

Fig. 353. *Pinnotheres maculatus* Say. *a*, Male in dorsal view, 2 mm indicated; *b*, female in dorsal view, 3 mm indicated (from Williams 1965).

propodus larger than carpus; dactyl narrow, curved, spatulate, attached near middle of propodus, and reaching to near extremity of propodus.

Chelipeds moderately stout, articles subcylindrical and more or less pubescent; carpus elongate; palm thick, blunt edged, increasing in size distally; fingers stout, fitting closely together with tips hooking past each other, fixed finger nearly horizontal, dactyl with tooth near base fitting into sinus with tooth at either side on fixed finger. Walking legs slender, hairy above and below; second pair longest, shorter than chelipeds; first 3 dactyls falcate, shorter than propodi; last leg shortest, turned forward and upward, with long dactyl equaling propodus.

Abdomen large, extending to bases of legs.

*Measurements in mm.*—Carapace: length 13.7, width 14.3.

*Color.*—Obscure brown.

*Recognition characters.*—Mature male: Carapace flat, subcircular, diameter about half as great as female, somewhat longer than wide, harder than female. Regions superficially defined more by color than by structural prominence, light areas mostly

elevated, usually allowing pubescence to wear; gastric, cardiac, and branchial regions separated by broad, shallow, confluent indentations. Front broad, prominent, depressed, slightly bilobed, approximately  $\frac{1}{3}$  width of carapace. Orbits subcircular, eyes large. Antennae somewhat longer than width of orbit.

Chelipeds shorter than in female, hands stouter. Walking legs wider, especially propodal articles of first 3 legs; posterior surface overlaid with thin fringe of hairs attached near upper margin; last leg relatively shorter than in female, not reaching propodus of third, dactyl more nearly like third than in female.

Abdomen at middle approximately  $\frac{1}{3}$  width of sternum, gradually narrowing from third to seventh segment, sides of third convex, of seventh obtusely rounded; sutures between segments of abdomen and sternum with narrow lines of dark pubescence.

*Measurements in mm.*—Carapace: length 9.1, width 8.7.

*Color.*—Striking, light dorsal color pattern of bare spots on background of dark pubescence consisting of median stripe constricted in middle and behind, a subtriangular spot on each side in front of middle, and a linear spot on each side behind. Chelipeds with dark pubescence on inner and upper surface of carpus, a bit on upper surface of merus and inner side of palm proximally, otherwise scattered flecks on hands and walking legs.

*Variation.*—Young females resemble dark-colored males except in shape of the abdomen and the character of its appendages. Such females are free swimming and range upward in length to 5.2 mm. More mature females, light colored and commensal or parasitic in habit, range from 3.3 mm in length upward. In such small and medium-sized females the long hair on the legs persists.

Some males resemble mature females in coloration and structure of legs, ranging in length from about 4 mm upward. Such males are commensal or parasitic in habit.

Individuals vary in stoutness of chelae, and in length and curvature of dactyls on the second legs. Normally this dactyl is like the dactyls on the first and third legs, but may be straightened and longer, and may occur on one or both sides of an individual and in different individuals in the same lot.

*Habitat.*—Mature males or females are commensal or parasitic in *Argopecten irradians concentricus*, *A. gibbus*, *Anomia simplex*, *Atrina serrata*, *A. rigida*, *Mytilus edulis*, *Modiolus modiolus*, *M. tulipa*, *Mya arenaria*, *Chlamys magellanica*, *C. tehuelcha*, *Ostrea puelchana* and a number of other bivalves, plus tubes of *Chaetopterus variopedatus*, from *Molgula robusta*,

the pharynx of *Bostrichobranchus pilularis*, on *Asterias vulgaris* (see Schmitt, et al. 1973; Fenucci 1975), and in *Laevicardium mortoni* (see Cooley 1978). The free-swimming stages have been found in bays, sands and ocean from surface to 45.7 m.

*Type-locality*.—Given as—"inhabits the muricated *Pinna* of our coast."

*Known range*.—Off Martha's Vineyard, Mass., to Golfo San Matias, Argentina (Fenucci 1975).

*Remarks*.—Ovigerous females have been found through most of the range of distribution. They have been reported in January from St. Thomas, March from Jamaica, May to November from Florida, June to January from North Carolina, July to September from Massachusetts and Rhode Island, and in June in Brazil (Rathbun 1918b and USNM).

Larval stages reared under experimental conditions in finger bowls of filtered seawater of 30‰ salinity at 25°C, and fed *Artemia salina* nauplii, passed through five zoeal stages and a megalopa (Costlow and Bookhout 1966b). Megalopae were segregated one to a bowl to avoid cannibalism. Morphological differences from other pinnotherid larvae were given both for the local fauna and that of other areas. In lower Chesapeake Bay and York River, Va., Sandifer (1973b, 1975) found the larvae from June to October over a salinity range of 10.91 to 32.34‰ at 20° to 28.1°C, peaking in August and September in a salinity range between 20 and 25‰, except for one specimen taken in February in the mouth of the Bay. The zoeae were common but never abundant, all stages being represented, but stage I was most numerous. Bottom samples contained 77% of all *P. maculatus* collected from the layer in which upstream drift is thought to favor retention in the estuary. He reviewed other studies on planktonic larvae of the species: common at Woods Hole from July to November (Fish 1925); July to October in Delaware Bay (Deevey 1960) and in low concentrations in Delaware River in summer (Cronin, et al. 1962); abundant in Narragansett Bay from June to September with peak in mid-bay in August (Hillman 1964); lower St. Johns River, Fla., in low densities (<1/m) from May to November (Tagatz 1968); off Cape Lookout, N. C., in November; and off Beaufort Inlet, N. C., from May to November (Dudley and Judy 1971), but never numerous.

Welsh (1932) found the swimming velocity of *P. maculatus* larvae to be greatly influenced by temperature and light intensity. The larvae are sensitive to only a small range of light intensity. At temperatures between 20° and 25°C the maximum velocity of swimming is attained at intensities between 10 and 25 meter-candles. When series of measurements were made to determine the effec-

tive light at different constant temperatures, it was found that, besides a marked effect on general activity, there was a change in the relationship of velocity to intensity; slopes of curves showing these relationships changed, and the maximum possible velocity of swimming for each temperature was reached earlier at the higher temperatures.

As in *P. ostreum*, the hard stage is found in both males and females, and though both swim actively, the males predominate in open water. An invasive stage may precede the relatively large hard stage as in *P. ostreum*. Unlike *P. ostreum* males, at least some *P. maculatus* males apparently live beyond the hard stage, for larger, somewhat globose males, resembling females in adaptation to parasitic or commensal life, occur in some hosts (see variation above).

Kruczynski (1973) found that distribution of *P. maculatus* living in the bay scallop, *Argopecten irradians concentricus*, fell into three areas in long, narrow, shallow Bogue Sound, N. C. (east, middle and west). Mature females were found only in the east and west ends of the sound near inlets but never really abundant (10% incidence in host); other crab stages were more abundant in these areas, but in reduced numbers also in the mid-sound scallop beds. Paradoxically, scallop density was highest in the mid-sound beds. The low percentage of infection in the sound as a whole may be controlled by a scallop fishery which diminishes crab incidence by harvest, but this does not explain why more crabs live near the inlets. Kruczynski explained this as follows: "larvae are swept to all reaches of the sound by tidal currents but survive best [in high salinity] near inlets. Scallops are invaded in great numbers in fall and early winter. Heavy rains at this time reinforce the salinity gradient in Bogue Sound. Many pre-swarmers and swarmers are lost because of scallop harvesting. Swarmers receive an external cue and begin a migration on ebb tides, becoming concentrated near inlets, or use tides to maintain near-inlet position. Copulation takes place and inseminated females seek a definitive host in the area where copulation occurs." Salinity thus seems a controlling element even though the host species tolerates a wide range throughout the sound. Experiment by others has shown that *P. maculatus* is a poor osmoregulator, surviving best in 20–30‰ salinity at 25°C.

More crabs infected *Mytilus edulis* growing subtidally on a piling at Woods Hole than were found in mussels in intertidal areas (Kruczynski 1974). This study demonstrated no correlation between salinity and temperature and presence of crabs, and no significant difference in mean shell height of mussels with and without adult female *P. maculatus*.

However, the crabs may choose subtidal hosts to assure a more constant environment than mussels in the intertidal would afford. Also, the longer the host is open, the more chance for entry by swarming young crabs.

Entry behavior of crabs into host scallops is related to scallop reaction to touch, attraction of crabs to excurrent water from scallops, sense of touch among invasive crabs, and phototactic responses of crabs (Eidemiller 1969). In sequence, the scallop mantle gapes apart at the point where the crab's legs touch it, the scallop then opens to its fullest [presumably the normal gape], closes abruptly but not completely as the margins usually do not make contact, and reopens within five seconds. The mantle seems most sensitive in the region of short guard tentacles. As long as a crab remains on the mantle the scallop continues to open and shut.

Kruczynski (1975) showed that adult female *P. maculatus* accumulate radioactivity when living in bay and calico scallops, *Argopecten irradians concentricus* and *A. gibbus*, fed *Nitzschia closterium* labelled with  $^{14}\text{C}$  and in blue mussels, *Mytilus edulis*, fed *Thalassiosira pseudonana* under laboratory conditions. Crabs also accumulated radioactivity when kept in fingerbowls with labelled *N. closterium*. This demonstration strengthened the argument for the crabs being the causative agent for stunting in host scallops under natural and experimental conditions, but it was not determined whether the accumulation activity came from ingestion of phytoplankton, feces, pseudofeces, molluscan tissue or from water. Crabs without chelae in dishes did not pick up the radioactivity.

Caine (1975a), with a different approach, showed that both hard free-living and soft commensal phases of the mussel crabs feed on fine particulate matter, but the methods of food acquisition differ. Free-living forms acquire food while swimming (setae on carpus, merus and dactyls of second and third walking legs filter water), but commensal crabs obtain food from the host. Ossicles of the gastric mill are similar in the two forms, but the commensal phase has four pairs of setae on the posterior margin of the urocardiac ossicle which are thought to aid in manipulation of mucus strands ingested from the bivalve host. Crabs from plankton, quiet bottom water and bivalves did not burrow when freed but were secretive; swimming by dorsoventral movements of the first through fourth walking legs in metachronal waves from posterior to anterior produced an upward and forward motion. Only the fourth pair of walking legs is modified for feeding in commensals. The grasping surface of the dactyl and propodus are acutely inclined distally while the opposite side of the dactyl is finely

serrate. Anteroventral scraping movements of this leg pull mucus from ctenidia of host for transfer to the setose margin of the maxillipeds. In great detail, Caine described this set of movements and similar feeding of the free-living stages by filtering water with the second and third walking legs, scraping with the fourth, and transfer to the chelipeds as above. Detail was also given on movement of food through the stomach and associated structures.

Wells and Wells (1966) described what might be considered a hyperparasitic bopyrid, *Dactylokepon hunterae*, from *P. maculatus* in *Argopecten gibbus* dredged off Core Banks, N. C.

### *Pinnotheres ostreum* Say

(Oyster crab)

Figs. 354–356

*Pinnotheres ostreum* Say 1817:67, pl. 4, fig. 5.—Rathbun 1918b:66, text-fig. 30; pl. 15, figs. 3–6.—Hay and Shore 1918:443, pl. 35, fig. 9.—Williams 1965:203, figs. 187, 188A-B, 189.—Coelho and Ramos 1972:195.—Felder 1973:75, pl. 10, figs. 12–14.—Schmitt, McCain, and Davidson 1973:61.—Powell 1977:124.

*Pinnotheres depressum* Say 1817:68.

*Pinnotheres depressus*.—Rathbun 1918b:79, pl. 17, figs. 1–2.

*Recognition characters*.—Mature female: Carapace subcircular in outline; surface glabrous for most part, smooth, shining, membranous, yielding to touch, convex from front to back and with broad, shallow, longitudinal depression each side of cardiac and gastric areas. Lateral margins thick and bluntly rounded; posterior margin broad. Front

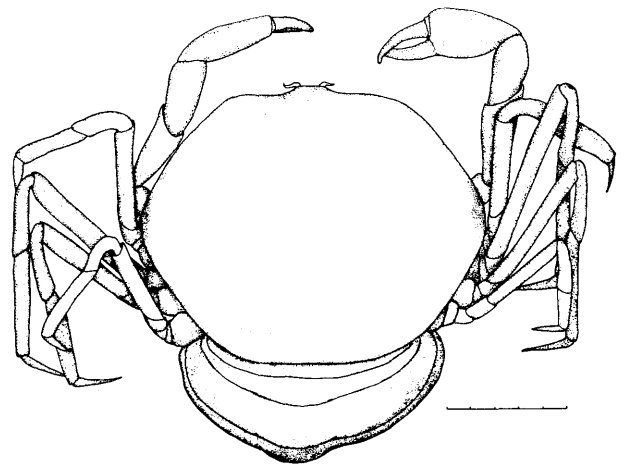


Fig. 354. *Pinnotheres ostreum* Say. Mature female in dorsal view, 5 mm indicated (from Williams 1965).

rounded, slightly produced, covering and concealing eyes. Orbits small, subcircular, anteriorly placed. Antennule large; antenna small, flagellum not so long as diameter of orbit. Buccal mass roughly quadrangular in outline but bent into broad crescentic arch, short anteroposteriorly. Outer maxilliped with ischium and merus fused; carpus or first article of palp short, oblong; propodus elongate, end rounded; dactyl inserted behind middle of propodus, minute, slender.

Chelipeds small, merus and carpus rather slender. Palm somewhat flattened inside, swollen outside, strongly widened from proximal toward distal end, then narrowed; width across base of fingers less than greatest width of palm; fingers, especially fixed one, stout, not gaping, tips hooked past each other, minute teeth on opposed edges, a larger tooth near base of each, fixed finger horizontal. Walking legs slender, subcylindrical; last 2 articles with thin fringe of hair; second and third legs about equal in length, first legs slightly stouter, last pair turned backward and upward.

Abdomen large, extending beyond carapace in all directions.

*Measurements in mm.*—Carapace: width, ranging from 4 to 15 (Christensen and McDermott 1958).

*Color.*—Whitish or salmon pink.

*Recognition characters.*—Mature male and hard-stage female: Carapace well calcified, flat dorsally, subcircular in outline, with truncate front more advanced than in mature female. Posterior margin straight; lateral margin thin, rather sharply bent from dorsal side, margin marked by raised band of short, dense hair. Eyes well developed. Buccal mass crescentic, arched, transversely broad but short anteroposteriorly; cavity completely closed by external maxillipeds formed as in mature female.

Chelipeds stout, merus and carpus not slender as in mature female. Palm slightly flattened inside, swollen outside and shaped as in mature female, both margins convex. Hand with bands of pubescence on upper and outer surface of palm, and outer surface of fixed finger. Fingers stout, especially fixed finger, with tips hooked past each other when closed; dactyl with small tooth proximally, tooth fitting between 2 protuberances on fixed finger when closed; both fingers with stiff hairs on gripping edges. Walking legs flattened, posterior margins thickened, and with plumose swimming hairs on second and third pairs.

*Measurements in mm.*—Carapace: male, width 1.4 to 4.6; female, width 1.3 to 2.7 (Christensen and McDermott 1958).

