (1968) described the larval development from eggs hatched in the laboratory. Among larvae held at 10°, 15°, 25° and 30°C, those held at 25°C and fed *Artemia* nauplii passed through pre-zoeal, two zoeal and megalopal stages lasting two hours, 12 and 12–14 days respectively before molting to first crab. No crab stages were obtained above or below 25°C and no megalopae below 20°C. Smith (1880b) reported swarms of zoeae of *Polyonyx gib-*

besi at the edge of tidal currents near the mouth of Narragansett Bay in summer, Hillman (1964) observed them once there in August, and Fish (1925) found them in plankton from July to October at Woods Hole. Sandifer (1973d) found the larvae to be fairly abundant in plankton from the mouth of Chesapeake Bay to lower reaches of York River, Va., over a salinity range of 15.74 to 30.37‰ with peak abundance from 20 to 25‰. The larvae were present from July to October over a temperature range of 19.4° to 28.1°C. Both zoeae and megalopae were in surface and bottom samples, with zoeal stage I making up 80% of the samples, most abundant near the bottom but stage II more abundant at the surface. Most megalopae were in bottom samples. Further south, Dudley and Judy (1971) found larvae at three stations off Beaufort Inlet, N. C.: May–November 1.6 km and 6.5 km offshore at 1–8 m, mainly 8 m; July–November 10–13 km offshore at 8 m.

Long, barbed rostral spines of the zoeae of *P. gibbesi* have been known to pierce the skin of children swimming in Quisset Harbor, Buzzards Bay, Mass., causing an itch that was alleviated soon after the youngsters dried themselves and dressed (Zinn 1954). Adults were not affected. Collections showed an unusually large swarm of zoeae in the plankton at time of the attack.

Genus *Porcellana* Lamarck 1801

Lamarck 1801:153.—Haig 1906:196.—China 1966:250.—Haig 1978:707.

Porcellana sayana (Leach)

Fig. 180

Pisidia sayana Leach 1820:54.

Porcellana sayana.—Hay and Shore 1918:403, pl. 29, fig. 7.—Haig 1956:31.—Williams 1965:110, fig. 87.—Coelho 1966a:62.—Gore 1970:963.

Recognition characters.—Carapace usually a little longer than wide, depressed; dorsal surface slightly convex, meeting lateral parts in slight shoulder a little behind base of antenna; surface minutely granulate and with fine oblique dorsal plications along sides, especially on posterolateral parts; few scattered small clumps of setae. Rostrum triangular, concave above, tip abruptly decurved, margins spinulate or tuberculate. Inner angle of orbit produced into strong tooth separated from rostrum by wide and rather deep notch; outer angle produced into broad, low tooth. Eyes well developed. Cervical groove lightly impressed, terminating an-

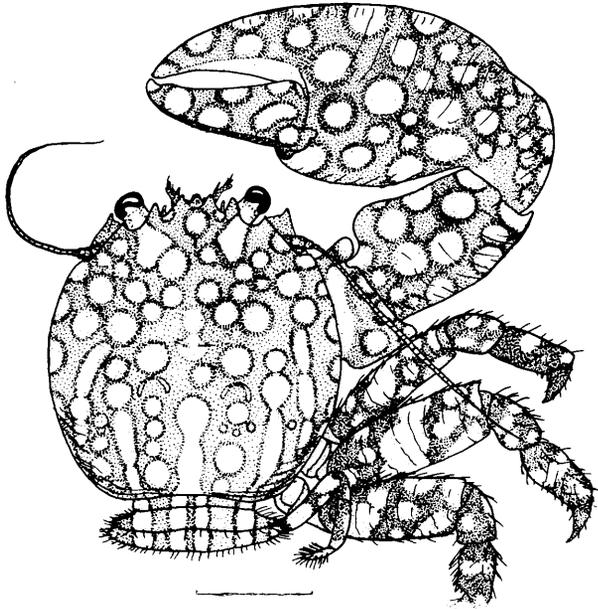


Fig. 180. *Porcellana sayana* (Leach). Animal in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

terolaterally in shallow indentation at edge of carapace. Antennae slender, smooth, longer than carapace; basal article strongly produced forward into spinelike projection; movable articles far removed from orbit.

Chelipeds strong, heavy, finely plicate, nearly smooth in old individuals; hand as long as or longer than carapace, outer margin fringed with long setae except in old individuals; fingers short, curved and bent; proximal inner angle of carpus and distal inner angle of merus produced, forming lobes, both articles with scattered setae near dorsolateral border; anterodistal angle of carpus ending in spine. First 3 pairs of walking legs normal, with scattered setae.

Telson composed of 7 elements.

Measurements in mm.—Carapace: males, length 14 (Wass 1955), width 12; nonovigerous females, length 8, width 8; ovigerous females, length 5 (Haig 1956) to 10, width 10. Specimens with length and width equal are unusual.

Color.—Ground color reddish or rusty brown; covered on all dorsal surfaces and abdomen with complicated irregular pattern of yellowish white, yellow, and some bluish-white spots or longitudinal stripes; stripes more prominent on rear center part of carapace and on abdomen. Walking legs banded with red on proximal edge, "white stockings" on distal edge (Gore 1970). Pattern quite variable in shape and shade, some specimens being predominantly light. Andrews (1911) noted males with a "sky blue" ring between the peripheral red line and

center of some spots.

Habitat.—This species is often found in crevices in clusters of oyster shells, among rocks of jetties or as a commensal of the hermit crabs *Pagurus pollicaris* and *Petrochirus diogenes* in the shell of some gastropod. Hildebrand (1954) found specimens attached to the decorator crab *Stenocionops furcata*. Telford and Daxboeck (1978) at Barbados, West Indies, found it confined to *Strombus gigas*, the queen conch, where it clung to the inner surface of the operculum or close to that structure even when the gastropod's foot was retracted, or more abundantly in association with the hermit crabs *Petrochirus diogenes*, *Dardanus venosus* and *Paguristes grayi* when they were housed in *S. gigas* shells. The authors remarked that the porcellanid has a color pattern similar to that of the host hermits. Shallow water to 92 m (Gore 1974); (713 m², Schmitt 1935a).

Type-locality.—Coast of Georgia and Florida.

Known range.—Cape Hatteras, N. C., around Gulf of Mexico and Caribbean Sea to Rio Grande do Sul, Brazil (Coelho and Ramos 1972).

Remarks.—This species is rather abundant off the Carolinas and in the western Gulf of Mexico (Hildebrand 1954, 1955; Rickner 1975), rare in southwestern Florida (Rouse 1970), but fairly common in less than 18-m depths around barrier islands off Mississippi (Franks, et al. 1972). Ovigerous females are known to occur from January to November in various localities from the Carolinas to the Guianas. Brooks and Wilson (1883) described the first zoeal stage of *P. sayana*. A long breeding season is indicated, as is true of a close relative in the Pacific, *P. cancrisocialis*. Haig (1960) suggested that these forms may be conspecific.

Randall (1967) reported *P. sayana* from stomach contents of the Spanish hogfish, *Bodianus rufus*.