*Color.*—Dark or medium-dark brown with 2 large, distinct, almost circular, pale white spots on both carapace and sternum; dorsal spots on branchial

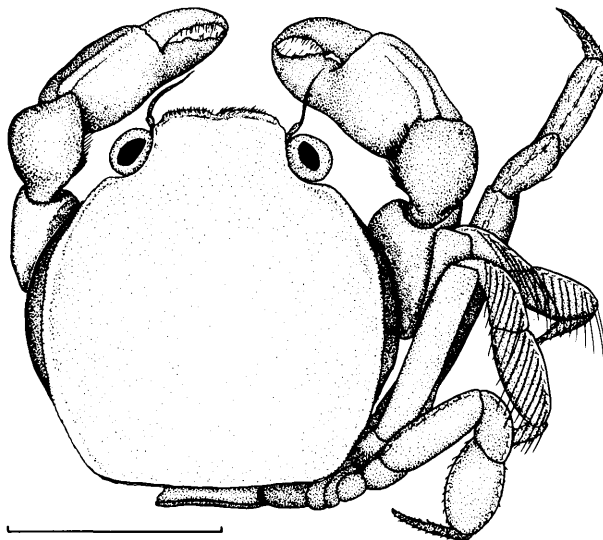


Fig. 355. *Pinnotheres ostreum* Say. Male in dorsal view, walking legs of left side not shown, 1 mm indicated (from Williams 1965).

regions, ventral spots flanking abdomen and mesial to first pair of legs; color and spots persistent in alcohol.

*Habitat.*—Parasitic [or commensal] chiefly in the oyster, *Crassostrea virginica*, also in *Pecten* spp. and *Anomia simplex* (see Christensen and McDermott 1958), in *Mytilus edulis* (see McDermott 1961), and in *Modiolus demissus* (see Sandifer and Van Engel 1970). Also occasionally found in *Chaetopterus* tubes (Gray 1961).

*Type-locality.*—“United States” (see Schmitt, et al. 1973); these authors mentioned six probable syntypes from the United States and Virginia in the British Museum (Natural History) and that, according to DeKay (1844), Say’s specimen was from New Jersey.

*Known range.*—Salem, Mass., to Santa Catarina, Brazil.

*Remarks.*—Say’s *P. depressus* appears almost certainly to be the hard-stage male as described above and discussed below.

The works of Hyman (1924a), Stauber (1945), Sandoz and Hopkins (1947), Christensen and McDermott (1958), and Beach (1969), together have made knowledge of the biology and life history of *P. ostreum* the most complete for any species of *Pinnotheres* in the world. The serious student should refer to these thorough works, for they can be summarized only in barest outline here. The complex life cycle of this species encompasses many developmental stages, as well as a striking sexual dimorphism in the mature animals, which, together with structural specializations and mode of existence, demonstrate a beautiful accommodation to an unusual habitat.



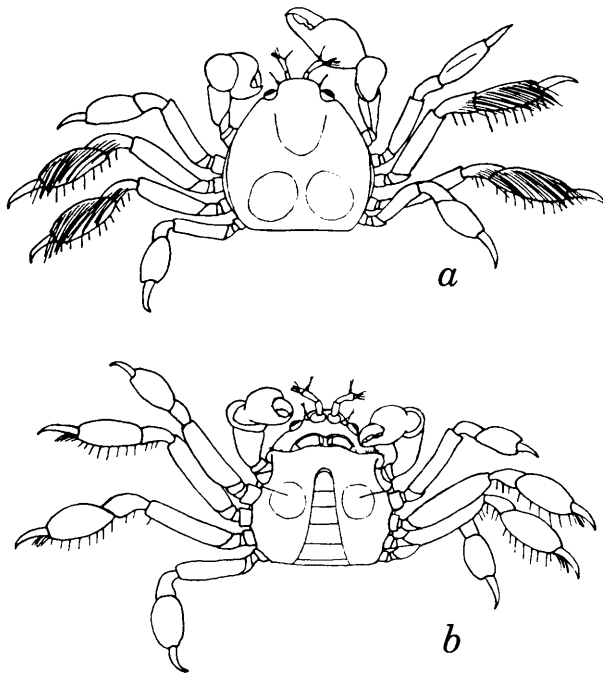


Fig. 356. *Pinnotheres ostreum* Say. *a*, Crab stage I female in dorsal view; *b*, same, ventral view; approximately  $\times 9$  (from Stauber 1945).

The larval stages include four zoeae followed by a megalopa. The first two zoeal stages were described by Hyman (1924a), and a description of all these stages (partial for fourth zoeal stage) was given by Sandoz and Hopkins (1947). In general, the zoeae and megalopa have no dorsal or lateral spines on the carapace. Time of development from hatching to molting of the megalopa to first crab stage is 25 days.

Sandifer (1973d, 1975) collected planktonic larvae of *P. ostreum* from lower Chesapeake Bay and York River, Va., in salinities of 3.94 to 31.86‰ from June to October, with a peak in the lower York in July. Stage I zoeae dominated the samples, mostly at the bottom where upstream drift tends to hold them in the estuary. He (1973d) summarized the findings of others: Deevey (1960) in Delaware Bay, Pinschmidt (1964) from May to October in Newport River, N. C., at somewhat higher salinities, and Tagatz (1968) from St. Johns River, Fla., from April to November. Dudley and Judy (1971) also collected larvae up to 13 km off Beaufort, N. C., from June to October. From the first crab stage on, development was summarized by Christensen and McDermott (1958:154). The first crab stage, actually the stage which invades oysters, was called the invasive stage by these authors. It was described by Sandoz and Hopkins (1947) and in many respects is similar to the later hard stage in its flattened shape, legs adapted for swimming, and characteristic color marking (carapace width, 0.59–0.73 mm).

In Delaware Bay, few invasions take place before August 1. The peak of oyster setting there is in July; spat will have grown to size sufficient to harbor one or more crabs by the peak of the crab invasions in September. Invasions as early as June are reported for North Carolina (Beach 1969). Though invasive stages in oysters are found all winter, growth and development stop about the first of November when water temperatures begin to drop below 15°C. Surprisingly small spat may be invaded. Two crabs were found in an oyster 4.2 mm long, and in larger spat up to seven crabs were found in a single specimen. The crabs prefer to invade spat or yearling oysters rather than older ones (76.7, 54.6, and 21.5, being respective infestation percentages for a given year class of crabs), but survival rate of crabs is better in yearlings and older oysters. Beach (1969), from studies in North Carolina, thought that salinities below 10–15‰ prevent settlement of invasive stages in some areas and that swift currents may suppress it in others through lack of easy access to the host and lack of sufficient food. High salinity near areas of high organic content seemed to invite the highest rates of invasion, but there the host might suffer greater mortalities as a result of multiple infection. Infection was greatest around the low-tide mark as opposed to intertidally.

Following the invasive stage are two ill-defined stages designated as prehard. These stages, described by Christensen and McDermott (1958), are soft and resemble later posthard stages of the females (carapace width: male, 1.4–4.6; female, 0.75–2.7 mm). The legs are rounded and not adapted for swimming. These stages are found in all parts of the water-conducting system of infested oysters. In the region of Delaware Bay, most young crabs reach the prehard stages before growth ceases in fall and they overwinter in these stages. Development resumes when temperatures rise above 15°C.

The hard stage, formerly regarded as the invasive stage, is characterized above. On the average, males are larger than females, as they are in the preceding stages. The form of this stage resembles that of the invasive stage, and males of this stage swim freely. This is the copulatory stage (Hartnoll 1969), and the males normally die in this stage.

The succeeding female stages, described by Stauber (1945), resemble the adult female, and are found only in the host on the gills. Stage II (the hard stage was designated as stage I by Stauber) has a thin flexible carapace but a narrow abdomen contained wholly in the sternal groove (carapace width, 1.3–3.1 mm). Stage III has an abdomen extending beyond the depression in the sternum (carapace width, 2.6–4.4 mm). Stage IV has a relatively wide abdomen reaching the coxae of the legs

in most cases (carapace width, 3.6–8.9 mm). Stage V is the adult female described above.

The posthard stages are passed through rapidly. In Delaware Bay by mid-July, 62% of the females have developed from the overwintering stage to maturity. By mid-August, 95% are mature and more than half are ovigerous; thus, *P. ostreum* reaches maturity within its first year. Males live one year or less, but females continue to grow after they have hatched their first batch of eggs and may live to an age of two or three years, though many probably die after they have hatched their eggs in the second summer. In the second or third year, females may become ovigerous as early as mid-June, and ovigerous yearlings may occur as late as mid-October. Farther south the breeding season is more extended, and ovigerous females have been collected near Ocracoke, N. C., as early as mid-April.

Ovigerous females measuring 9.4 and 10.8 mm in width carried 7,957 and 9,456 eggs respectively. It is not known how long a female carries eggs, but it is believed to be three to five weeks. The females produce only one batch of eggs the first year but in a second or third year may produce twice (also Beach 1969).

Except for the brief free-swimming periods in the invasive hard stages, the crabs lead a parasitic existence. Stauber (1945) and Christensen and McDermott (1958) found that the crab feeds on food filtered from water by the host by picking food strings from the margins of the gills with its chelipeds. The crab also will catch newly formed mucus-food masses with its walking legs and then reach beneath the abdomen with its chelipeds, comb the legs, and pass the food on to the mouth. The method of feeding for young crabs not on the gills is unknown, but they may filter food with the mouthparts. Posthard stages are found only on the

gills, indicating that feeding on the food-laden mucus alone can insure adequate energy supplies for rapid growth and egg production. Growth of females is positively correlated with size of host and probably related to food supply and amount of water pumping by the host.

The ordinary feeding activities are harmful to the host (Stauber 1945), particularly causing gill erosion of two types, local erosion of one or more demibranchs, and an extensive shortening of demibranchs from the anterior end of gills to a point ventral to the adductor muscle. Christensen and McDermott (1958) noted that this erosion is a progressive process and nearly all infested oysters show some gill damage, some few older oysters having hardly any gill tissue left. Usually, however, only presence of a mature crab over a long time will noticeably affect growth of an oyster in normal environmental circumstances.

#### Genus *Parapinnixa* Holmes 1894

Rathbun 1918b:107.—Schmitt, McCain, and Davidson 1973:30.

Carapace calcified, much broader than long; anterior margin nearly straight, front depressed. Orbits nearly round. Antennules folded obliquely or transversely, fossettes communicating with each other beneath front. Buccal area small, broadly subtriangular. External maxillipeds with ischium rudimentary; merus large, subtriangular; palp 3-jointed, terminal article joined to distal end of preceding one. First walking leg largest, others successively diminishing in length, last very small. Abdomen of female small, not covering sternum. (From Rathbun 1918b.)

#### Key to Species

1. Carapace less than twice as wide as long . . . . . *P. bouvieri*  
Carapace more than twice as wide as long. . . . . *P. hendersoni*

#### *Parapinnixa bouvieri* Rathbun

Fig. 357

*Parapinnixa bouvieri* Rathbun 1918b:111, text-fig. 60, pl. 25, figs. 4–10.—1933:83, fig. 75.—Williams 1965:208, fig. 191.—Schmitt, McCain, and Davidson 1973:31.—Powell 1977:122.

*Recognition characters*.—Minute. Carapace smooth, shining, not more than twice as wide as long, longitudinally very convex transversely, sides arcuate; widest part with thin pubescent margin on lower

edge; anterior margin nearly straight, a row of 4 distinct pits behind margin. Frontoorbital width about  $\frac{1}{3}$  carapace width. Front broadly triangular, deflexed, tip invisible in dorsal view, edge emarginate and pubescent; a pubescent groove running parallel to and immediately behind front terminating in orbital margins. Orbits circular, filled by eyes, cornea black, visible from above. Antennular cavities large, not wholly separated from each other or from orbits, extending laterally beyond minute antennae. Outer maxilliped subtriangular when folded in place, 2 free corners rounded, longitudinal side

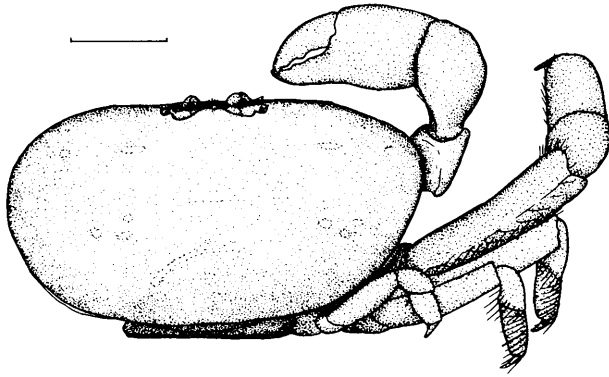


Fig. 357. *Parapinnixa bouvieri* Rathbun. Ovigerous female in dorsal view, legs of left side not shown, 1 mm indicated (from Williams 1965).

approximately  $\frac{2}{3}$  as long as posterior side; ischium and merus fused, obliquely truncate distally leaving first joint of palp exposed; propodus elongate, distally tapering; dactyl small, suboval, both articles folding under merus.

Chelipeds short, stout, merus especially, partly hairy inside; palms thick, hairy outside; lower margin convex; fixed finger subtriangular, broad at base, small tooth on gripping edge near tip; dactyl with small basal tooth, remainder of edge finely and irregularly denticulate. Walking legs with edges more or less pubescent, second and third pairs with line of long hairs applied to posterior surface of carpus and propodus; first leg thick, merus not reaching laterally beyond carpus of cheliped; second and third leg about equal; fourth small, not exceeding merus of third; dactyls of second and third legs longer and more slender than of first and fourth.

Male abdomen with sides gradually convergent, seventh segment not more than 1.5 times as long as wide; female abdomen with sides of triangular part straight.

*Measurements in mm.*—Carapace: female, length 1.6, width 3.1; male, length 2, width 3.5.

*Habitat.*—Approximately 3.5 to 73 m.

*Type-locality.*—Off Cape Catoche, Yucatan, [Mexico], 22°08'30"N, 86°53'30"W, 45.7 m, Albartross Stn. 2362.

*Known range.*—Off Charleston, S. C.; south of Tortugas, Fla.; Puerto Rico; and type-locality.

*Remarks.*—Ovigerous females have been taken in Florida in August. The ovigerous specimen taken in Puerto Rico (no date) was found among ventral spines of a rose sea urchin (J. A. Rivero, USNM).

### *Parapinnixa hendersoni* Rathbun

Fig. 358

*Parapinnixa hendersoni* Rathbun 1918b:109, text-fig.

59, pl. 26, figs. 1–5.—Righi 1967:99, figs. 7, 8.—Coelho and Ramos 1972:197.—Schmitt, McCain, and Davidson 1973:32.—Powell 1977:122.

*Recognition characters.*—Resembling *P. bouvieri* except as follows: Carapace more than twice as wide as long. Shallow pit to either side and one in mid-line of raised transverse area behind frontal margin; posterior to this a pubescent groove.

Chelipeds with palms thick, protuberant inside at middle, partly hairy inside, hairy outside at juncture of fingers and along 2 bands leading toward carpus; fingers stout, not gaping, tips hooked and overlapping; dactyl with granulate, pubescent crest and shallow, nearly hidden basal tooth fitting in basal excavation on fixed finger. Walking legs with dactyls similar, falcate, fitting closely in groove on propodus when flexed.

Abdomen of male covering nearly all of sternal width basally, third segment widest, rounded laterally, fourth partly invaginated in third, sides concave from fourth to angle near base of telson, latter long with rounded tip; female widest at third segment, subtriangular with concave sides beyond that, telson almost equilaterally triangular with blunt tip, margin fringed with long hairs; genital opening exposed at either side of telson.

*Measurements in mm.*—Carapace: male, length 4, width 8.3; female, length 3.5, width 8 (Rathbun 1918b).