Porcellana sigsbeiana A. Milne Edwards

Fig. 181

Porcellana sigsbeiana A. Milne Edwards 1880:35.—
Haig 1956:33.—Williams 1965:111, fig. 88.—
Gore 1970:964.

Recognition characters.—Carapace longer than wide, evenly convex in posterior half, broadly ridged in gastric region; lateral margins thin, produced and slightly upturned; surface faintly rugose. Front strongly tridentate; rostrum exceeding narrower lateral teeth, irregularly pentagonal. Orbit with outer angle produced into broad, oblique tooth; eyes well developed. Anterolateral borders concave, ending in shoulder separated from acute

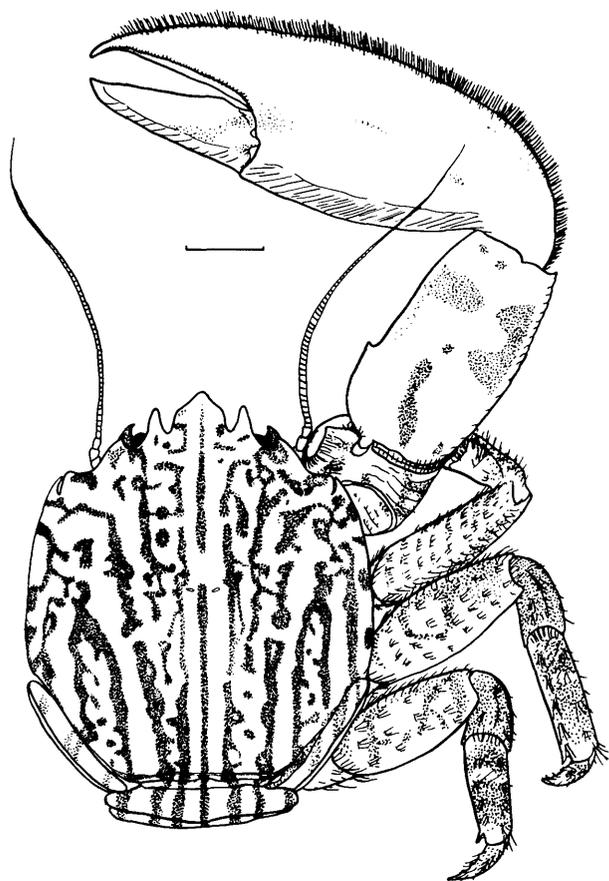


Fig. 181. *Porcellana sigsbeiana* A. Milne Edwards. Animal in dorsal view, fifth leg only of left side shown, 5 mm indicated (from Williams 1965).

marginal tooth by elongate notch at terminus of cervical groove. Antennae slender, smooth, about as long as carapace; basal article strongly produced forward in spinelike projection; movable articles far removed from orbit.

Cheliped strong, heavy, nearly smooth but slightly rugose; hand longer than carapace, outer margin fringed with setae, fingers less than half as long as palm, nearly straight, hooked at tips; length of carpus more than 1.5 times width, small spiniform tooth at outer distal angle with variable small spines mesial to it and shoulder at proximal inner angle tipped by similar spine preceded by variable smaller ones; merus with broad tooth and variably smaller ones on lobe at internal angle. First 3 pairs of walking legs with scattered tufts of setae.

Telson composed of 7 elements.

Measurements in mm.—Carapace: male, length 24, width 22; ovigerous female, length 16, width 14.5.

Color.—Irregular pattern of reddish longitudinal mottlings on white background (specimens preserved in alcohol).

Habitat.—Gore (1971) characterized *P. sigsbeiana*

as a sublittoral species; it is usually found in deeper water than the related and similar *P. sayana*; 16 to 393 m (Wenner and Read 1982).

Type-locality.—Blake Stations: 49, off delta of Mississippi River, 216 m; 36, north of Yucatan, 154 m; 142, Flannegan Passage [Virgin Islands], 49 m.

Known range.—Off Martha's Vineyard, Mass., to southwestern Caribbean Sea off Colombia (Gore 1970); West Indies to Virgin Islands.

Remarks.—This is the largest porcellanid species in the region (Benedict 1901c). Spines on the legs become worn or obliterated in old individuals.

Ovigerous females have been taken in April, May, June and November off northwest Florida, Alabama, Mississippi and Louisiana, in July off Venezuela and Colombia (Gore 1974), and in midwinter off Yucatan. Gore (1971) studied the complete larval development under laboratory conditions at temperatures of 10°, 15°, 20°, 25° and room temperature of 19°–27°C (\bar{x} = 24.4°C). Duration of stages appeared to be temperature dependent. There is a pre-zoeal stage that persists for ½ hour followed by two zoeal stages and a megalopa; the first zoeal stage lasted 8–9 days, the second 10–14 days, and the megalopa at least 15 days. Although the lowest mortality was observed at 20°C, the only crab stage reared was obtained at room temperature 33 days after hatching.

Comparing larvae of *P. sigsbeiana* with those of other porcellanids, Gore (1971) recognized two groups: a *Porcellana* group that includes *Polyonyx*, *Euceramus* and *Pisidia*; and a *Petrolisthes* group that includes *Pachycheles* and *Megalobrachium*. A third group may include aberrant *Petrolisthes* from the eastern and Indo-Pacific ocean regions. Gore included an excellent bibliography of papers on larval porcellanids.

Section Hippidea

Superfamily Hippoidea

Abdomen reduced in size, bent under thorax; appendages of sixth segment not adapted for swimming. First pair of legs simple or subchelate, second to fourth legs with last article curved and flattened. Rostrum small or absent. Third maxillipeds without epipodites.

Family Albuneidae

Carapace flattened and without wings covering legs. First pair of legs subchelate. Third maxillipeds narrow. Telson not conspicuously lengthened, almost oval.

Key to Genera

1. Eystalks narrow, triangular. *Albunea*
 Eystalks broad, oval *Lepidopa*

Genus *Albunea* Weber 1795

Gordon 1938:190.—China 1966:203.

Key to Species

1. Dactyl of second and third legs with blunt, rectangular lobe at base of anterior border. *A. gibbesii*
 Dactyl of second legs with asymmetrically mucronate spur, and third legs with acute, falciform spur at base of anterior border *A. paretii*

Albunea gibbesii Stimpson

Fig. 182

Albunea symnista Gibbes 1850:187.

Albunea gibbesii Stimpson 1859:78[32], pl. 1, fig. 6.—Benedict 1901c:139.—1904:625.—Hay and Shore 1918:414, pl. 30, fig. 11.—Schmitt 1935a:208.—Gordon 1938, figs. 3e, 4b.—Williams 1965:136, fig. 112 (part).

Recognition characters.—Carapace about as broad as long, convex from side to side, nearly straight from front to back; front with minute rostrum, and strong spine at either side followed by 7 to 10 slender spines; anterolateral angle with stout conical spine below *linea anomurica* projecting little if any beyond anterior border; posterior margin deeply

and broadly notched; dorsal surface with numerous irregular, more or less transverse, impressed lines, short ciliated one near front and another crossing near middle in shape of spread M being most conspicuous.