*Variation.*—A juvenile male from North Carolina (UNC-IMS 2124) has an upper and lower row of remote granules on the external surface of the palm; above the upper row are a few similar, scattered granules, and the upper and lower crests of the

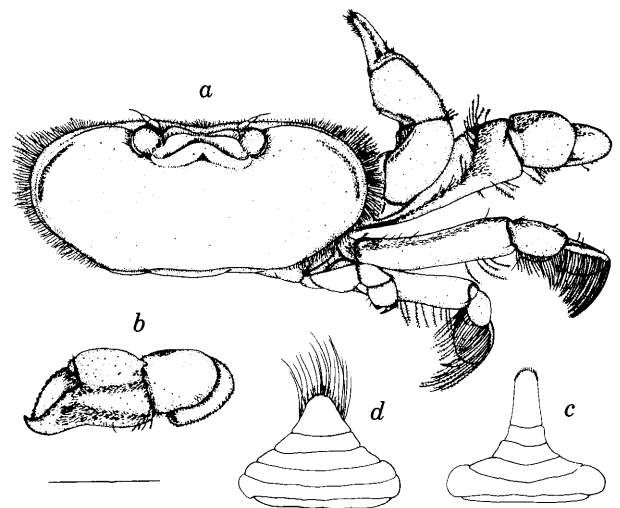


Fig. 358. *Parapinnixa hendersoni* Rathbun. Male: a, dorsal view, legs of left side not shown; b, left chela, external view; c, abdomen; d, female, abdomen; 3 mm indicated (USNM, Biscayne Bay, Fla).

merus are beaded. None of the larger specimens show these granules, although the dactyl of both adults and this tiny male has a granulate crest.

*Color*.—Small brownish pigment spots in alcohol (Rathbun 1918b).

*Habitat*.—Free swimming in surface plankton at night (Rathbun 1918b); surface to 84 m.

*Type-locality*.—Los Arroyos, Cuba.

*Known range*.—SE Cape Lookout, N. C. (UNC-IMS 2124 and 2448, 34°29'N, 76°13'W, 33 m; USNM 101505, 34°34'N, 75°50'W, 64 m); off Tampa Bay, Fla., through West Indies to Curaçao (USNM); Maranhão to Bahia, Brazil (Coelho and Ramos 1972).

*Remarks*.—The specimens from North Carolina are so small that they are questionably included in *P. hendersoni*. Whether the granular features on the palm of the chela are lost during growth or represent a character on an undescribed species is unknown. More material from the same area should help to resolve this question.

### Genus *Pinnaxodes* Heller 1865

Rathbun 1918b:174.—Schmitt, McCain, and Davidson 1973:33.

### *Pinnaxodes floridensis* Wells and Wells

Fig. 359

*Pinnaxodes floridensis* Wells and Wells 1961:269, figs. 1A-F, 2A-G.—Schmitt, McCain, and Davidson 1973:34.

*Recognition characters*.—Carapace convex, suborbicular, slightly wider than long, widest anterior to midpoint, moderately calcified, smooth, minutely punctate. Males with front usually somewhat produced and orbits visible in dorsal view; females with front usually deflexed and orbits often concealed in dorsal view. Lateral margins indistinct, rounded. Buccal mass subtriangular; line of long hairs extending lateral to buccal cavity. Outer maxilliped broad, with large palp; mesial edge of merus bearing distinct angle at midpoint; propodus larger than carpus, spatulate, about twice as long as wide; dactyl  $\frac{2}{3}$  length of propodus, spatulate, articulated proximally on flexor surface of propodus and slightly exceeding it; both terminal articles with long hairs.

Chelipeds slightly asymmetrical, moderately long, smooth, minutely punctate; carpus slightly swollen; palm elongate, subcylindrical, swollen proximally but dorsoventrally broadening distally, line of hairs on low mesioventral crest extending along palm and fixed finger; fingers tapering, gapping

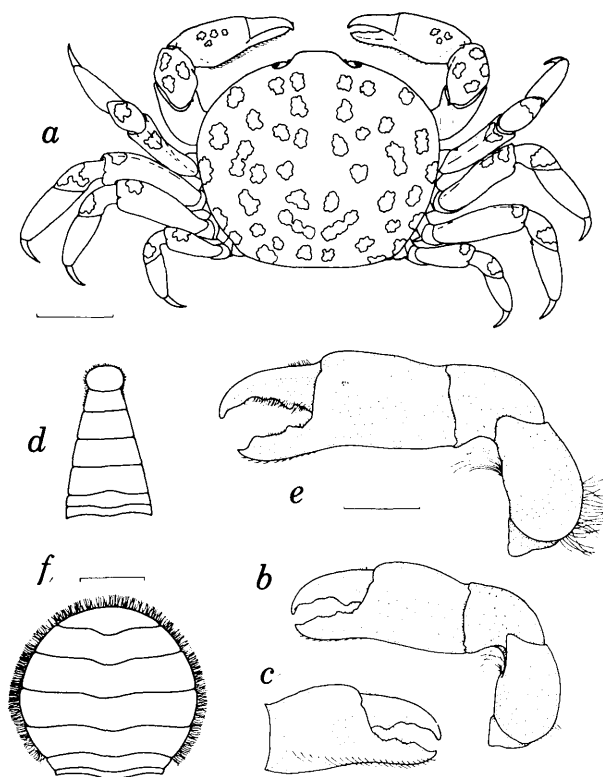


Fig. 359. *Pinnaxodes floridensis* Wells and Wells. Male: *a*, dorsal view showing color pattern in outline; *b*, left cheliped, outer view; *c*, chela, inner view showing line of hair; *d*, outline of abdomen. Female: *e*, left cheliped, outer view; *f*, outline of adult abdomen. Scales: *a*=3 mm; *b-c*, *e*=2 mm; *d*, *f*=4 mm (from Wells and Wells 1961).

through most of length, distal shearing edges crossing at tips, somewhat spooned and with hairy internal crest; dactyl curved inward, basal tooth on cutting edge and an inconspicuous dorsal tuft of hair near articulation; fixed finger deflexed, small sinus and tooth on cutting edge. Walking legs moderately short and stout, second pair longest but shorter than chelipeds; last pair shortest; propodi elongate; dactyls curved, corneous at tip; merus with line of hair along dorsal crest and posterior ventral margin, continued also on propodi and dactyls.

Abdomen of male narrow triangular, with rounded telson; of mature female broad, subcircular and fringed with hair, telson broad and rounded distally; of immature female broadly triangular with narrow telson.

*Measurements in mm*.—Carapace: male, length 8.0, width 9.0; ovigerous female, length 9.5, width 11.0 (Wells and Wells 1961).

*Variation*.—Wells and Wells (1961) analyzed morphometric variations. In addition to sexual dimorphism mentioned above, mature females are generally wider than males; the carapace of immature females closely resembles the male form.

In males there are often distinct shallow grooves or depressions in the cardiac region, and the transition from dorsal to lateral surfaces is often marked by a low anterolateral ridge. The separation of merus and ischium on the third maxillipeds is complete in males, but in females the suture line between these articles extends only  $\frac{2}{3}$  the width of the limb.

*Color*.—Many small red spots on white ground color dorsally, less developed ventrally, distributed in an imperfectly symmetrical pattern; typically, a distal spot of color on carpus of walking legs and on merus of external maxillipeds (Wells and Wells 1961).

*Habitat*.—Adults in cloaca and respiratory tree of *Holothuria princeps*, juveniles in anterior part of digestive system; shore (washed up in storm) to 38 m (Wenner and Read 1982).

*Type-locality*.—"Outer beach near Fort Walton Beach, Florida."

*Known range*.—Off North Carolina (USNM) to Georgia; northwest Florida.

*Remarks*.—Nearly all that is known of this species was given by Wells and Wells (1961); Patton (1967) and others have reviewed their findings. The original description and morphometric and reproductive analyses were based on a large number of specimens associated with the host holothurians that were either beached (on February 28, 1960) or stranded in shallow water following a severe storm. Sixty-one percent of the sea cucumbers examined contained these crabs. Female crabs outnumbered males 4:1. Females were present in a wide range of sizes and reproductive stages, juvenile, immature, mature and ovigerous, and some immature females contained sperm in the spermathecae. Wells

and Wells concluded that oviposition occurs over an extended time and that the crabs are filter feeders.

### Subfamily Pinnothereliinae

Carapace transverse, usually broadly so. Ischium of external maxilliped usually distinct from merus, though smaller and sometimes imperfectly united with it. Merus longitudinal or somewhat oblique; palp of good size, sometimes as large as merus-ischium (Rathbun 1918b).

### Genus *Pinnixa* White 1846

Rathbun 1918b:128.—Hemming 1958b:35.—Schmitt, McCain, and Davidson 1973:101.

Carapace much wider than long; integument usually firm; front narrow, nearly transverse, with median groove. Orbit broadly ovate or nearly circular, with wide inner hiatus partly occupied by basal antennal article. Antennules transversely or obliquely folded in wide fossettes open to each other beneath front. Eystalks very short. Epistome transversely broadened. Ischium of maxillipeds small, merus large, distal part of outer margin convex; palp articulated to summit of merus, its third article arising on inner side of second article near base. Chelipeds moderate; hand large, compressed. Second walking leg larger than first, third largest, fourth shorter than third and relatively stouter than first and second. Abdomen of both sexes 7-segmented, narrower at base than last sternal segment. (Adapted from Rathbun 1918b.)

### Key to Species

(By Richard E. Dowds)

1. Posterior part of carapace with conspicuous, sharp, transverse ridge extending uninterruptedly from side to side . . . . . *P. cristata*  
Posterior part of carapace without transverse ridge, or with ridge falling well short of lateral margin of carapace . . . . . 2
2. Chela with inner margin of dactyl not smoothly bent 90° at  $\frac{1}{4}$  to  $\frac{1}{2}$  distance from its proximal end when flexed . . . . . 3  
Chela with inner margin of dactyl smoothly bent about 90° at  $\frac{1}{4}$  to  $\frac{1}{2}$  distance from its proximal end (adult male with dactyl flexed) . . . . . 8
3. Fixed finger of chela with prehensile edge variously toothed, merging with lower margin at tip . . . . . 4  
Fixed finger of chela with prehensile edge and lower margin connected distally by subterminal, oblique margin (female and juvenile male) . . 8
4. Prehensile edge of fixed finger horizontal or inclined at less than 30° angle . . . . . 5  
Prehensile edge of fixed finger inclined at more than 40° angle (juvenile male) . . . . . 8

5. Third walking leg with greatest length of merus more than twice greatest width, posterodistal end of ischium prolonged into stout curved spine (may be lacking in juvenile) . . . . . *P. retinens*  
Third walking leg with greatest length of merus less than twice greatest width, ischium lacking stout curved spine . . . . . 6
6. Outer surface of chela with numerous scattered granules and long hairs above mid-horizontal row of granules; upper margin of dactyl bearing numerous long hairs . . . . . *P. floridana*  
Outer surface of chela with few, if any, granules; few short hairs (mainly on fixed finger and upper margin of dactyl) . . . . . 7
7. Third walking leg with posterior surface of merus not deeply excavate behind smoothly beaded posterior margin . . . . . *P. cylindrica*  
Third walking leg with posterior surface of merus deeply excavate behind nearly entire length of laminate and strongly beaded or tuberculate posterior margin . . . . . *P. lunzi*
8. Third walking leg with greatest length of propodus less than twice its greatest width . . . . . *P. chaetoptera*  
Third walking leg with greatest length of propodus twice or more than twice its greatest width. . . . . 9
9. Third walking leg with inferoposterior margin of merus coarsely granulated or toothed (may be concealed by hair). . . . . juvenile *P. chaetoptera*  
Third walking leg with inferoposterior margin of merus finely toothed or granular. . . . . *P. sayana*

### *Pinnixa chaetoptera* Stimpson

Fig. 360

*Pinnixa chaetoptera* Stimpson 1860a:235.—Rathbun 1918b:151, text-figs. 93–94, pl. 33, figs. 3–6.—Hay and Shore 1918:445, pl. 36, fig. 4.—Williams 1965:210, fig. 194A–C.—1974:57, fig. 104A–D (key).—Righi 1967:100, figs. 1–6.—Felder 1973:74, pl. 10, fig. 8.—Schmitt, McCain, and Davidson 1973:104.—Powers 1977:125.

*Recognition characters.*—Carapace transversely oval, somewhat more than twice as wide as long, more swollen in female than in male, surface uneven, sides densely pubescent. Front narrow, with deep median groove; epistome partly exposed in dorsal view. Regions well defined by pubescent grooves; cardiac region with acute transverse crest broadly interrupted in middle forming 2 dentiform prominences, more conspicuous in male than in female; subbranchial region advanced, forming prominent shoulder with granulated edge. Posterior margin concave.

Chelipeds stout, smooth, pubescent. Hand in adult male with perpendicular, distal palmar edge bearing prominent, rounded tooth near base of short, deflected fixed finger; dactyl smoothly curved about 90° ¼ to ½ distance from its proximal end, almost vertical when closed, forming oval gape with tips of fingers meeting. Hand of female relatively smaller, fixed finger having shorter upper and longer lower margins connected distally by subter-

minal, obliquely cusped margin; dactyl with tooth at basal ⅓ of length, longer than in male, prehensile edge of fingers crenulate, agape proximal to cutting portion when closed with tips crossing each other. First and second pairs of walking legs slender, propodi with distal V-shaped row of spinules on lower border; dactyls with 1 or more short rows of spinules. Third pair longer and much stouter, conspicuously pubescent, and with inferoposterior margins of ischium, merus, and propodus dentate; fourth pair like third but smaller, with minute spinules on dactyls.

Male abdomen with sixth segment slightly constricted laterally at middle; telson semicircular.

*Measurements in mm.*—Carapace: male, length 5.9, width 13.8; female, length 6.4, width 14.

*Variation.*—In small crabs, third walking legs have teeth on the inferoposterior margin of the merus large and few in number (as few as 8), but with increasing age they become relatively short, more numerous (up to 30), and increasingly concealed by hair. Chelae of male *P. chaetoptera* and *P. sayana* change with age. In very young males (carapace width less than about 3.5 mm) the chela is similar to that of young females. As males grow, the chela passes through intermediate forms in which the upper and terminal margins of the fixed finger merge to form a single steepening margin, and the dactyl becomes more bent and loses the tooth located about midway along its inner margin. By the time the carapace width reaches about 7 mm in *P. chaetoptera* or 4.5 mm in *P. sayana*, the

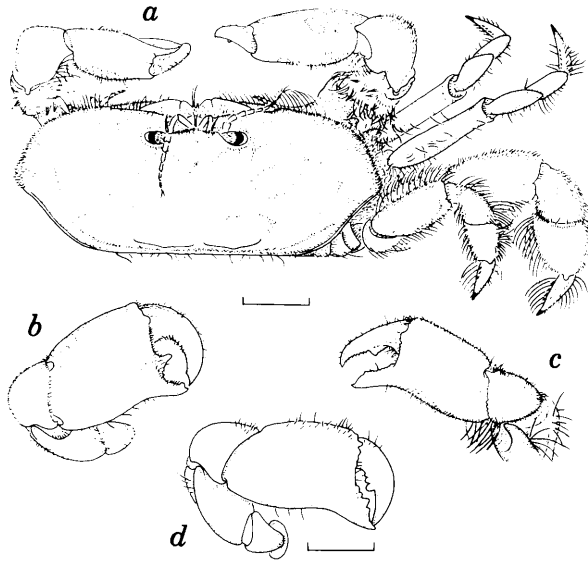


Fig. 360. *Pinnixa chaetopterana* Stimpson. *a*, Male in dorsal view, walking legs of left side not shown; *b*, male right chela and carpus, external view; *c*, female left chela and carpus, external view; *d*, juvenile male cheliped external view of chela; *a-c*, 2 mm; *d*, 0.5 mm indicated (USNM 57302).

chela has almost fully achieved the adult male form (R. E. Dowds, personal communication).

Wass (1955) pointed out that larger and smaller forms of *P. chaetopterana* occur on the northern Gulf of Mexico coast.

*Color*.—Nearly white, but usually much obscured by brown or blackish hairs and by dirt accumulated in them; eggs bluish (various authors).

*Habitat*.—The large form of this crab lives commensally with the worms *Chaetopterus variopedatus* and *Amphitrite ornata*, and is seldom found outside their tubes. The small form lives in the upper portion of *Callianassa jamaicensis* burrows (Biffar 1971a:650) on the northern Gulf coast (Chace in Wass 1955). Frankenberg and Leiper (1977) reported *P. chaetopterana* as dominant from June through November in grab samples from near-shore fine sand habitat in Georgia, apparently associated with the also dominant *Callianassa atlantica*. Intertidal to 15.5 m.

*Type-locality*.—Charleston Harbor, S. C., on muddy or clayey shores in tubes of *Chaetopterus variopedatus* [= *pergamentaceus*].

*Known range*.—Wellfleet, Mass., to Rio Grande do Sul, Brazil.

*Remarks*.—Ovigerous females have been reported from Beaufort, N. C., between April (Gray 1961) and late October (Enders 1905), from Florida in October (Wass 1955) and February (Gray 1961), from southern Massachusetts in July and August (Pearse 1913; Rathbun 1918b), and from São Paulo, Brazil in August (Righi 1967). Other-

wise they are known from South Carolina in February. Faxon (1879) and Hyman (1924a) described the first zoeal stage.

Sandifer (1973d) reported *P. chaetopterana* larvae as common (97.6/kl) in lower Chesapeake Bay, being most abundant near the bottom, with zoeae I-III more common than IV-V. Larvae were collected in salinities of 20.3–32.34‰ in temperatures of 19.8°–28.1°C from July to October, but few were taken below 23°C and most were in the 24°–27°C range. He summarized other scattered reports of larvae: June to October in Narragansett Bay where they were most abundant in August (Hillman 1969); June to late October at Woods Hole (Fish 1925); and July to September in Delaware Bay (Deevey 1960). Other records, year-round in St. Johns River, Fla. (Tagatz 1968), and May to November near Beaufort, N. C., (Dudley and Judy 1971) were given for genus only. Subadults have been taken in surface mero-plankton from March to November in Bogue Sound, N. C., at the UNC-IMS pier, Morehead City.

Some habits of this crab were observed by Pearse (1913) at Woods Hole, Mass. The species is strongly thigmotactic. Crabs placed on sand in an aquarium usually buried themselves, but soon explored the surface and entered and remained in glass tubes left lying on the sand. In experiments, crabs found a buried, artificial “*Chaetopterus* tube” by accident. Adult crabs could enter or leave this tube. The crabs moved either forward or sideways on sand. The third walking leg was the chief locomotor organ, but in tubes the crabs braced themselves with all the legs.

Crabs placed in standing water in an artificial worm tube were able to exist for 8 days before leaving the tube for better aerated water. The crabs’ respiratory currents were feeble and inconstant in direction and force. Crabs were usually fouled with encrusting organisms and they took no trouble to clean their bodies except for mouthparts, eyes, and antennae. They fed by extending the fringed external maxillipeds and sweeping them toward the mouth, filtering small particles from the water, then cleaning the fringe with other mouthparts.

Gray (1961, see also account for *Polyonyx gibbesi*) described *Pinnixa chaetopterana* as primarily a mud crab and a facultative commensal of *Chaetopterus*. He found that the crabs readily enter and leave the tubes of the host, and if diameter of the parchment chimney of the worm tube is too small, the crab cuts a hole at the base of the chimney to make an entrance or exit.

Davenport and Hickok (1960), from choice experiments in an experimental trough designed to provide mixing streams from point sources, determined that *P. chaetopterana* shows marked reaction

to host-factor from *Chaetopterus* and *Amphitrite*, but not from *Nereis* or *Arenicola*. The crab shows marked akinesis when it first encounters host-factor, after which a klinokinetic reponse occurs. Intensity of the latter is proportional to the concentration of host-factor; with rise in concentration there is an increase in rate of random turning. There was also a tendency for the crabs to remain within the pool of host-factor in the experimental trough, not tending to transgress the steep gradients at its boundaries. However, there is no experimental evidence that the animals tend to be displaced toward the source of host-factor, and rheotactic responses are not present. Evidence indicates that the host-factor is a protein.

### *Pinnixa cristata* Rathbun

Fig. 361

*Pinnixa cristata* Rathbun 1900a:589.—1918b:134, text-fig. 78, pl. 29, figs. 8–9.—Hay and Shore 1918:446, pl. 36, fig. 5.—Williams 1965:210, fig. 193.—Felder 1973:74, pl. 10, fig. 6.—Schmitt, McCain, and Davidson 1973:106.—Powers 1977:126.

*Recognition characters*.—Carapace short, surface punctate, wrinkled, and microscopically granulate, slightly pubescent at extreme outer corners; high, sharp, almost straight ridge extending without a break entirely across carapace somewhat in front of posterior border; deep furrow behind gastric region. Front deflexed, not advanced. Orbit no wider than half of front. Anterolateral margin with low raised crest stopping short of hepatic region; posterior margin wide, concave.

Chelipeds rather stout; palm oblong with upper and lower margins convex, surface covered with reticulate pattern of fine granulations. Male with distal palmar margin almost perpendicular and bearing median, truncate tooth nearly obscured by hair; fixed finger short, deflexed, truncate; dactyl

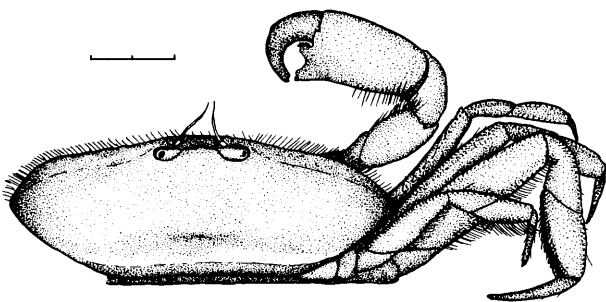


Fig. 361. *Pinnixa cristata* Rathbun. Male in dorsal view, legs of left side not shown, 2 mm indicated (from Williams 1965).

smoothly bent at approximately right angle at proximal  $\frac{1}{3}$ – $\frac{1}{2}$  of length, gaping. Female with fixed finger short, deflexed, subtruncate, gripping edge with truncate, subbasal tooth; dactyl smoothly bent at approximately right angle at proximal  $\frac{1}{3}$  of length, gaping, tips of fingers slightly notched and partly crossed when closed. Walking legs somewhat longer than in related species, sparsely hairy along margins only, third walking leg strongest; dactyls slender, slightly curved on first 3, straight on last walking legs.

*Measurements in mm*.—Carapace: male, length 3.5, width 9.1; female, length 4, width 11.

*Color*.—Two distinct color patterns are often found in the same area at the same time near Beaufort, N. C. First: predominantly yellowish-orange to tan, occasionally spots of gray or black on carapace and legs; abdomen and sternum often mottled gray overall. Second: nearly entire crab dark gray to black except for translucent white on dactyls and distal ends of propodi on walking legs; dactyls of chelae may be same light color and their propodi mottled with white spots. Intermediates are also found. The dark phase turns yellow-orange in 70% ethanol, and that color, as in the first phase, persists (R. E. Dowds, personal communication).

*Habitat*.—"Intertidal beaches and shallow sand and muddy-sand bottoms in brackish to marine waters; usually commensal with callianassids or other burrowers" (Felder 1973; also Pearse, et al. 1942).

*Type-locality*.—Beaufort, N. C.

*Known range*.—Beaufort, N. C., to Edisto Island, S. C.; Grande Isle, La., to Long Lake, Blackjack Peninsula, Aransas County, Tex. (Hedgpeth 1950, USNM).

*Remarks*.—This species has been taken from the mouth of the fish *Galeichthys felis* in Louisiana.

The anterolateral crest in many males and some females is elevated very little and in a few cases is barely discernible (R. E. Dowds, personal communication).

### *Pinnixa cylindrica* (Say)

Fig. 362

*Pinnotheres cylindricum* Say 1818:452.

*Pinnixa cylindrica*.—Rathbun 1918b:159, text-fig. 99, pl. 35, figs. 5, 8.—Hay and Shore 1918:446, pl. 36, fig. 2.—Williams 1965:213, fig. 197.—Schmitt, McCain, and Davidson 1973:106.—Powers 1977:126.

*Recognition characters*.—Carapace smooth polished, with punctations small and scarce in middle



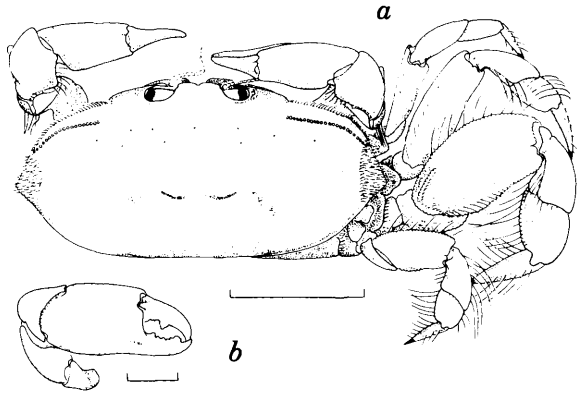


Fig. 362. *Pinnixa cylindrica* (Say). Male: *a*, dorsal view, walking legs of left side not shown; *b*, right cheliped, external view of chela; *a*, 5 mm; *b*, 2 mm indicated (USNM 102840).

third, large and more numerous elsewhere; pubescent at extreme outer corners; depressed in middle; anterior cardiac region separated from gastric and branchial regions by a groove. Anterolateral portions with sharp, granulate crest not reaching cervical suture, shoulder above lateral angle lacking blunt prominence; middle of cardiac region crossed by transverse (sometimes inconspicuous) ridge; posterior border short, somewhat concave. Front not prominent, bilobed, with submarginal groove.

Chelipeds moderately stout, smooth, punctate; hands suboval, approximately 1.5 times as long as wide, fingers horizontal, subequal in length, tips strongly hooked, overlapping when closed, leaving a gape; fixed finger with tooth near tip; dactyl with tooth near middle; finely milled crest running from tip of fixed finger backward and upward approximately  $\frac{2}{5}$  length of palm on outer surface. First walking leg slender, reaching to propodus of second; second stouter, reaching to middle of dactyl of third; third leg stoutest, merus 1.6 times as long as wide, distally narrowed, upper and lower margins finely granulate; fourth short; dactyls nearly straight, that of fourth leg convex posteriorly, slightly concave anteriorly.

Abdomen of male with sixth segment constricted laterally, constriction narrower than telson.

*Measurements in mm.*—Carapace: male, length 7, width 14; ovigerous female, length 9.5, width 21.5.

*Color.*—Yellowish gray, light to dark brown, or sometimes grayish, and mottled with dark gray and/or white. Rhythmic chromatophore changes as well as genetic differences may control observed variations (McDermott 1963).

*Habitat.*—The species lives in burrows of *Arenicola cristata* (Wass 1955; McDermott 1963), and possibly with other large annelids; shallow water to 36.6 m.

*Type-locality.*—Jekyll Island, Ga.

*Known range.*—North Falmouth, Mass., to Pen-

sacola, Fla. (Cooley 1978), including Dry Tortugas.

*Remarks.*—McDermott (1963) summarized existing knowledge of the habits of this species and added numerous ecological observations. He reported the crab for the first time from New Jersey, finding it associated with 76% of the lugworms collected during summer. Crabs and worms were collected by manual digging. With one exception, single crabs were found on worms.

Of 18 female crabs found in July, 16 were ovigerous. One captive female produced eggs on July 7 and liberated zoeae "around" August 5. Crabs which liberated zoeae when collected produced new sponges of eggs which were in late stages of development approximately 30 days later. McDermott judged that this species produces at least 2 egg masses in a breeding season. Molting between broods did not occur in the laboratory.

Associates of *P. cylindrica* were found to be a peritrich ciliate, *Zoothamnium* sp., attached little boat shells, *Crepidula convexa*, and colonies of the bryozoan, *Triticella elongata*.

A few larvae attributed to *P. cylindrica* (zoeal stages I, II, III, and V) were reported from the mouth of Chesapeake Bay from July to October in salinities of 27.28–31.19‰ at 19.8°–26.2°C, nearly all in bottom samples (Sandifer 1973d), and subadults have been taken in surface meroplankton in September at the UNC-IMS pier, Bogue Sound, Morehead City, N. C.

### *Pinnixa floridana* Rathbun

Fig. 363

*Pinnixa floridana* Rathbun 1918b:138, text-fig. 82, pl. 30, figs. 4–7.—Williams, McCloskey, and Gray 1968:57, fig. 13.—Schmitt, McCain, and Davidson 1973:110.—Powers 1977:126.

*Recognition characters.*—Carapace suboblong, narrower in male than in female, anterolateral angle forming slight shoulder; surface smooth, punctate; cardiac region elevated but without ridge, gastroducardiac groove shallow; anterolateral walls steep, sharp milled crest along margin up to cervical suture, male with anterolateral wall steeper and shoulder more prominent than in female; posterior margin concave. Front truncate, not advanced. Orbits inclined anterolaterally in dorsal view.

Chelipeds weak, hairy; chelae tapering distally. Hand of female with denticulate upper margin, row of granules near lower margin continued somewhat on fixed finger, another horizontal row of granules near middle of palm and scattered granules and long hairs above that as well as on dactyl; fingers nearly horizontal, few small teeth on pre-

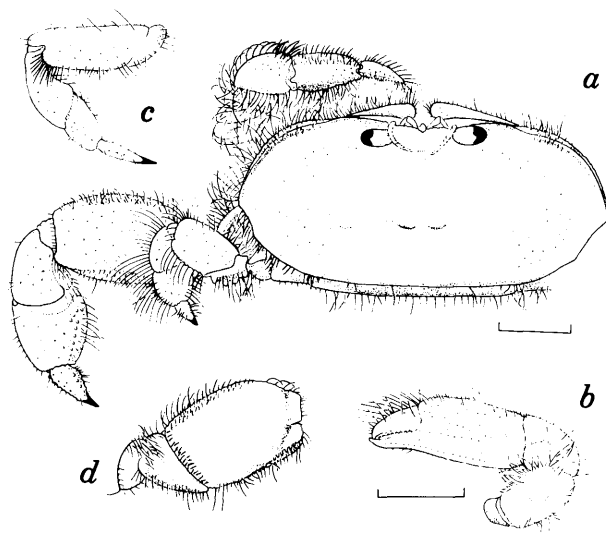


Fig. 363. *Pinnixa floridana* Rathbun. Female: *a*, dorsal view, legs of right side not shown; *b*, left cheliped, external view of chela; *c*, left walking leg, dissociated; *d*, third walking leg, merus and ischium in anterior view; *a-d*, 1 mm indicated (USNM 173017).

hensile edges, not gaping, tips hooked, dactyl with 2 rows of sharp granules. Hand of male with palm proportionately wider, fixed finger somewhat shorter, fingers gaping slightly. First walking leg narrower than second, reaching middle of second dactyl; second leg reaching middle of propodus of third; third leg very wide, lower margin denticulate, merus and propodus tapering rapidly toward dactyl; fourth leg not exceeding merus of third, wide in proportion; dactyls of all legs straight or nearly so.

Line of hair at distal end of second abdominal segment continued along sternum; telson of male abdomen broadened, truncate, arched at sides, margin hairy.

*Measurements in mm.*—Carapace: male, length 2.4, width 4.4; female, length 3.5, width 8; ovigerous female, length 1.8, width 4.3.

*Habitat.*—Commensal with compound ascidian growing at base of *Eugorgia virgulata* [*Leptogorgia virgulata*] washed ashore at Alligator Point, Fla., and under rocks (Wass 1955, amended by Schmitt, et al. 1973); perhaps living in *Diopatra cuprea* tubes (Williams, et al. 1968); to about 55 m.