Eystalks narrow, triangular, cornea at tip minute. Antennules about twice as long as carapace; flagella slender and densely setose above and below along inner surface, forming respiratory tube when approximated. Basal article of antenna with acute, small, lateral spine; flagellum about half as long as peduncle. First pair of legs stout, setose, all but distal articles inflated; hand subchelate; inferior distal angle of propodus produced into spine; dactyls curved and rather slender. Second, third, and fourth legs stout, hairy, and with falcate dactyls; dactyl of third leg almost rectangular at base of anterior margin and second with similar broader structure. Fifth legs weak, borne above others.

Second, third, and fourth abdominal segments with expanded pleura, fifth and sixth segments small. Female with long uniramous pleopods on second to fifth segments. Uropods consisting of rather large basal article and two small falcate blades. Telson of male ovate to ovate with bluntly mucronate tip, central shield heavily calcified, round patch of setae near basal corners and elongate V-shaped patch distally on midline, wide margins lightly calcified and thickly fringed with setae; of female ovate and well calcified overall, setae less developed.

Measurements in mm.—Length of carapace, male and female, 20.

Variation.—Spines on the anterior margin of the carapace may vary in number, spaced occasionally so close as to appear doubled. In a limited sample, males from southern Brazil appear to have a more attenuated tip on the telson than males from North America and the Greater Antilles.

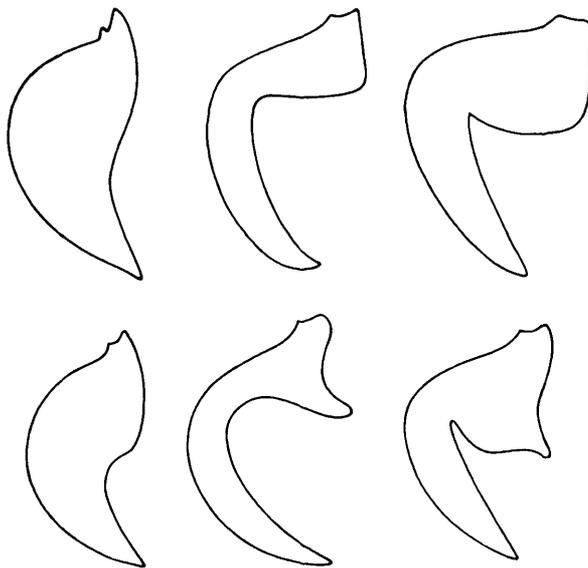


Fig. 182. *Albunea gibbesii* (upper) and *A. paretii* (lower), dactyls of second to fourth legs.

Color.—Light brown to orange-tan above, cross striae lighter, with irregularly placed iridescent areas; antennules with alternating light and dark bands; eyestalks with a white ring behind cornea; underparts light (from recently preserved specimens). Pink hand and finger (M. Gray, notes on Georgia specimen). Light purple with whitish markings, more or less iridescent (various authors).

Habitat.—Sandy bottoms; extreme low tide mark to 64 m; (70–90 m?).

Type-locality.—St. Augustine, Fla.

Known range.—East of Cape Lookout, N. C., to Texas; through West Indies to São Sebastião, São Paulo, Brazil.

Remarks.—*Albunea gibbesii* is occasionally found on exposed sandy shoals, especially at times of extremely low tides when heat from the sun warms the exposed sand and drives the animals to the surface. Occasionally specimens are found by digging, and have been taken in the Carolinas by dredging to depths of 64 m. This also may be the species reported by Cain (1972) at 70–90 m on the *Lithothamnion* reef SE of Cape Lookout, N. C.

Ovigerous females have been taken in North Carolina in June.

Pearse, et al. (1947) showed that *A. gibbesii* burrows backwards into the sand like the similar highly specialized sand dwellers, *Lepidopa websteri* and *Emerita talpoida*. These authors stated that *A. gibbesii* scrapes food from the setose antennules with the mouthparts; however, the chelate first legs and well-developed mandibles suggest feeding habits more like those of *Lepidopa* species. Function of the antennules as a possible feeding device was discussed by Benedict (1904).

Randall (1967) reported *A. gibbesii* from stomach contents of the margate, *Haemulon album*, and permit, *Trachinotus falcatus*.

Albunea paretii Guérin-Méneville

Figs. 182–183

Albunea oxyophthalmus Leach (MS) in White 1847b:57 (nomen nudum).—Snodgrass 1952, fig. 11A.

Albunea paretii Guérin-Méneville 1853:48, pl. 1, figs. 10–10a.—Rodrigues da Costa 1962:6, pl. 1, figs. 5, 7; pl. 3, figs. 1–3.—Williams 1965:137, figs. 112 (part), 113.

Albunea parettoi.—Monod 1956:37, figs. 2–9.

Albunea paretii.—Fausto-Filho 1967a:12.

Recognition characters.—Similar to *A. gibbesii*, differing chiefly in characters given in key and shape of male telson. Dactyl of second legs with asym-

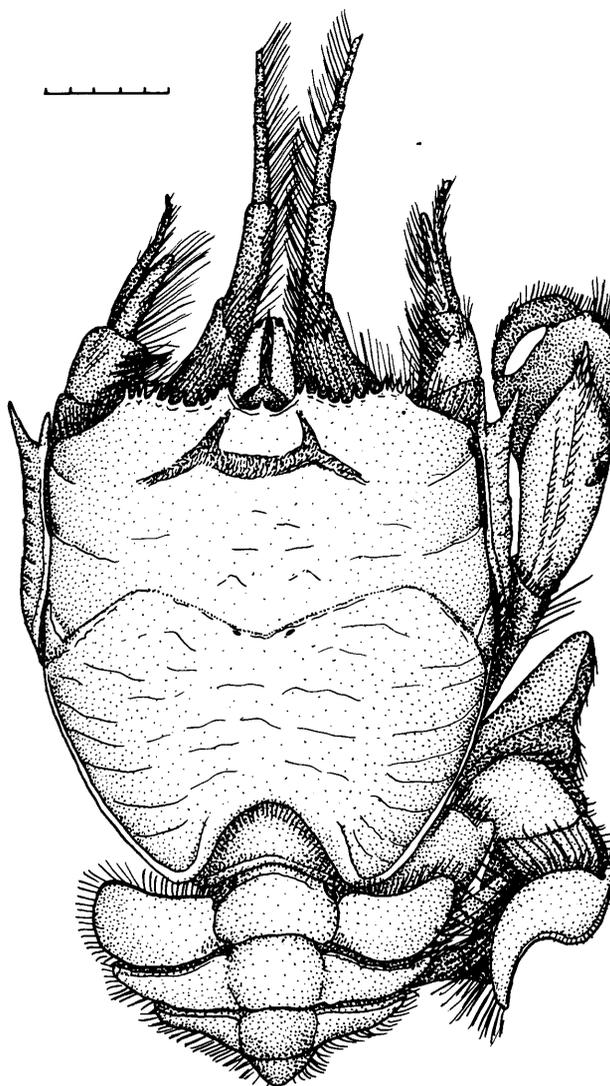


Fig. 183. *Albunea paretii* Guérin-Méneville. Animal in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

metrically mucronate spur, of third legs with acute, falciform spur at base of anterior border. Telson of male pentagonal, central shield heavily calcified, with line of setae near each basal corner and in closed V-pattern distally along midline, wide margins lightly calcified and thickly fringed with setae; of female ovate and well calcified overall, setae much less developed.