*Type-localities.*—Marco, Fla., also Sarasota Bay.

*Known range.*—SE off Cape Lookout, N. C.; Hutchinson Island, east central Florida (Camp, et al. 1977); west coast of Florida.

### *Pinnixa lunzi* Glassell

Figs. 364–365

*Pinnixa lunzi* Glassell 1937:3, figs. 1.8.—Williams 1965:214, figs. 198, 199A-E.—Felder 1973:71,

pl. 10, fig. 4.—Schmitt, McCain, and Davidson 1973:114.—Powers 1977:127.

*Recognition characters.*—Carapace slightly more than twice as wide as long, punctate, regions indicated, borders flanged, with shoulder formed near wide lateral angle; anterior border with fringe of long setae, and variable setae elsewhere on carapace and margin of limbs. Front prominent, bilobed, truncate, upturned over antennules. Gastric and cardiac regions separated by depression connecting with deeper depression on each side of these regions; beaded ridge on anterolateral slope, especially pronounced in smaller specimens; prominent cardiac ridge extending transversely almost across carapace with abrupt slope from crest of ridge to posterior border.

Chelipeds stout; hands of male shorter and stouter than in female, appearing disproportionately small in female; palm with margins subparallel in female, widest at base of dactyl in male; in both sexes fingers gaping, fixed finger horizontal, armed with row of small teeth, distal tooth largest; dactyl stout, curved, armed with median lobe. Walking legs stout. First 2 lightly crested with setae on merus; carpus crested with sharp beaded rim; propodus armed with row of fine, sharp, brown spinules; dactyls contorted, sharp pointed, fluted, with rows of small, sharp, forward-pointing spinules on crests. Third leg large; merus with 2 separated, upper, crenulate margins, lower border tuberculate, posterior surface with deep, pubescent concavity, smooth within; ischium at lower distal end extending well past base of merus and with meral concavity continued on posterior face, lower border tuberculate; carpus and propodus together equal in length to upper length of merus; dactyl stout, nearly straight, without minute spinules. Fourth leg similar to third but smaller, merus with lower border tuberculate, dactyl slightly upturned at tip.

Male abdomen with telson semioval, sides not wider than concave-sided sixth segment; third, fourth, and fifth segments partially fused.

*Measurements in mm.*—Carapace: male, length 9, width 21; female, length 9, width 21.

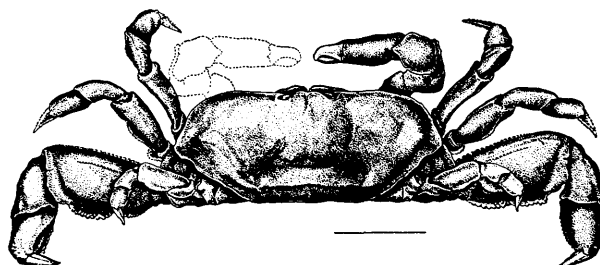


Fig. 364. *Pinnixa lunzi* Glassell. Male holotype in dorsal view, 7 mm indicated (from Glassell 1937).

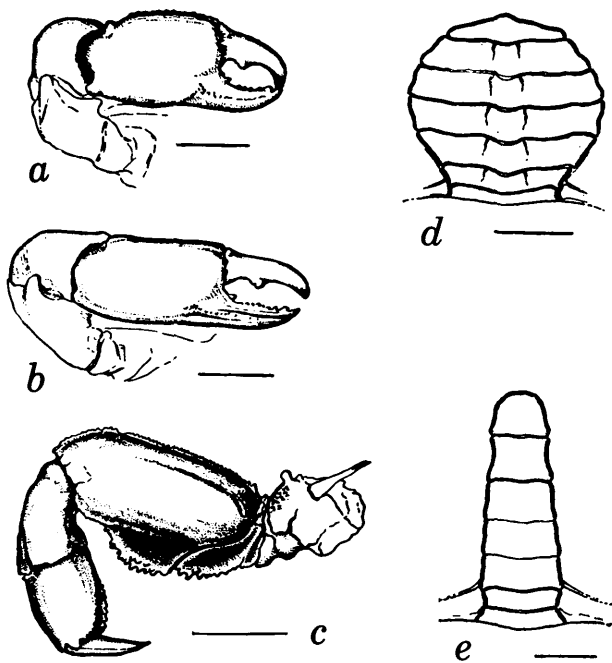


Fig. 365. *Pinnixa lunzi* Glassell. a, Male right chela; b, female right chela; c, female left third walking leg; abdomen, d, female, e, male; a-b, e, 3 mm; c, 4 mm; d, 6 mm indicated (from Glassell 1937).

*Color*.—In alcohol, a muddy bluish brown; legs, abdomen, and chelipeds ivory.

*Habitat*.—Beach under drift material to mud-shell bottom and fine silts and coarse sand-shell around offshore ridges or reefs; in burrow of echinuran *Thalassema hartmani* and probably other shallow burrowers (see remarks below); shore to 26 m.

*Type-locality*.—Isle of Palms (about 15 mi. north-east of Charleston, S. C.), washed on beach under drift material.

*Known range*.—Off Delmarva Peninsula, Va., North and South Carolina, Georgia; off Mississippi River delta and Seven and One-Half Fathom Reef off Texas near 26°51'N, 96°18'W.

*Remarks*.—Since its discovery in beach drift, this crab has been reported in a number of associations. Boesch (1971) found it off Virginia in grab samples from medium to coarse sand-shell ridges parallel to shore, separated by troughs of fine sand. There it was associated with the polychaetes *Clymenella torquata* and *Pherusa affinis*, the coelenterate *Ceriantheopsis americanus*, amphipod *Ampelisca vadorum*, sipunculid *Golfingia margaritacea*, and holothurian *Caudina arenata*. Boesch also reported the occurrence with *Thalassema* in burrows in Georgia. Woodward dug a male from a burrow in a normally subtidal sand flat back of Long Beach, Brunswick County, N. C. (USNM). Boothe (1977) reported an adult male in dredge samples from

mud-shell bottom in the Ashepoo River system (18‰ salinity) along with non-burrowing invertebrates. Felder (1973) reported Mississippi delta specimens and (1973a) a specimen from the stomach of a red snapper, *Lutjanus campechanus*, on a Texas reef. The fish was judged to have eaten this crab in the immediate vicinity shortly before it was collected. Reef temperature records varied from 14.8 to 26.3° C with salinities of 28.1 to 39.9%. Other food items in snappers from this area indicate that they prey on crustaceans that are swimmers, vagrants, or shallow burrowers in substrates surrounding the reef. Boesch (1971) had earlier deduced that *P. lunzi* is a facultative commensal capable of existence for periods without a host.

### *Pinnixa retinens* Rathbun

Fig. 366

*Pinnixa retinens* Rathbun 1918b:139, text-figs. 83–84, pl. 41, figs. 1–2.—Williams 1965:196, fig. 196A–D.—Felder 1973:74, pl. 10, fig. 7.—Schmitt, McCain, and Davidson 1973:118.—Powers 1977:127.

*Recognition characters*.—Carapace nearly twice as wide as long, almost flat, except sloping toward toward margins; regions indicated. Anterolateral margin marked by sharp, granulate ridge reaching to subhepatic sulcus, usually no cardiac ridge; posterior margin preceded by subparallel groove. Outer maxilliped with obliquely spatuliform dactyl attached to middle of inner margin of propodus.

Legs setose. Chelipeds small, approximately as long as first leg; hand flattened, with lower margin straight, suboblong, marginate below; fingers long, slender (especially females), subequal, hardly gaping; dactyl with tooth at proximal third of gripping edge. First and second walking legs similar; second little longer, dactyls slightly curved, long, pointed. Third walking leg stout, exceeding second by length of dactyl and half of propodus; lower edge of ischium, merus, and propodus armed with stout spinules; greatest length of merus more than twice its greatest width; posterodistal end of ischium prolonged in stout, curved spine with point directed upward and backward; dactyl more curved than in first and second legs, pointed. Last leg extending to distal end of third merus; dactyl stout, nearly straight, tip curved slightly upward.

Abdomen constricted at base of second segment, widest between second and third, and tapering to base of telson; telson wider than long; anterior and posterior margins of sternal segment granulate.

*Measurements in mm*.—Carapace: male, length 4,

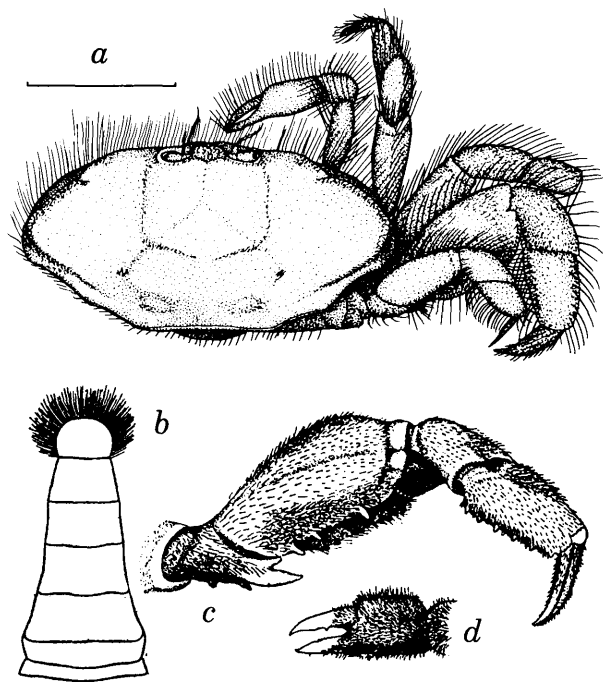


Fig. 366. *Pinnixa retinens* Rathbun. *a*, Female in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965); male, *b*, abdomen; *c*, third walking leg, lower side; *d*, left chela; *b-d*, holotype approximately  $\times 9$  (from Rathbun 1918b).

width 7; ovigerous female, length 6, width 12.

*Variation*.—Juveniles may lack the posterodistal ischial spine on the third walking leg.

*Habitat*.—An ovigerous female was taken from the burrow of *Upogebia affinis* at Alligator Harbor, Fla., in June (Wass 1955). Small specimens have been taken from mud bottom in Chesapeake Bay (Wass, personal communication). Near low-tide mark to 36.6 m.

*Type-locality*.—Chesapeake Bay, off Poplar Island, Md., 36.6 m, soft bottom.

*Known range*.—Delaware Bay (Watling and Maurer 1976); Little River Inlet, S. C., Alligator Harbor, Fla.; Aransas area of Texas coast (USNM).

*Remarks*.—*Pinnixa retinens* is common in Chesapeake Bay (Van Engel and Sandifer 1972). Wass (1955) found an ovigerous female in a burrow of the mud shrimp, *Upogebia affinis*, in Alligator Harbor, Fla., in June, and Boothe (1977) reported it along with the possible host worm *Abarenicola* sp., with other associates, from Little River Inlet, S. C.

### *Pinnixa sayana* Stimpson

Fig. 367

*Pinnixa sayana* Stimpson 1860a:236.—Rathbun 1918b:156, text-fig. 98, pl. 34, figs. 2–4.—Hay and Shore 1918:446, pl. 36, fig. 3.—Williams

1965:212, fig. 195.—Righi 1967:102, figs. 9–14.—Coelho and Ramos 1972:196.—Felder 1973:74, pl. 10, fig. 9a, b.—Schmitt, McCain, and Davidson 1973:119.—Powers 1977:128.

*Recognition characters*.—Carapace similar to *P. chaetoptera* but less hairy, less inflated anterolaterally, and with front more produced; smooth, polished, lightly pubescent on sides, depressed at middle; low, ill-defined, transverse ridge parallel with and close to posterior margin extending about  $\frac{1}{3}$  width of carapace. Front narrow, with deep median groove, produced to cover epistome in dorsal view. Anterolateral slope crossed by beaded crest most pronounced in lateral  $\frac{2}{3}$ .

Chelipeds with hands stout, compressed, basically similar to *P. chaetoptera* but those of female with straighter fingers; female (and juveniles) with fixed finger having shorter upper and longer lower margins connected distally by subterminal, obliquely cusped margin; male with perpendicular palmar edge bearing prominent truncate tooth near base of short, deflected fixed finger, dactyl strongly curved about  $90^\circ \frac{1}{4}$  to  $\frac{1}{2}$  distance from its proximal end. Walking legs long and slender; smooth; first walking leg reaching propodus of second; second and third leg same length; fourth reaching beyond middle of carpus of third; merus of third leg approximately 3.5 times as long as wide, propodus twice or more than twice its greatest width; inferoposterior margin of merus finely toothed or granular; dactyls of first 2 legs slightly curved, of third straight, posterior edge of last dactyl slightly convex.

*Measurements in mm*.—Carapace: male, length 5, width 10; female, length 4.3, width 8.7 mm.

*Variation*.—Females differ from males in that the cardiac ridge is lower and less sharp, the fingers do not gape, the fixed finger is longer and less bent, and the dactyl on the chela is more oblique. Growth changes in chelae of *P. sayana* are compared with changes in *P. chaetoptera* in the account for that species.

*Color*.—Almost white, but lightly stained with brown.

*Habitat*.—The species has been found free in the water, has been dug out of mud (not found in the tubes of *Arenicola cristata*); shore to 47.5 m (Schmitt, et al. 1973), 75 m (Coelho and Ramos 1972).

*Type-locality*.—Mouth of Beaufort Harbor, N. C., 10.97 m, sandy mud.

*Known range*.—Vineyard Sound, Mass., to Beaufort, N. C.; Hutchinson Island, east central Florida (Camp, et al. 1977), Sarasota Bay, Fla., to Grand Isle, La.; Amapá, Pará, Pernambuco, São Paulo, Brazil.

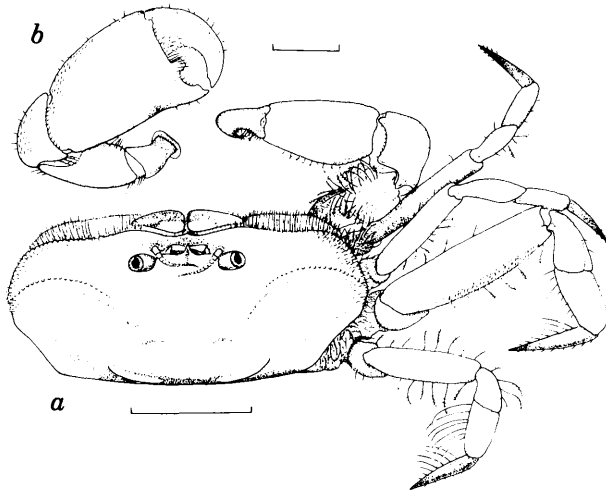


Fig. 367. *Pinnixa sayana* Stimpson. Male: a, dorsal view, legs of left side not shown; b, right chela, external view; 1 mm indicated (USNM 173396).

**Remarks.**—Ovigerous females have been reported in August from Narragansett Bay, R. I. (Rathbun 1918b), are known in September from Louisiana, and in January-February from São Paulo, Brazil (Righi 1967). The last zoeal stage of a *Pinnixa* commonly found off the New England coast and described by Faxon (1879), was tentatively referred to this species by Smith (1880a). Both Faxon and Smith found the first crab stage to follow immediately the last zoeal stage. These stages in development of *P. sayana* were summarized and illustrated by Hyman (1924a).

Sandifer (1973d) reported all 5 zoeal stages of *P.*

*sayana* from the middle York River, Va., to the mouth of Chesapeake Bay, being most abundant in bottom samples with stage III dominating. Larvae were collected in salinity of 18.1–32.34‰ (mainly in 20–30) in temperatures of 19.8°–27.9°C from June to October, with a peak in September. He also found the larvae in the Cape Hatteras region in November and summarized other scattered reports of larvae: June to October in Narragansett Bay (Hillman 1964); July to September at Woods Hole (Fish 1925); July to October in Delaware Bay (Deevey 1960); and August to December in Pamlico and Neuse Rivers, N. C. (Williams and Deubler 1968). Subadults have been taken in surface meroplankton in October at the UNC-IMS pier, Bogue Sound, Morehead City, N. C.

**Superfamily Grapsoidea**

**Family Grapsidae**

Front quite wide; carapace usually quadrilateral, with lateral borders either straight or slightly arched and orbits at or near anterolateral angles. Buccal cavern square; generally a gap, often large and rhomboidal, between external maxillipeds. Male openings sternal. Palp of external maxillipeds articulating either at anteroexternal angle or at middle of anterior border of merus, exognath either slender or broad. Interantennular septum broad. Division of orbit into two fossae accented (Rathbun 1918b).

**Key to Subfamilies, Genera, and Some Species**

- 1. Antennules folding beneath front of carapace in usual way. . . . . 3  
    Antennules visible dorsally in deep clefts in front of carapace . . . . .  
    . . . . . [subfamily Plagusinae] 2
- 2. Carapace broader than long . . . . . *Plagusia depressa*  
    Carapace longer than broad . . . . . *Percnon gibbesi*
- 3. Third maxillipeds without hairy, oblique ridge. . . . . 4  
    Third maxillipeds with oblique, hairy ridge crossing ischium . . . . .  
    . . . . . [subfamily Sesarminae] *Sesarma*
- 4. Lower border of orbit continuing downward toward buccal cavern . . . . .  
    . . . . . [subfamily Grapsinae] 5  
    Lower border of orbit not continuing downward toward buccal cavern but  
    supplemented by remote suborbital crest in line with anterior border of  
    epistome . . . . . [subfamily Varuninae] *Euchirograpsus americanus*
- 5. Carapace decidedly broader than long . . . . . *Pachygrapsus transversus*  
    Carapace about as long as broad; legs strongly fringed with hairs. . . . .  
    . . . . . *Planes minutus*

**Subfamily Grapsinae**

Front usually strongly deflexed. Lower border of orbit running downward toward buccal cavern.

Antennal flagellum very short. External maxillipeds usually separated by wide rhomboidal gap, merus not traversed by oblique hairy crest; palp articulating at or near anteroexternal angle of

merus; exognath narrow and exposed throughout. Male abdomen filling all space between last pair of legs (Rathbun 1918b).

### Genus *Pachygrapsus* Randall 1840

Rathbun 1918b:240.—Manning and Holthuis 1981:233 (synonymy).

#### *Pachygrapsus transversus* (Gibbes)

(Mottled shore crab)

Fig. 368

*Grapsus transversus* Gibbes 1850:181.

*Pachygrapsus transversus*.—Rathbun 1918b:244, pl. 61, figs. 2–3.—Hay and Shore 1918:447, pl. 36, fig. 9.—Williams 1965:217, fig. 202.—Forest and Guinot 1966:91.—Christiansen 1969:92, fig. 38.—Chace and Hobbs 1969:169, fig. 52k.—Coelho and Ramos 1972:201.—Felder 1973:79, pl. 11, figs. 5, 10.—Powers 1977:130.—Manning and Holthuis 1981:234.

**Recognition characters.**—Usually a small species. Carapace anteriorly rectangular, about  $\frac{1}{4}$  broader than long, depressed, polished, with fine transverse plications, except oblique ones on branchial regions. Sides slightly arched, strongly converging posteriorly and armed with well-marked tooth behind orbital angle. Front slightly more than half as wide as carapace, edge sinuous and granulate, upper surface with 4 low elevations. Orbits oblique, approximately  $\frac{2}{5}$  width of front, lower border denticulate.

Chelipeds equal, much stouter than other legs, 1.6 times longer than carapace in male, finely granulate; inner edge of merus produced in lami-

nate, toothed expansion. Meri of all legs and carpus of cheliped transversely striated; latter with blunt internal tooth; upper surface of palm with marginal line, oblique striae on inner and lower side, an oblique line on outer surface near lower edge; fingers narrowly gaping except for large triangular tooth near middle of fixed finger. Merus of walking legs with posterodistal angle dentate; first and fourth walking legs subequal, last 3 articles bristly and thorny. Female with conspicuous feathery hairs on carpus and propodus of first walking legs.

Male abdomen with telson broadly triangular.

**Measurements in mm.**—Carapace: male, length 16.9, width 21.2 (freshly molted and slightly shrunken, Nicteroy, Brazil); ovigerous female, length 13.0, width 16.7 (Balboa, Panama); male, length 21.7, width 26.4; female, length 15.4, width 19.5 (Port Said, Egypt) (USNM).

**Color.**—Variable; ground color almost black, olive green, yellowish, yellowish brown or dull gray, covered by irregular mottlings of dark brown, reddish or dark olive; usually darkest anteriorly with transverse ridges edged with greenish gray, reddish or dark brown; chelae often plain or reddish brown, tips light; walking legs brown or blackish with gray spots (various authors).

**Habitat.**—Mainly intertidal among rocks, also on pilings, roots of mangroves, and sandy shores.

**Type-locality.**—Key West, [Fla.].

**Known range.**—Cape Lookout, N. C., to Montevideo, Uruguay; Bermuda; Mediterranean Sea to northern Angola; eastern Pacific from California to Peru, Galapagos Islands. The species has been carried to higher latitudes than it normally inhabits by transport on ships' bottoms, and, as Verrill (1908b) suggested, the range may have been greatly extended by commerce in modern times.

**Remarks.**—Ovigerous females are known virtually year-round from various part of the normal range: Caribbean Sea—western Gulf of Mexico, February–August (Rathbun 1918b; Rickner 1977); year-round, eastern Florida (Gore, et al. 1978); Bermuda, April–July (Verrill 1908a) but the species is common there from April to October (Lebour 1944); North Carolina, August–September; Galapagos Islands, Egypt, July; west Africa, March, May–October, December (Manning and Holthuis 1981); Brazil, August–February; Ecuador, September. Females taken off northern Brazil bore 9,222 ( $\bar{x}$ ) ova (carapace length 6.0–15.5 mm) (Ogawa and Rocha 1976). Lebour (1944) illustrated some of the larval stages reared from eggs hatched at Bermuda. Dudley and Judy (1971) found the larvae numerous near Beaufort Inlet, N. C., in June, but rare in October.

Pearse (1932b) reported the protozoan *Epistylis*,

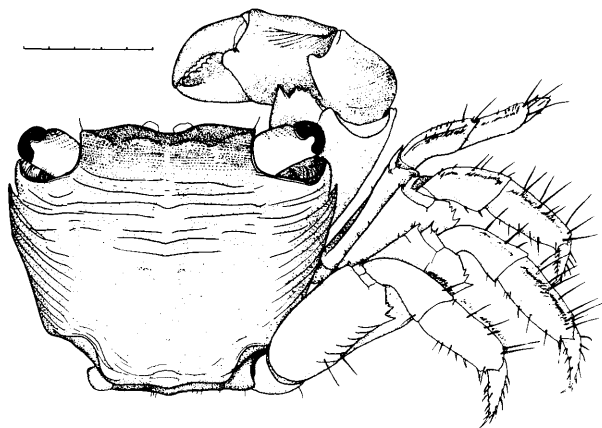


Fig. 368. *Pachygrapsus transversus* (Gibbes). Animal in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

and Verill (1908a) the isopod *Leidyia distorta* in the gill cavities of this crab.

Gore, et al. (1978) found *P. transversus* to be the third most abundant decapod on a sabellariid reef off eastern Florida where its feeding role was that of an omnivore-scavenger.

### Genus *Planes* Bowdich 1825

Rathbun 1918b:253.—Chace 1951.—Hemming 1958b:36.—Manning and Holthuis 1981:235 (synonymy).

#### *Planes minutus* (Linnaeus)

(Gulf weed crab; turtle crab; Columbus crab)

Fig. 369

*Cancer minutus* Linnaeus 1758:625.

*Planes minutus*.—Hay and Shore 1918:448, pl. 36, fig. 6.—Chace 1951:81, figs. 1a, 2a, d, g, j, k, l, 3a-h.—Holthuis 1959:240.—1977:160.—Williams 1965:218, fig. 203.—Christiansen 1969:94, fig. 39.—Coelho and Ramos 1972:201.—Manning and Holthuis 1981:235.

*Recognition characters*.—Carapace approximately as wide as long, subquadrate in young, trapezoidal in medium-sized, laterally convex in old individuals, convex dorsally, smooth, but with faint oblique lines on outer part of branchial region. Front approximately half as wide as carapace, decurved, usually slightly emarginate in middle, edges minutely denticulate or smooth. Eyes large; orbits large, lower margin granulate, tooth at inner angle equilateral, subacute, outer angle spiniform, small sinus behind it.

Chelipeds large and heavy; merus and ischium with thin serrate crest along inner margin termi-

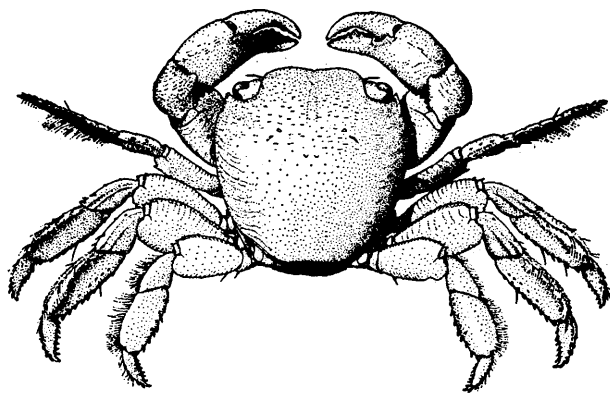


Fig. 369. *Planes minutus* (Linnaeus). Male in dorsal view, approximately  $\times 2$  (from Chace 1951).

nating in 2 or 3 spines at distal end of merus; carpus with strong blunt spine on inner face; hands inflated and smooth except for small, sharp granules near lower margin; fixed finger bent downward, especially in males, dactyl curved, both with blunt teeth throughout length. Walking legs long, slender, and flattened; second and third legs subequal, fourth legs shortest; meri occasionally with inconspicuous anterior subterminal tooth and few posterior denticles; last 3 articles thorny and with dense fringe of hair on anterior edge.

Abdomen of male rather broadly triangular; telson rather narrowly triangular, approximately as long as basal width.

*Measurements in mm.*—Carapace: male, length 19, width 19. Length of large series reported by Chace (1951) 3.7 to 19.

*Color*.—Extremely variable; irregularly mottled or blotched with light greenish yellow or pale yellow on darker olive-green ground color; or reddish-fawn color, more or less blotched with dark brown, and usually with small white spot on each side or one large white spot on front of carapace (various authors).

Crozier (1918) observed no color change in a mahogany-colored *P. minutus* placed for a day on a lighter background. Hitchcock (1941) found three types of chromatophores in *P. minutus*: white, black, and yellow. The most prominent chromatophore is white. Color adaptation to different background is slow and though the chromatophores are responsive to such changes, extracellular pigment in the hypodermis and exoskeleton prevents the animal from effecting an immediate change in appearance. Hitchcock concluded that the pattern of the individual crab is probably genetic. Chace (1951) remarked that in view of these findings, the apparent color of any individual can be changed only at the time of molting.

*Habitat*.—These crabs are more abundant on *Sargassum* in the Sargasso Sea than elsewhere, but throughout their range they depend on flotsam or on floating or swimming organisms to which they cling (Chace 1951).

*Type-locality*.—On sargasso and other submarine sea plants on the north side of Jamaica (Sloane in Holthuis 1959).

*Known range*.—“Northern Atlantic Ocean south of the line connecting Newfoundland with the south coast of England and the southern North Sea” (Holthuis 1959; also Oord and Holthuis 1959), including the Mediterranean Sea, south to  $11^{\circ}05'N$ , exclusive of the Gulf of Mexico (Chace 1951). The authors regarded occurrences outside this region as doubtful, although Chace found the species at one locality in the Indian Ocean at  $90^{\circ} E$  on the

equator and Holthuis recorded a specimen from Surinam. Fausto-Filho (1968) reported the species from Ceará, as did Coelho and Ramos (1972) from Pernambuco, Brazil, in floating debris, placing the southern range limit at 5°S, but both Chace and Holthuis were uncertain about records south of 11°05'N.

*Remarks.*—The genus *Planes* was thoroughly reviewed by Chace (1951), and the serious student should consult this paper. Chace included remarks on relative growth, stating that:

“The carapace length-width relationship remains fairly constant with a slight tendency toward narrowing, from the smallest immature specimens examined to a carapace length of about 11 mm. At this stage the carapace seems to become somewhat narrower rather abruptly and continues to become narrower at a slightly more rapid rate than during the younger stages. A similar, but even more striking, trend is noticed in the relative shortening of the walking legs.”

Chace conjectured that specimens larger than about 11 mm are found on flotsam and turtles rather than on *Sargassum*, and that the shorter legs may be more adapted to this existence than to life on floating weed. It is also possible that these sizes represent different taxonomic forms, but Chace deferred such a designation until a time when more material is available for study.

Both Hyman (1924b) and Lebour (1944) illustrated some larval stages of *Planes minutus*. In the region of the Carolinas, ovigerous females have been taken virtually throughout the year.

#### Subfamily Varuninae

Front moderately or little deflexed, sometimes sublaminar. Branchial region with downward-sloping posterolateral portion set off from rest of region by more or less distinctly marked line. Sub-orbital crest, supplementing defective lower border of orbit, rather distant from orbit and usually running in a line with anterior border of epistome. Antennal flagellum usually of good length. External maxillipeds moderately or slightly gaping, without oblique hairy crest; palp articulating with middle of anterior border or near anteroexternal angle of merus; exognath in American genera rather narrow, sometimes partly concealed. Male abdomen rarely covering all space between last pair of legs (Rathbun 1918b).

#### Genus *Euchirograpsus* H. Milne Edwards 1853

Rathbun 1918b:281.—Hemming 1958b:31.—Türkay 1975:104.

#### *Euchirograpsus americanus* A. Milne Edwards

Fig. 370

*Euchirograpsus americanus* A. Milne Edwards 1880:18.—Rathbun 1918b:282, text-fig. 144, pl. 74 (part).—Hay and Shore 1918:448, pl. 36, fig. 7.—Williams 1965:220, fig. 204 (except Pacific material).—Türkay 1975:114, figs. 6–7, 16b, 20a, b, 24.

*Recognition characters.*—Carapace slightly broader than long; sides nearly straight and parallel, flattened posteriorly, sloping gently down toward sides and front; surface covered with granules and short, soft hair. Front somewhat produced, lamellate, with narrow median notch. Eyes large; orbits large, small blunt tooth at inner angle; upper margin oblique, sinuous; outer angle spiniform, behind it 3 smaller spines on lateral margin; lower margin of orbit denticulate. Third article of antennae hollowed out on inner side.

Chelipeds stout, 1.5 times as long as carapace; merus with surface crossed by fine granulated line, margins spinose, a superior subdistal spine; carpus with inner distal margin spinulose; palm with 3 spinulose ridges above, outer ridge near lower edge, and another less distinct through middle; fingers slender, grooved, pointed, gripping edges with low, irregular teeth fitting together. Walking legs slender, compressed, hairy; second pair over twice length of carapace; all meri crossed by fine granulated lines, and with superior, subdistal spines; flexor surface of all meri except last with inner distal spine, all with outer distal spine, and first with another spine proximal to it; dactyls armed with long spines.

*Measurements in mm.*—Carapace: male, length 15.1, width 16.3; female, length 15.1, width 16.5.