Measurements in mm.—Length of carapace: male, 15; female, 20.

Habitat.—Sandy bottom; low tide mark to 38 m. Döriges (1977) found it associated with unprotected sand flats, shoals, and from 10 m seaward in nearshore waters of Georgia.

Type-locality.—[Uncertain], America.

Known range.—Beaufort Inlet, N. C., to Corpus Christi, Tex.; through West Indies to Santa Cata-

rina, Brazil (Coelho and Ramos 1972); West Africa from Cape Verde Islands and Senegal to Ghana.

Remarks.—Ovigerous females have been taken in June in North Carolina.

Genus *Lepidopa* Stimpson 1858

Stimpson 1858:230.—Holthuis 1960a:27.—China 1966:248.

Lepidopa websteri Benedict

Fig. 184

Albunea scutellata.—Gibbes 1850:187 (not Fabricius 1793, and H. Milne Edwards 1837).

Lepidops venusta.—Kingsley 1880:410.

Lepidopa websteri Benedict 1903:892, fig. 3.—Hay and Shore 1918:415, pl. 30, fig. 12.—Williams 1965:138, fig. 114.—Efford 1971:91, figs. 1b, k; 2j; 3r; 4h, m; 5g, i; 60.

Recognition characters.—Carapace considerably shorter than wide, slightly narrowed behind lateral spines, then widening before sides converge toward truncated posterior margin; anterior margin fringed with long setae; posterior concavity just short of being semicircular; dorsal surface traversed near front by impressed lines crossing at about middle of carapace. Rostrum narrowly acute (tip somewhat obscured by setae), its concave sides continuous with margin of ocular sinus; margin running from base of orbit almost straight out to anterolateral projection (tipped by spine) with only slight tendency to convexity; anterolateral margin extending backward and then nearly straight laterally before curving to lateral spine.

Eyestalks lamellate, irregularly oval, underside densely setose. Antennules with peduncles exceeding eyestalks; major flagella straight, slender, nearly 3 times as long as carapace, fringed mesially with setae and forming respiratory tube when approximated; second flagella exceedingly short, each extending only to end of second article of first flagella. Short antennae with broad basal article; antennal scale reduced to short point just overlapping fourth article of peduncle, fifth article only about half width of distal end of fourth; flagellum stout, curved, composed of 8 articles (first very short). Carpus of third maxilliped overlapping propodus but not reaching its distal end. First legs with broad, flat articles; dactyl turned back on propodus to form subchela. Second, third and fourth legs with terminal article bifurcate. Fifth legs much reduced, slender and folded.

Abdomen short and partly flexed beneath thorax;

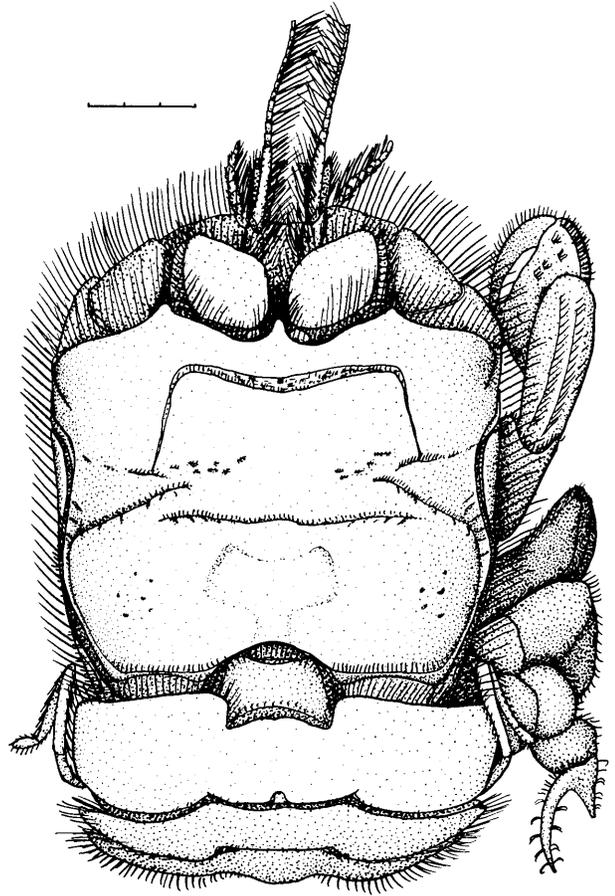


Fig. 184. *Lepidopa websteri* Benedict. Animal in dorsal view, first to fourth legs of left side not shown, 5 mm indicated (from Williams 1965).

second, third, and fourth segments with expanded pleura. Uropods small, with slender basal article and long, oval blades, their margins and those of abdominal segments fringed with long silky hairs. Telson heart shaped.

Measurements in mm.—Length of carapace, to 19 (A. M. Young, personal communication).

Color.—All parts white, iridescent, with pink being most conspicuous tint on anterior part of carapace, and blue showing along sides, in depressions of carapace, and on extremities of fifth legs; dorsal plates of abdomen faintly pink tinged, bordered by a delicate blue-green; on either side of middorsal line, pink shading into red, and blue becoming deeper in shade (from note by A. Shaftsbury, USNM).

Habitat.—Usually found on gradually sloping sand beaches of open ocean at or immediately below low tide mark (Pearse, et al. 1942); shallow water, limits unknown.

Type-locality.—Beach near Fort Macon [Carteret County], N. C.

Known range.—Around mouth of Chesapeake Bay

(larvae); Drum Inlet, N. C., to Sapelo Island, Ga.; Tampa Bay, Fla.; Ship Island and Petit Bois Island, Miss. (Efford 1971; Sandifer and Van Engle 1972a; Sandifer 1973d).

Remarks.—Efford (1969) outlined his view of evolution of the Albuneidae and (1971) revised the genus *Lepidopa*, discussed zoogeography, and reviewed all published information. The biology of *L. websteri* is best known among species in the genus but information is largely limited to the brief account given by Pearse, et al. (1942) which included detailed drawings of the specialized legs as well as a lateral view of the whole animal. The species is highly adapted for burrowing in sand, and is usually found in small numbers. It burrows backward, and at rest lies at an angle to the surface with the long antennules extended in the water above. If disturbed, the animals may descend several centimeters into the sand. Benedict (1904) commented on the possible feeding function of the antennules in the genus *Lepidopa*. In 1903, he found setae of annelids, skin of a small *Synapta* and parts of the flagella of some small crustaceans among stomach contents of *Lepidopa scutellata* (= *L. benedicti*, see Holthuis 1960a:31). Such finding would be in accord with the fact that *Lepidopa*, like *Albunea*, has well-developed mandibles (Snodgrass 1952). Under experimental conditions Howard (1969) X-rayed *L. websteri* in its U-shaped burrows. He suggested that it may be a detritus feeder.

Ovigerous females have been taken in July in North Carolina, and both larvae and juveniles have been taken in plankton tows there in July and Au-

gust. Sandifer and Van Engel (1972a) described three zoeal stages from plankton collected at six stations near the mouth of Chesapeake Bay and one location north of the Bay off the eastern shore of Virginia in July and August of 1960, 1961, and 1969. Most of these were first zoeae. Presuming an 8–10 day duration of stage I (as in *L. californica*), and taking into account the summer circulation patterns for the region, a breeding population on Virginia beaches was proposed as likely rather than transport of the larvae from North Carolina.