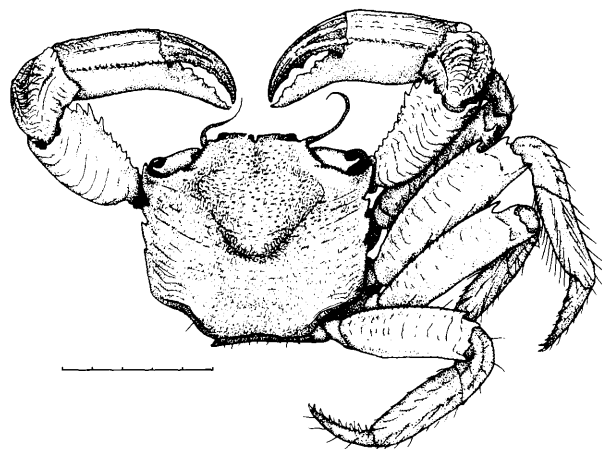


Fig. 370. *Euchirograpsus americanus* H. Milne Edwards. Animal in dorsal view, walking legs of left side not shown, 5 mm indicated (from Williams 1965).



*Color*.—Yellowish gray, arranged in marblings on carapace and in alternately light and dark bands on legs, or light brown with 5 or 6 bands of red on legs (various authors).

*Habitat*.—31 to 508 m.

*Type-locality*.—Barbados, 126.2 m, Blake Stn. 278.

*Known range*.—Off Oregon Inlet, N. C., Florida through West Indies, and Colombia to Venezuela.

*Remarks*.—Türkay (1975), in his generic revision, split a genus that had contained two species into a group of six species. Two of these occur in the western Atlantic, *E. americanus* having essentially the Atlantic distribution formerly attributed to it but not occurring in the Galapagos Islands, and between the Bahamas—east Florida and the Yucatan peninsula.

The northernmost record for *E. americanus* is the shallowest, represented by an ovigerous female taken in February (Cerame-Vivas, et al. 1963). Ovigerous females are otherwise known in Florida from March to September.

#### Subfamily Plagusiinae

Front cut into lobes or teeth by antennular clefts visible in dorsal view. Lower border of orbit curving down into line with prominent anterior border of buccal cavity. External maxillipeds neither completely closing buccal cavity nor leaving wide rhomboidal gap, not crossed by an oblique hairy crest; palp articulating near anteroexternal angle of merus, often no flagellum on exposed exognath. Antennal flagella short. Male abdomen filling all space between last pair of legs (Rathbun 1918b).

#### Genus *Percnon* Gistel 1848

Rathbun 1918b:337.—Hemming 1958b:35.—Manning and Holthuis 1981:237 (synonymy).

#### *Percnon gibbesi* (H. Milne Edwards)

(Spray crab)

Fig. 371

*Acanthopus Gibbesi* H. Milne Edwards 1853:180.

*Percnon gibbesi*.—Rathbun 1918b:337.—Schmitt 1939:24.—Garth 1965:34.—Williams 1965:224.—Fausto-Filho 1975:82.—Powers 1977:131.—Manning and Holthuis 1981:238.

*Percnon ?gibbesi*.—Fausto-Filho 1974:15.

*Recognition characters*.—Carapace thin, dislike, longer than wide, covered with small short bristles

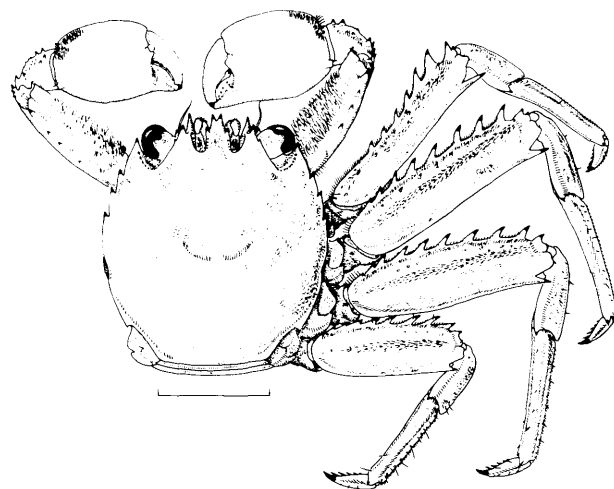


Fig. 371. *Percnon gibbesi* H. Milne Edwards. Male in dorsal view, walking legs of left side not shown, 1 cm indicated (USNM 151485).

except for bare raised patches; dorsal surface with few low tubercles. Front deeply cut by antennular furrows; part between antennules narrow and extended in form of rostrum armed with 2 erect spines on each side distally, and row of inconspicuous spinules just within and parallel to each margin proximally. Eyes large, cornea reniform. Inner margin of orbit bearing 3 spines, 2 distal spines prominent; outer half of upper orbital border more or less serrate. Anterolateral border of carapace with 4 acute spines, counting large spine on outer orbital angle; second spine on outer orbital angle; second spine in series with its lateral margin shorter than that of third spine.

Chelipeds varying in size with age and sex, small in females but large and unequal in adult males; merus and carpus armed with spines, merus in males with dense patch of feathered hairs along dorsomesial side, patch lacking in females; palm nearly smooth, oval and somewhat compressed, upper surface with ill-defined, proximal groove extending  $\frac{1}{3}$  length and flanked by usually 2 proximomesial spines, pubescence filling groove continued behind proximal spines to small triangular zone on inner surface; fingers short, blunt, with tips concave on opposed surfaces. Merus of each walking leg with large, nearly uniform spines on anterior margin, upper surface covered with short bristles similar to carapace, longer along margins; flexor margin ending in distal spine; merus of first 2 legs with second row of spinules parallel with anterior border, row indistinct on third merus and absent on fourth.

*Measurements in mm*.—Carapace: male, length 30, width 28; female, length 33, width 34 (Garth 1946).

*Color*.—Carapace and meri of walking legs brown

or mottled above; usually a median longitudinal stripe of white or pale blue; legs banded with reddish, brown, and light pink distally; eyestalks and chelae orange; ventral side of body pale blue with legs pale pink (Garth 1946; Verrill 1908a). Greenish or light green, central light blue longitudinal band dorsally (Fausto-Filho 1974).

*Habitat*.—The usual habitat for this species is the underside of rocks at the low-tide level (Verrill 1908a), or in the surf at knee to hip depth, where it is extremely difficult to capture because of its propensity for rapidly keeping to the underside of turned objects (Garth 1946).

*Type-locality*.—Antilles.

*Known range*.—Fort Macon, N. C.; southern Florida and Bahamas to Brazil; Bermuda; Azores to Angola; Cape San Lucas, Lower California, to Chile; Galapagos Islands.

*Remarks*.—Rathbun (1918b) and Schmitt (1939) separated *P. gibbesi* from *P. planissimum* (Herbst) as, with some reservations, did Crosnier (1965), Garth (1965), Williams (1965) and Fausto-Filho (1974, 1975), but Forest and Guinot (1961; 1966) and Coelho and Ramos (1972) united them as *P. planissimum*. Admittedly, the species are close (carapace, male abdomen and pleopods identical; see Crosnier 1965; Fausto-Filho 1974), but they can be separated on the basis of cheliped characters. The palm of *P. gibbesi* has a small proximal, triangular, pilose zone on the internal surface and a pilose groove on the proximal  $\frac{1}{4}$ – $\frac{1}{3}$  of the inner dorsal surface; this groove is noticeably shorter in *P. planissimum*, and the internal pilose zone is almost absent (Crosnier 1965; Garth 1965). As Garth observed, in material available for study the two forms are clearly separable, although study of a more complete series may show these characters to vary in a regular and continuous manner over the geographic range.

Ovigerous females are known from May to September in the Gulf of Mexico-Caribbean-Bahamian-Bermuda region (Rickner 1977; USNM). Muraokoa (1967) described the megalopa of *P. planissimum* taken from Sagami Bay, Japan.

Juveniles in the rocky sublittoral of Colombia were observed exclusively in the immediate vicinity of *Diadema antillarum*, apparently using the long urchin spines as protection against predation, for when the urchins were removed the associated crabs were eaten by fishes (Schmalzfuss 1976). Schmalzfuss hypothesized that the dimorphically ornate, larger chelipeds of male *P. gibbesi* are used in courtship or copulation and that the elaborate pattern of rows and fields of feathered hairs on the walking legs and dorsal surface of the carapace serve a purpose in suspension feeding. He noted that the

brush of hairs on the antennule displays a conspicuous yellowish color when the antennule is flicked up and down in quick strokes, following which it is brushed through the maxillipeds. He interpreted antennular motion as either a lure to attract small fish which are caught and eaten or as an active filter, considering these possibilities to be compatible.

Randall (1967) reported *P. gibbesi* from stomach contents of the coney, *Cephalopholis fulva*, rock hind, *Epinephelus adscensionis*, soapfish, *Rypticus saponaceus*, schoolmaster, *Lutjanus apodus*, puddingwife, *Halichoeres radiatus*, porcupine fish, *Diodon hystrix*, and longlure frogfish, *Antennarius multiocellatus*.

### Genus *Plagusia* Latreille 1804

Rathbun 1918b:331.—Monod 1956:455.—China 1966:257.—Manning and Holthuis 1981:238 (synonymy).

#### *Plagusia depressa* (Fabricius)

Fig. 372

*Cancer depressus* Fabricius 1775:406.

*Plagusia depressa*.—Rathbun 1918b:332, text-fig. 154, pl. 101.—Monod 1956:455, figs. 614–617.—Williams 1965:223, fig. 207.—Forest and Guinot 1966:93.—Chace and Hobbs 1969:192, figs. 62r–t, 63.—Felder 1973:75, pl. 11, fig. 5.—Fausto-Filho 1974:15.—Powers 1977:131.—Manning and Holthuis 1981: 239.

*Recognition characters*.—Carapace subhexagonal, wider than long, depressed, covered with short, plumose hairs forming scalelike pattern around flattened tubercles and elsewhere; regions distinct, front of gastric region with series of approximately 6 prominent, acute tubercles arranged in an arc. Indefinite front broad, with deep median furrow and deep notches for antennules; spiniform tubercle on each side between median furrow and antennular notch. Eyes with cornea slightly narrower than eyestalks; orbits deep; outer orbital angle produced into strong, curved spine followed on anterolateral margin by 3 similar spines of diminishing size; lower orbital margin produced, armed with 2 teeth slanting toward anterolateral angle of mouth area. Epistome prominent beyond anterior border of carapace and cut into central and 2 or more lateral lobes on each side.

Chelipeds of adult male moderately heavy, subequal, approximately as long as carapace; in female slender,  $\frac{3}{4}$  as long as carapace; merus with 3 small spines above at distal end; carpus rugose, inner tooth triangular; palm and dactyl (male) with

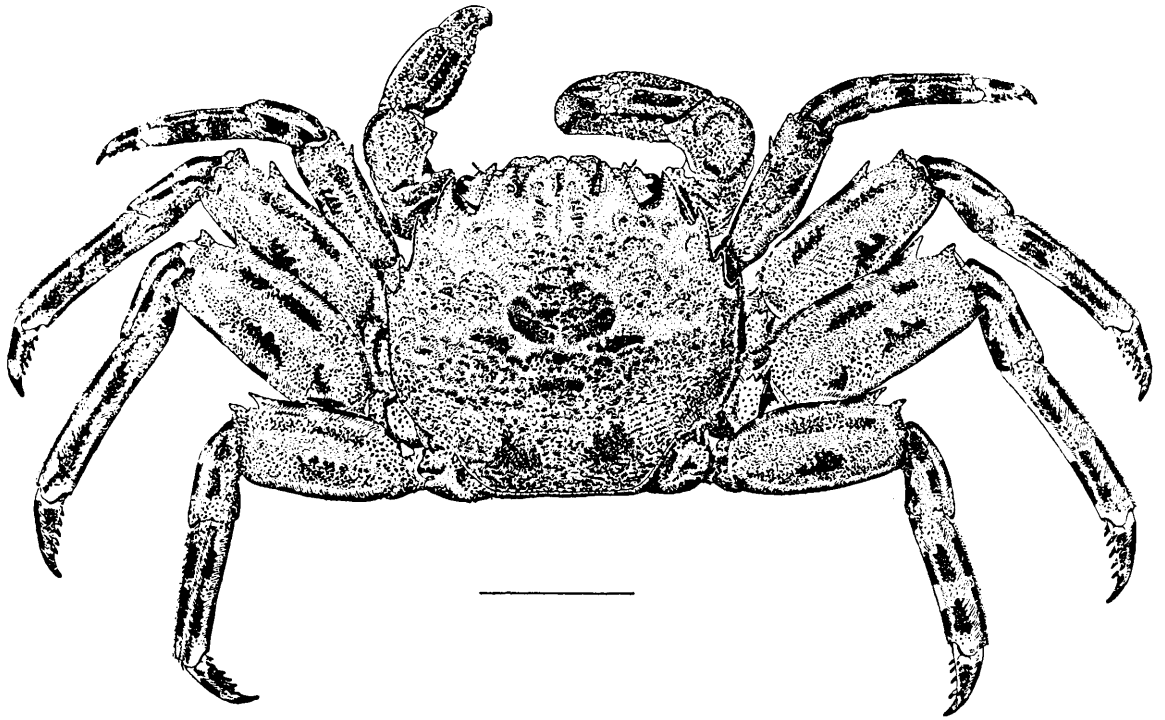


Fig. 372. *Plagusia depressa* (Fabricius). Male in dorsal view, 20 mm indicated (from Chace and Hobbs 1969).

tubercles arranged in 3 longitudinal ribs separated by setose furrows, outer surface smooth, inner surface with scattered small tubercles; fingers blunt, spoon tipped with corneous edges. Walking legs strong, somewhat flattened, increasing in size from first to third, fourth shorter than second; second and third legs with dentate crest above on coxae; meri with subterminal spine on anterior border; distal 3 articles with dense strip of long hair; dactyls with 2 rows of strong spines on flexor side.

*Measurements in mm.*—Carapace: male, length 50, width 53; female, length 59, width 62.

*Color.*—Light reddish, dotted with blood red, tubercles bordered with blackish hairs having gray extremities; blood-red spots on legs; underside of body yellowish (Latreille in Rathbun 1918b). Light to dark blue green (Fausto-Filho 1974). "Carapace olive tan with brown to black tubercles and dark brown or black areas dorsally." Chelipeds with white basal articles; merus, carpus and chela pinkish with purple spots and stripes, fingers white distally. Walking legs olive with purple spots and stripes, dactyls white to olive with purple band and corneous tips. Underparts white, including third maxillipeds (Chace and Hobbs 1969).

*Habitat.*—Found among rocks, on jetties, in tide pools, and thought to be transported on ships' hulls.

*Type-locality.*—"In mari mediterraneo" (erroneous).

*Known range.*—Beaufort, N. C., through Gulf of Mexico and West Indies to Pernambuco, Brazil; Bermuda; Azores; Madeira; Morocco to northern Angola; St. Helena Island (Chace 1966). Felder (1973) and Haburay (1975) considered the species uncommon in the Gulf of Mexico.

*Remarks.*—Chace (1966) compared male gonopods of the species of *Plagusia*, pointing out that *P. depressa* from the Atlantic is probably a distinct species.

Ovigerous females are known from samples collected in April to August in the main part of the range, and February at St. Helena Island (USNM). Muraoka (1965) described the megalopa of the Pacific *P. depressa tuberculata* in plankton taken in early autumn from Sagami Bay, Japan.

#### Subfamily Sesarminae

Front strongly deflexed. Lower border of orbit commonly running downward toward angle of buccal cavern. Side walls of carapace finely reticulated with granules and hairs or hairs only. External maxillipeds separated by wide rhomboidal gap, an oblique hairy crest traversing them from point near anteroexternal angle of ischium to point near anterointernal angle of merus; palp articulating either at summit or near anteroexternal angle of

merus; exognath slender and either partly or almost entirely concealed. Male abdomen either filling or not quite filling all space between last pair of legs (Rathbun 1918b).