Family Hippidae

Carapace subcylindrical, and with wings covering legs. First legs simple. Third maxillipeds broad. Telson lengthened, lancet-shaped.

Genus *Emerita* Scopoli 1777

Heegaard and Holthuis 1960:181.—China 1966:236.

Body convex, oval. Carapace firm, crossed more or less by overlapping rugosities. Rostrum small; impressed transverse line behind rostrum and deeper more strongly curved one farther back. Anterolateral margins concave. Eyestalks long, slender, cornea small but dilated. Antennules with peduncles and flagella setose mesially, forming respiratory tube when approximated. Antennae normally held concealed beneath third maxillipeds. First legs directed forward.

Key to Species

(After Schmitt 1935a)

1. Dactyl of first leg subacute or sharply pointed distally, anteroventral extension of propodus similar; transverse rugosities more or less continuous over dorsum and continued in posterior part of carapace to inferior margin *E. benedicti*
- Dactyl of first leg rounded or obtuse distally, anteroventral extension of propodus bluntly pointed or rounded; lateral expansion of carapace smooth and punctate for greater part *E. talpoida*

Emerita benedicti Schmitt

Fig. 185

Emerita benedicti Schmitt 1935a:215, figs. 71a, b.—Lunz 1939:336.—Williams 1965:139, fig. 115A.

Recognition characters.—Carapace subcylindrical, firm; transverse rugosities more or less continuous, close set, and crossing whole of dorsum, those

on posterior part continued to inferior margin. Rostrum equilaterally triangular, separated by rounded sinus on each side from prominent and subacute tooth. Anterolateral margins concave and subserrate. Antennules about 3 times length of slender eyestalks. Antennae normally held beneath third maxillipeds, at least as long as carapace when extended; first peduncular article short, second largest with outer margin produced into strong

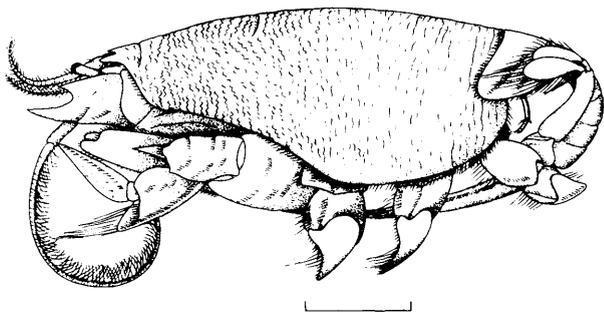


Fig. 185. *Emerita benedicti* Schmitt. Female in lateral view; 5 mm indicated (USNM 119091).

superior and much longer inferior spine; flagellum densely beset laterally with 8 rows of fringed setae, outer rows longest.

First pair of legs with articles more or less setose and with impressed, interrupted, transverse ciliated lines; dactyl subacute distally; anteroventral extension of propodus similarly pointed; carpus terminating in spine distally. Second, third, and fourth legs less strong, setose, tips curved and foliaceous. Fifth legs almost filamentous, entirely concealed beneath abdomen.

Abdomen broadest anteriorly, narrow posteriorly, flexed so that telson and sixth segment lie beneath body. Uropods turned forward, resting along sides of proximal segments. Telson elongate, lanceolate, margined with reflected setae above and inflected ones on edge; base with 2 short, impressed lines.

Measurements in mm.—Length of carapace, ovigerous female, 21.

Habitat.—Shell bottom, and probably other types (Lunz 1939) [coarse grained substrate?]; to 3.5 m.

Type-locality.—Tampa Bay, Fla.

Distribution.—Charleston County, S. C., to Veracruz, Mexico (Efford 1976).

Remarks.—Ovigerous females are known from South Carolina in June (Lunz 1939) and from South Carolina, Georgia, and Mississippi in July.

Emerita talpoida (Say)

(Mole crab; sand bug)

Fig. 186

Hippa talpoida Say 1817:160.

Hippa emerita.—Ortmann 1896 (in part):232.

Emerita talpoida.—Hay and Shore 1918:41, pl. 30, fig. 8.—Schmitt 1935a:216, figs. 74a, b.—Snodgrass 1952.—Williams 1965:140, figs. 115B, 116.

Recognition characters.—Carapace subcylindrical, with overlapping rugosities anteriorly, smoother and

polished posteriorly. Rostrum small, blunt, separated by rounded sinus on each side from more prominent and acute tooth. Anterolateral margins concave and subserrate. Antennules approximately twice length of slender eyestalks; basal article with strong external spine. Antennae nearly twice as long as carapace when extended; first peduncular article short, second largest with outer margin produced into strong, anteriorly directed spine bifid at tip with deep fissure below; flagellum densely beset laterally with 8 rows of fringed setae, outer rows longest.

First pair of legs with articles more or less setose and with impressed, interrupted, transverse ciliated lines; dactyl rounded or obtuse distally; anteroventral extension of propodus bluntly pointed or rounded; carpus terminating in spine distally. Second, third and fourth legs less strong, setose, tips curved and foliaceous. Fifth legs almost filamentous, entirely concealed beneath abdomen.

Abdomen broadest anteriorly, narrow posteriorly; flexed so that telson and sixth segment lie beneath body. Uropods turned forward, resting along sides of proximal segment. Telson elongate, lanceolate, margined with reflected setae above and inflected ones on edge; base with 2 short, impressed lines.

Measurements in mm.—Length of carapace: males 19.4; ovigerous females, 36.

Color.—Uniform pale yellowish brown (Snodgrass 1952).

Habitat.—Sandy beaches in and below surf line; to 3.5 m in winter.

Type-locality.—[East] coast of United States.

Known range.—Harwich [Barnstable County], Mass. to Horn Island, Miss.; Progreso, Yucatan, Mexico (Schmitt 1935a; Efford 1976).

Remarks.—The morphology, life history and general ecology of *Emerita talpoida*, a representative of the specialized sandy-beach fauna, have been studied by a number of workers. The spawning season lasts from winter to autumn, varying in length with latitude and season, more extended in the south than in the north. Ovigerous females have been reported in scattered records as early as February at Egmont Key, Tampa Bay, Fla. (Dragovich and Kelly 1964), are known in April from Pensacola, Fla., and as late as September at Cape Henry, Va., October in Charlotte County, Fla., and November at Flagler Beach, Fla. (USNM). Diaz (1974) found them from January to October in North Carolina, with spring and summer pulses of abundance. Hunter (1972), working in Virginia, thought the reproductive cycle to be related to temperature.

The eggs are bright orange when first laid and

gradually fade to a translucent dirty gray just before hatching. Johnson (1964) gave details on the histology of the male reproductive system and Diaz (1974) showed that large females in spring have greater numbers of and larger eggs than the smaller females of midsummer. Wharton (1924) gave a figure of the mature sperm cell. Herrick (1892:25) gave figures of developmental stages in the egg. Rees (1959) described the larval stages and a megalopa, which resembles the adult, from rearing experiments in the laboratory. He found development to last 28 days and encompass at least 6 larval stages, and Diaz (1974) added details showing some variation in development time. Shield (1973) described a constant pattern of red-colored chromatophores in each of the zoeal stages which is apparently distinctive for the species.

Sandifer (1973d) reviewed published records of larvae found in plankton. These occurrences are later than the spawning records, being as early as May off the St. Johns River in Florida, and around Beaufort Inlet, N. C., off Chesapeake Bay in June, Delaware Bay to Woods Hole in July, ranging from St. Johns River, Fla. to Woods Hole in September, and receding in autumn with records in Delaware Bay in October and at Cape Hatteras, N. C., in November. Most of these records are from along shore or in bays or lagoons near the sea. A few records show that there is some offshore movement. Dudley and Judy (1971) found larvae at 1–8 m depths at three stations off Beaufort Inlet, N. C.: 1.6 km offshore, May–September; 6.5 km offshore, May–October; 8–10 km offshore, June–October. Sandifer (1973d) reported them from a comparable station in the mouth of Chesapeake Bay. Efford (1970) pointed out that all species of *Emerita* live along continental shores, except one in Puerto Rico. All, with the possible exception of that one (da Costa 1962), have extended larval developments, and da Costa concluded that longshore countercurrent systems are essential to maintenance of the populations (also Efford 1976).

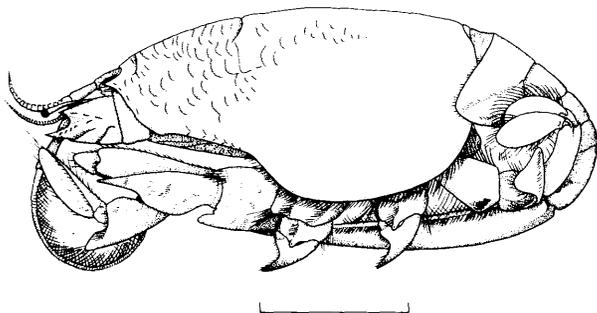


Fig. 186. *Emerita talpoida* (Say). Female in lateral view; 1 cm indicated (USNM 91082).

Wharton (1942) found megalopae and young adults distributed evenly in the wave-washed zone rather than in colonies as are adults. Megalopae swim with the abdomen extended, whereas young adults swim with the abdomen flexed. He traced development of the pleopods of females from the truly swimming appendages of the megalopae to the uniramous non-swimming pleopods of adults. Adult males lack pleopods.

Diaz (1974) was able to resolve the results of earlier observations on spawning, breeding, and growth with his own. He found that recolonization occurs in June–July and September–October, corresponding to the earlier spawning pulses if one allows time for larval development and settlement of the megalopae. With the aid of individuals tagged with corks tied to monofilament line, he observed no massive migrations, rather there is net displacement along the shore in currents moving from 10–15 m to 4–5 km/day.

Aggregations were seen clearly in fall and spring along Bogue Banks, N. C., their occurrence usually corresponding with appearance of a cusp on the beach. By midsummer, there were aggregations 5–10 m wide in bands several km long.

Females grow at rates related to time of settlement; those arriving on the beach in June might overwinter once, but those arriving in September through November could overwinter twice. Females commonly attained a carapace length of 22 mm (smallest ovigerous was 14.1 mm) and there were a few above 29 mm. Large females tend to die after spawning in spring. Males reach their maximum size in 9–10 months, commonly attaining lengths of 14 mm and occasionally as much as 19.4 mm. The sex ratio was 50% except in May, August, and September when females rise to 65% and in July when they reach a low of 43%.

Sexually mature at very small sizes, the males are neotenic, occurring in densities of up to 7/female with no correlation between size of female and number of male consorts. Multiple matings of a female with males were observed, ribbons of sperm usually being deposited between the third and fourth pairs of legs. Females had molted prior to copulation.

Efford (1967) suggested that neotenus males in *Emerita* are probably advancing toward incipient parasitism, precocious sexual maturity insuring that many males find females and enhancing their chances of sticking on in turbulent surf. However, Wenner (1972) pointed out that deviation from 1:1 sex ratios in different size classes is apparently widespread in marine crustaceans and may have been obscured by usual methods of computation. He felt that size within class should be observed for

computing sex ratios, and that one of the types of skewed ratios could indicate sex reversal. To bolster his evidence for *Emerita*, 85 males of *E. analoga* were maintained in a cage in open water for 40 days. At the end of that time 79 survived and 16 were females. Diaz (1974) essentially repeated this experiment for *E. talpoida* but observed no sex reversal among males kept 48–85 days in aquaria and fed *Artemia* nauplii or dockside plankton in turbulent water. He analyzed groups of 100 in June–July 1972, April and October 1973, at carapace lengths of 3.5–13.9 mm. Females, some ovigerous, introduced in the same tanks with the males also had no effect. Fusaro (1978) found that differential growth rate of males and female *E. analoga* between 9 and 14 mm carapace length may account for the size frequency distribution and sex ratio pattern observed by Wenner, rather than protandry.

Wharton (1942) estimated that growth of large female *E. talpoida* may be as much as 0.08 mm per day from early June to late August. However, both Wharton and Williams (1947) noticed that there is considerable annual fluctuation in size at the same locality, and Williams further stated that there is considerable variation in size between localities in the same year.

The beautiful adaptations of this species for life in the shifting sand of the surf zone were treated by Wharton (1942) and the anatomical specializations exhaustively discussed by Snodgrass (1952). Adults can swim by means of the uropods, but they are primarily adapted for burrowing backward into wet sand. This is accomplished by rotating the uropods and fourth legs in unison (Trueman 1970, for *E. portoricensis*) and moving the first, second and third legs laterally and posteriorly in oarlike unison. Digging is initiated by tactile stimulation of the base of the telson. Like many crustaceans adapted for life in sand, the exoskeleton is ornamented with ridged burrowing sculptures (Seilacher 1973; Schmalfuss 1978). The ridges can be described as cuestas or terraces with sharp edges above steep anterior slopes. The ridge patterns are only vaguely symmetrical, and on different individuals are as different and personalized as fingerprints. Ontogenetically, ridge patterns are replicated in considerable detail except for size increase; new ridge elements are introduced as short lateral extensions of preexisting ridges, links between these, or incipient ridges in smooth areas; new incisions appear in previously simple saddles, particularly of incipient ridges, but partial disappearance of ridge elements is less common. Seilacher proposed that minute fibers pull the new cuticle off the old one in the direction of molting. At every point the pull produces V-shaped wrinkles which link with adja-

cent wrinkles to form smoothly curved pull-off saddles. Larger setae are not involved in the process because their pores are never placed in the tie-point incisions, but they influence the course of the ridges. This remains to be proved. The process does not allow formation of completely straight ridges, but for burrowing ribs the fabricational irregularity increases friction rather than reducing it, introduces chance effect in pattern, allows step by step increase of ridge length at molts, and produces frictional symmetry only in one direction (conformable with direction of molting); therefore, this type of sculpture is restricted to the carapace whereas different types of ornamentation (setate ridges) fulfill the same function in other parts of the exoskeleton.

Emerita talpoida moves up and down the beach with the tide, following shallow waves toward the water or moving up the beach with deep waves. Each time the animal is buried, the antennae are allowed to lie on the sand extended anterolaterally to strain the receding waves. Stomach contents consist of small particulate matter, the method of transferral of food from the antennae to the mouth being explained in detail by Caine (1975). Jones (1936) compared the habits of *E. emerita* to those of *E. talpoida* and devised a clever method of marking animals with string for the purpose of tracing their movements on the beach.

Edwards and Irving (1943) studied the influence of temperature and season on oxygen consumption in *E. talpoida* at Woods Hole. They found that oxygen consumption of winter animals at 12°C is about the same as that of the smallest summer animals at 17°C; consumption of winter animals at 3°C is about the same as that of summer animals at 13°C. They concluded that *E. talpoida* from the Woods Hole area become adjusted to seasonal changes in temperature in such a manner that rate of metabolism in winter is kept at a level comparable to that in summer. This explains why growth is uniform throughout the year, by their estimates, though the animals live in 2 to 4 m of water in winter rather than in the surf. The method of feeding in winter was not discussed, and Efford (1966) pointed out that *E. talpoida* cannot feed in standing water whereas *E. analoga* can do this.

Emerita talpoida tolerates sea water concentrations of 40 to 180‰ (Bursey and Bonner 1977). Crabs transferred directly from one salinity to another experience changes in hemolymph concentration toward that of the new salinity and less than two hours are required to establish a new steady state. Hyperosmotic regulation occurs over the entire range of tolerance, but may be entirely due to protein concentration of the hemolymph since its

osmotic concentration is always greater than the external medium at equilibrium (Burse 1978). Tolerance is greatly influenced by temperature, and is optimal at 20°C for test exposures of limited time.

Cronin and Johnson (1958) described a fungus from the hind gut of *E. talpoida* from the beaches of North Carolina near Beaufort.

Infraorder Brachyura

Crabs with abdomen much reduced in size, straight, symmetrical, closely bent under thorax, never used for swimming, and with uropods rarely present, never biramous. Cephalothorax depressed, fused with epistome at sides and nearly always in middle. Antennal scales immovable. Third maxillipeds broad. First pair of legs chelate and nearly always much stronger than other legs.

Borradaile's (1907) hierarchical arrangement of brachyurans, essentially adopted by Rathbun (1918b, 1925, 1930a, 1937), has been the accepted standard for American workers. However, independent lines of evidence from adult morphology of recent crabs, the fossil record, and larval studies are beginning to offer a more complex picture of evolutionary radiation in the group than the "standard" ideas based on adult morphology alone. Števíć (1971) drew the lines of evidence together, feeding a host of ideas into concise analysis which offers new views of old problems. Incorporating the more modern views, especially those derived from larval studies, the following arrangement deviates from Rathbun's standard in some respects, especially among the primitive crabs.

Key to Genera

1. Carapace firm and hard, body covered with short pubescence . . . *Dromidia*
Carapace soft and membranous, body mostly naked *Hypoconcha*

Genus *Dromidia* Stimpson 1858

Rathbun 1937:32

Carapace convex and pilose, hair often of considerable length; front narrow, hepatic region more or less concave, or excavated anteriorly. Palate strongly ridged on either side. Sternal sulci in female approximate in their extremities in either a single or more or less bifurcated tuberculiform projection between bases of chelipeds. (After Rathbun 1937.)

Section Dromiacea

Carapace subglobose or subquadrate, frontal region narrow. Last 1 or 2 pairs of legs small, subdorsal in position. Abdomen folded under thorax, penultimate segment usually without appendages; 5 pairs of appendages in female, first pair rudimentary. Lateral thoracic apodemata united in common center, forming a sternal canal. External maxillipeds with merus and ischium subquadrate (Rathbun 1937).

Superfamily Dromioidea

Family Dromiidae

Carapace subglobular, rarely flattened; no *lineae anomuricae* (a pair of longitudinal suture lines on carapace). Sternum of female traversed at least in part by 2 obliquely longitudinal grooves. External maxillipeds generally operculiform. Legs of moderate size; fourth and fifth pairs short, subdorsal in position, furnished with small hooklike nail or dactyl. Sixth segment of abdomen generally with rudimentary uropods (Schmitt 1921).

Gordon (1950; 1963) found the obliquely longitudinal sternal grooves on the females of this family to be external evidence of a pair of involuted tubes (variously developed in different species) leading from an external opening at the anterior end of the grooves posteriorly to paired spermathecae enclosed in the endophragmal system. (See also Wear and Batham 1975.)

The North American fossil record for this family dates from the Paleocene of the Gulf of Mexico coast (Glaessner 1969), though no modern species possesses a fossil record.

Dromidia antillensis Stimpson

Fig. 187

Dromidia antillensis Stimpson 1859:71.—Hay and Shore 1918:417, pl. 31, fig. 5.—Rathbun 1937:33, fig. 12, pl. 7, figs. 1–3.—Guinot-Dumortier 1959:428, fig. 4a, b.—Williams 1965:143, fig. 118.—Coelho and Ramos 1972:177.—Felder 1973:44; pl. 6, figs. 1, 3 (key).—Powers 1977:19.

Recognition characters.—Body and legs covered

with thick coat of short pubescence, leaving little but parts of fingers and tips of dactyls exposed. Carapace convex in all directions, longer than broad; frontal region longitudinally grooved along middle; front strongly deflexed, with 5 small teeth, median 3 subequal and approximately as long as distance between them at bases, teeth over eyes somewhat shorter but acute. Anterolateral margin of carapace deflected toward corner of buccal area, armed with 4 or 5 teeth.

Chelipeds rather thick and heavy; carpus dentate with small teeth at anterior angle; palm shorter than dactyl and armed with 3 blunt spines on upper margin; fingers curved, with strongly interlocking teeth. Walking legs rather slender; last pair turned forward over back and much longer than fourth pair; dactyls of fourth and fifth legs hooked, closing against unequal pair of distal spines on propodus.

Measurements in mm.—Carapace: male and female, length 32, width 31.

Color.—Quite variable. General ground color dirty yellowish green, olive buff, white, coral-mud gray, orange buff or various shades of red with lighter pubescence; fingers with bases darker than white tips, shades of orange, pink, or red; cornea of eyes gray, hazel, reddish speckled or brown; some

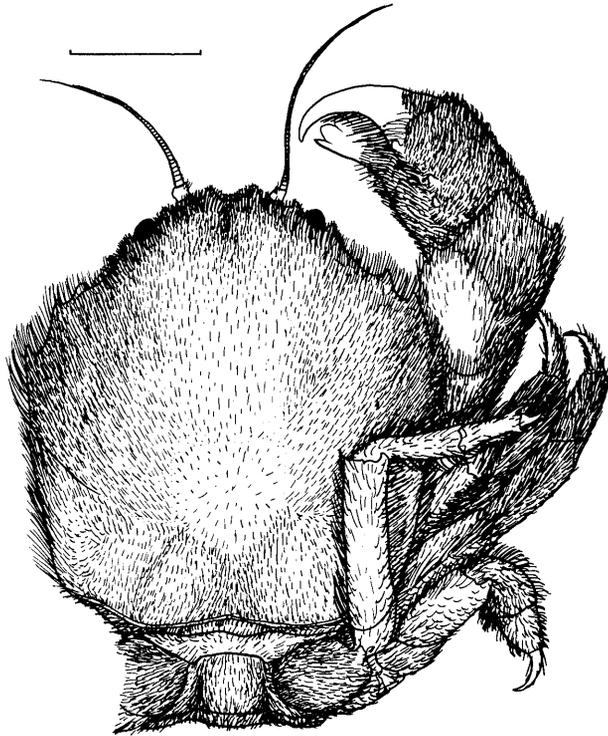


Fig. 187. *Dromidia antillensis* Stimpson. Male in dorsal view, legs of left side not shown, 1 cm indicated (from Williams 1965).

specimens with bluish cast on maxillipeds and antennular peduncles. Rathbun (1937) gave great detail on a number of individuals which appear to vary from light to dark in a harmonious set of colors.

Habitat.—Shore to 311 m.

Type-locality.—St. Thomas, V. I., Key Biscayne and Tortugas, Fla.

Known range.—Off Cape Hatteras, N. C., through Gulf of Mexico and Caribbean Sea to Rio de Janeiro, Brazil; Bermuda; Saint Helena (Forest 1974).

Remarks.—This species is usually found carrying a covering of compound ascidians, sponges, or zoanthoid polyps. The North Carolina records represent marginal occurrences in a favorable northern locality. Hildebrand (1955) found it common on the Campeche Banks shrimping grounds.

Rathbun (1937) reported ovigerous females from Florida and the West Indies in winter, spring and summer, and they are known from North Carolina in June. Rice and Provenzano (1966) described 6 zoeal stages and a megalopa from eggs hatched in February and reared in 100% and 75% sea water at 25°C, and in 100% sea water at 20°C. Development time in 100% sea water at 25°C averaged 40 days. At lower salinities and temperatures no developing animal passed through all stages. From eggs hatched in June and reared in 100% sea water between 25° and 28°C, development through megalopa averaged 30 days. Relationships of the species to the Dromiacea were discussed in light of larval studies.

In temperature tolerance experiments, specimens taken from an offshore reef off North Carolina in September and October died after a 7-hour exposure to 4°C (F. J. and W. B. Vernberg, 1970).

Genus *Hypoconcha* Guérin-Méneville 1854

Rathbun 1937:44.

Front and lateral margins expanded, covering eyes and all parts of head except flagella of antennae; margin of anterior half usually hairy, also lower surface and appendages; dorsal surface very thin and membranous. Appendages capable of being folded compactly against body; fourth and fifth pairs of legs prehensile without being subchelate; dactyl lunate.

Shape adapted to fit inside valve of lamelli-branch mollusk; this protective covering held over carapace by posterior pairs of legs and insertion of angular abdomen under hinge. (After Rathbun 1937.)

Key to Species

1. Ventral surface of carapace with 3 granulated nodules forming a triangle on either side; not hairy. *H. sabulosa*
 Ventral surface of carapace often granulate or spiny but without 3 nodules forming a triangle on either side; often hairy 2
2. Ventral surface of carapace visibly granulate; posterior side of orbit raised but never conspicuously spined *H. arcuata*
 Ventral surface of carapace with scattered, sharp granules or spines often partly or wholly concealed by thick pubescence; posterior side of orbit surmounted by a strong spine *H. spinosissima*

Hypoconcha arcuata Stimpson

Fig. 188

Hypoconcha arcuata Stimpson 1858:226.—Hay and Shore 1918:418, pl. 31, fig. 2.—Rathbun 1937:47, pl. 11, figs. 1–4.—Williams 1965:144, fig. 119.—Coelho and Ramos 1972:178.—Powers 1977:20.

Recognition characters.—Body short, broad, flattened, solid and roughly granulate ventrally. Front margin of carapace nearly semicircular in outline, margin densely ciliated, deeply fissured in middle and with shallow notch on each side near middle. Ventral surface without ridges but coarsely granulate and pubescent, sloping evenly to anterior margin, with eyes, antennules, antennae and mouthparts deeply seated in depressions; narrow fissure in front of eye for lodgment of antennal flagellum; outer posterior margin of orbit fissured. Third maxillipeds completely closing buccal cavity.

Legs all stout, hairy and coarsely granulate. First pair chelate; fingers somewhat spatulate and toothed at tip, fixed finger articulated at angle with hand. Second and third legs with sharp, corneous tips; fourth and fifth legs borne on dorsal surface, with penultimate article quite short and terminal article reduced to small contorted claw. Abdomen short and flexed so that last 2 segments lie on thoracic sterna.

Measurements in mm.—Carapace: male, length 24, width 24; female, length 24, width 25; ovigerous females, length 7.7–20, width 8.4–22.

Variation.—Most specimens are more granulated than the one figured.

Color.—Gray.

Habitat.—This curious crab is always found occupying a valve of some lamellibranch shell, preferably a clamshell (often *Trachycardium muricatum* or *egmontianum* [see Rouse 1970]) which it carries about upon its back after the manner of a hermit crab. By means of the claws on its fourth and fifth

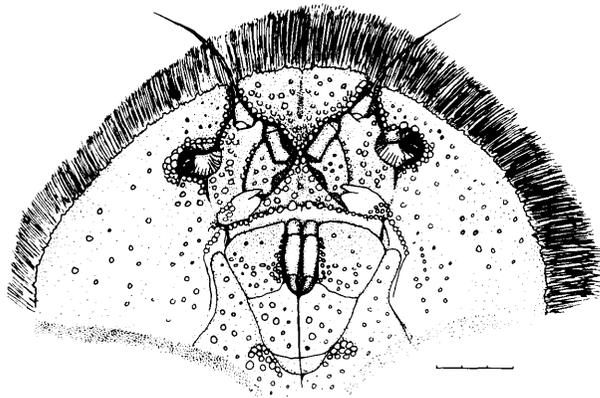


Fig. 188. *Hypoconcha arcuata* Stimpson. Anterior part of animal in ventral view, 3 mm indicated (from Williams 1965).

pairs of legs, perhaps aided by pressure of its body against the shell, it clings so tightly that removal from the shell without crushing it is almost impossible. Shallow water to 66 m (Wenner and Read 1982).

Type-locality.—South Carolina sandy shores and St. Thomas [V.I.].

Known range.—Off Cape Lookout, N. C., to west Florida; St. Thomas, V. I.; Surinam (Holthuis 1959) to Espirito Santo, Brazil.

Remarks.—Ovigerous females are known from eastern Florida in April and May. Kircher (1967, 1970) reared larvae from ovigerous females taken at an unspecified time off Cape Lookout, N. C. In controlled temperature BOD boxes at 25°C, newly hatched larvae subjected to 15, 20, 25, 30, 35 and 40‰ salinity on a photoperiod of 14 h light, 10 h dark survived to first crab stage in 25, 30, and 35‰ salinity. Three zoeal stages and a glaucothoe stage were described and figured. The early zoeae had higher survival rates in the lower salinities but the inverse was observed in later stages. There was an inverse relationship between duration and survival of each stage at a given salinity.

Kircher compared morphology of these larvae