### Genus *Sesarma* Say 1817

Rathbun 1918b:284.—Manning and Holthuis 1981:241.

### Key to Species

1. Lateral margin of carapace straight; distal articles of first 3 walking legs with long hairs but not densely pubescent; body nearly flat . . . . . *S. (Chiromantes) cinereum*
- Lateral margin of carapace sinuous; last 3 articles of first 3 walking legs densely pubescent; body strongly convex . . . . . *S. (S.) reticulatum*

#### *Sesarma (Chiromantes) cinereum* (Bosc)

(Wharf crab; wood crab; friendly crab; square-backed fiddler)

Fig. 373

*Grapsus cinereus* Bosc [1802]:204, pl. 5, fig. 1.

*Sesarma cinerea*.—Hay and Shore 1918:449, pl. 36, fig. 11.

*Sesarma (Holometopus) cinereum*.—Rathbun 1918b:300, text-fig. 149, pl. 83.—Abele 1973:377, fig. 1B, H.—Powers 1977:133.

*Sesarma (Holometopus) cinerum* [sic].—Williams 1965:222, fig. 206.

*Sesarma cinereum*.—Felder 1973:78, pl. 11, fig. 6.

*Sesarma (Chiromantes) cinereum*.—Manning and Holthuis 1981:242 (implication).

*Recognition characters*.—Carapace rectangular, nearly uniform in width throughout; regions well marked; surface nearly smooth, punctate, rough with squamiform tubercles toward front; suprafrontal lobes well marked, inner pair widest. Front 4 times as wide as high, widening below, somewhat 4-lobed in dorsal view, lower edge sinuous. Outer orbital angle acute. Lower surface of carapace covered with fine net of geniculate hairs.

Chelipeds heavy; merus and carpus covered with short transverse lines of scabrous granules; merus with upper edge sharp, inner edge irregularly dentate with triangular laminar expansion on distal half; carpus with inner angle rounded. Palm nearly twice as high as upper length; outer surface covered with scabrous granules arranged in parallel lines near upper margin; inner face coarsely granulate, with short prominent ridge near distal end; fingers gaping narrowly, largest tooth at middle of fixed finger. Walking legs rather narrow, meri with superior subdistal spine; third pair of legs over twice as long as carapace.

Abdomen of males broadly triangular; telson much narrower than sixth segment.

*Measurements in mm*.—Carapace: male, length 18, width 20; female, length 20, width 23; ovigerous

females, width 9.2–20.2 (Seiple 1979).

*Color*.—Brown varying toward olive.

*Habitat*.—Supralittoral zones of marshes characterized by high salinity ( $\bar{x}$  = 27.9%) and sandy substrates (Seiple 1979). Found actively crawling about on wharves and stone jetties or resting in shallow burrows above tidemark along shores. The crabs have often been found on vessels along the coast hiding anywhere out of sight or reach and coming forth at night to feed.

*Type-locality*.—"La Caroline."

*Known range*.—Magothy River, Chesapeake Bay, Md., to Palm Beach, E Fla.; Collier County, W. Fla., to Veracruz Mexico (Abele 1973). Older records from the West Indies and elsewhere are erroneous.

*Remarks*.—Ovigerous females occur from mid-April to November in North Carolina, also reported May-June in Mexico (Rickner 1977), and have been found along the Potomac River in January (USNM). Females in North Carolina produce 4–6 egg batches in close synchrony with lunar phases, each female carrying her eggs approximately one lunar month, with peak reproductive activity occurring from April to June (Seiple 1979). Hyman (1924b) briefly described the first zoeal stage. Costlow and Bookhout (1960) described four

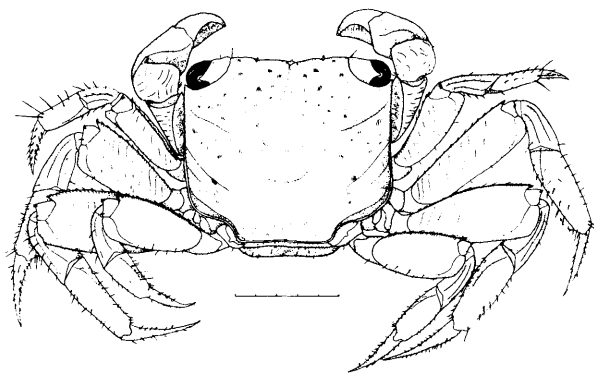


Fig. 373. *Sesarma (Chiromantes) cinereum* (Bosc). Animal in dorsal view, 5 mm indicated (from Williams 1965).

zoal stages and the megalopa from 1,200 zoeae reared on *Artemia* nauplii and *Arbacia* eggs under constant conditions of temperature, salinity, and light. Costlow, et al. (1960) found that optimum salinities exist for each larval stage, but development proceeds best in the 20–26.7‰ salinity range (among those tested). Temperature was found to have more effect on length of larval development than on mortality, with higher temperature speeding development. No “extra stages” were observed. The authors concluded that salinity is the chief physical factor confining *S. cinereum* to estuaries. No allozyme genetic variation is shown in life-history stages (Gooch 1971).

Records of the larvae from plankton vary with site of sampling. Pinschmidt (1963), in Newport River near Beaufort, N. C., found stage I and II zoeae in low concentration from June to September in water of 19° to 13°C and 7 to 36‰ salinity, but most numerous in August at 25° to 31°C. Sandifer (1973d) found the larvae rarely in York and Pamunkey rivers Va., in June and August, the three samples being from bottom water or 24.8° to 26.6°C in 11.9 to 19.64‰ salinity. Dudley and Judy (1971) found larvae of the genus *Sesarma* more abundant inshore (1.6 km) than offshore (6.5 km) from June to September off Beaufort Inlet, N. C., and more numerous at 8-m depth than at the surface. Tagatz (1968) found larvae of the genus *Sesarma* the second most abundant form in St. Johns River, Fla., in samples taken from April to October, with greatest number in August.

*Sesarma cinereum* feeds on *Spartina* shoots (Seiple 1979). The species can survive for a considerable period of time in dilutions of sea water and also shows considerable resistance to desiccation (Pearse 1929). Oler (1941) maintained captive specimens from a Maryland tidal river in a house basement for about a year. The animals burrowed in mud in an aquarium where the only moisture provided was tap water. Vegetable matter was fed at irregular intervals. After several months, the larger animals ate the smaller ones, presumably at the time of ecdysis. Duncker (1934), in Germany, secured three live females identified as *S. cinereum* (see Abele 1973) which had been transported by chance in a cargo of logs from the West Indies. The animals were kept alive in a glass jar with damp peat and a container for a source of fresh water. One lived 4 years and 72 days from date of captivity. The crabs were fed shredded beef or fish and commercial fish food plus *Collembola* that appeared in the jar. All eating was done on land. Some regeneration of lost appendages occurred, and the longest lived specimen molted four times, molting always taking place in water. To the author's surprise, eggs were re-

leased six times (about 4,700 to 13,400 per mass) always in water, the longest lived female producing five of these batches. Larvae hatched from all but one of the egg masses, but survived only a short time. Duncker concluded that one mating was effective for three years or more. Incubation lasted approximately 30 days. The female ate eggs that protruded over the edge of the abdomen. Duncker considered that the crabs acted more like land than aquatic animals, each individual having its own burrow.

Teal (1959) implied the same conclusion, for in experiments under water *S. cinereum* was relatively inactive, thus holding its oxygen consumption down. There was some evidence for thermal acclimation of metabolism, but more evidence for acclimation by selection of microclimate. Gray (1957) also emphasized the terrestrial habits of the species but showed that its relative gill area is nearly double that of the similar species, *Ocypode quadrata*.

#### *Sesarma (Sesarma) reticulatum* (Say)

Fig. 374

*Ocypode reticulatus* Say 1817:73, pl. 4, fig. 6.

*Sesarma reticulata*.—Hay and Shore 1918:448, pl. 36, fig. 12.

*Sesarma (Sesarma) reticulatum*.—Rathbun 1918b:290, pl. 77.—Williams 1965:221, fig. 205.—Abele 1973:380, fig. 1E.—Powers 1977:136.

*Sesarma reticulatum*.—Felder 1973:78, pl. 11, fig. 7.

*Recognition characters*.—Carapace about  $\frac{4}{5}$  as long as broad, convex, regions distinct, surface punctate and with scattered clumps of setae above and in front; sides concave behind widest point, convergent at orbital angles. Posterolateral regions obliquely striated and setose; inferolateral and frontal regions with irregular rows of tubercles bearing short, curved hairs. Dorsal portion of carapace overhanging sides; beneath projecting shelf a line of cilia. Lower surface of carapace covered with fine net of geniculate hairs. Front broad, slightly sinuate above basal articles of antennae. Eyestalks short and stout, set in deep oval orbits; deep gap below outer orbital angle leading into system of grooves opening into notch at anterolateral angle of buccal cavern. External maxillipeds separated by wide rhomboidal gap largely filled by hairy fringe, and obliquely traversed by conspicuous line of hairs from point behind anteroexternal angle of ischium to anterointernal angle of merus.

Chelipeds stout, subequal in male; merus and carpus lightly rugose; merus with obtuse subterminal tooth above, both lower margins denticu-

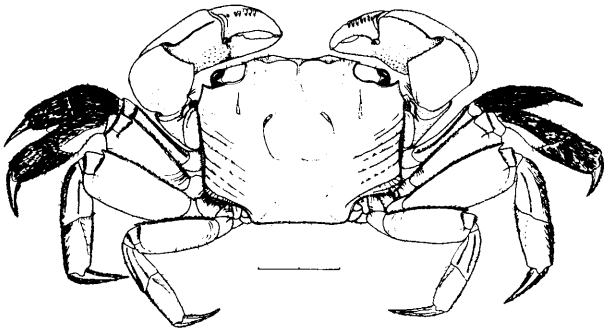


Fig. 374. *Sesarma (Sesarma) reticulatum* (Say). Animal in dorsal view, 1 cm indicated (from Williams 1965).

late; carpus with inner angle rounded. Palm almost smooth, in male slightly higher than midlength, upper edge with single granulate line, inner surface with short irregular ridge of tubercles near distal end; dactyl with 7 of 9 depressed spinules above on basal  $\frac{2}{3}$ ; fingers agape, enlarged tooth near each end. Palm of female half again as high as midlength, fingers slightly agape. Third pair of walking legs approximately twice as long as carapace, last 3 articles densely pubescent.

*Measurements in mm.*—Carapace: male, length 23; width 28.

*Color.*—Carapace dark olive, nearly black or purple; dark plum-colored or bluish-black speckles crowded on grayish background, grayish color showing little except on posterior part; upper part of chelipeds similarly colored but brighter, greater part of palm yellowish, tips of fingers white or yellowish; upper part of legs as carapace; under parts grayish (various authors).

*Habitat.*—Burrows in muddy salt marshes with mean salinity of 16.2‰ (Seiple 1979).

*Type-locality.*—Muddy salt marshes [east coast of United States].

*Known range.*—Woods Hole, Mass., to Volusia County, E Florida; Sarasota, W Florida, to Calhoun County, Tex. (Abele 1973, and personal communication).

*Remarks.*—Ovigerous females are reported from Massachusetts in July, and mid-April to mid-September at Beaufort, N. C., with peak reproduction in April-June (Seiple 1979). Females produce 2–3 egg masses per season, carrying each batch approximately 45 days. Crichton (1960) found 8,000 to 10,000 eggs per egg mass. Hyman (1924b) described the first zoeal stage, comparing it with *S. cinereum*. Costlow and Bookhout (1962a) described the complete larval development of three zoeal stages and a megalopa, comparing these to similar stages they had described for *S. cinereum*. They concluded that photoperiod has no observable ef-

fect on development. Costlow (1966) discussed effects of eyestalk extirpation on larval development, showing that removal of both eyestalks results in acceleration of metamorphosis in megalopae but not in zoeae, suggesting that the X-organ-sinus gland complex is a phased storage organ for more than one endocrine substance which regulates rate of development. No allozyme genetic variation is shown in life history-stages (Gooch 1977).

Sandifer (1973d) took larvae of *S. reticulatum* in the York and Pamunkey rivers, but never abundantly, in a salinity range of 2.04 to 20.24‰. Few larvae occurred below 10‰ salinity, most being between 15 and 20‰, but there was one occurrence off the mouth of Chesapeake Bay. The larvae appeared in June, increased in July-August, and disappeared by October, living in a temperature range of 22.8° to 27.9°C. Stage I made up 73% of the larvae taken, and > 80% of all taken were at the bottom. Sandifer (1975) regarded this depth distribution as an adaptation for retention in estuaries. Pinschmidt (1963) found the same trends.

Foskett (1977) found that larvae are hyperosmotic over the salinity range 10 to 35‰ and hypertonic in salinities above that throughout zoeal stages and the early megalopa. He felt that this trend may serve to increase density of the larvae, helping to promote retention within the estuary. Hyperregulation may also act to provide turgor pressure insuring integrity of the thin larval cuticle, but the rapid molting cycles do not affect blood osmotic concentrations. Foskett also noted that adults hyperregulate in salinities up to 27.5‰ and hypo-regulate in salinities above that, acquiring the adult regulatory pattern during early juvenile crab stages.

Crichton (1960, 1974) in Delaware, with the aid of rubber casts, found that the species digs burrows which may have several openings leading at a gentle slope to a depth of 7.5–10 cm where a series of more or less level corridors curve, twist, and often interconnect. Each corridor usually leads to a vertical shaft as much as 0.75 m deep, usually filled with water. Burrows are communal, containing a male or two and several females. Crichton found that this species will eat fiddler crabs (the burrows occasionally intersect) when it can capture them; however, the usual diet is *Spartina*, the crabs often cutting swaths through this marsh grass. From experiments it was deduced that 42% of energy harvested by *Sesarma* is passed directly to the marsh surface in fecal deposits. Burrowing action of the crab tills the land, increases erosion, and turns over the cord grass more rapidly than the annual decay cycle could do it unaided. The role of this crab among macroinvertebrates in marsh ecosystems was further discussed by Day, et al. (1973) and Subrah-

manyam, et al. (1976), and analysis of its burrowing habits by Allen and Curran (1974).

Teal (1959) found the species active on Georgia marshes when the tide was high or the sky cloudy. When the marsh was exposed, the crabs were in burrows, usually near the top, in air or water. Respiration rates were higher in water than in air. Teal and Carey (1967) additionally found that *S. reticulatum* can regulate its metabolism down to 6% atmosphere; however, marsh crabs do not encounter low oxygen conditions in air, only in burrows in water. There, during periods of submergence, the respiration rate may decline with decreasing oxygen pressure, and below critical pressures the crabs must convert metabolism to fermentation. Lactic acid is probably formed from glycogen, to be oxidized at the next period of emergence. Gray (1957) found the gill area of *S. reticulatum* to be relatively low as compared with other species living in a similar habitat (*Uca pugnax* and *minax*). He found *S. reticulatum* to be more robust but less active than

the close relative *S. cinereum*.

Humes (1941) described a harpacticoid copepod (*Cancrincola plumipes*) from the gill chambers of this crab.

## Superfamily Ocypodoidea

### Family Ocypodidae

Palp of external maxillipeds coarse, articulating at or near anteroexternal angle of merus; exognath generally slender and often somewhat concealed. Front usually of moderate width, and often a somewhat deflexed narrow lobe. Orbits occupying entire anterior border of carapace outside front, and with their outer wall often defective. Buccal cavity usually large and somewhat narrowed anteriorly, external maxillipeds often, but not always, completely closing it. Abdomen of male narrow. Male openings sternal. (Rathbun 1918b.)

### Subfamily Ocypodinae

#### Key to Genera and Species

(Modified in part after Felder 1973)

1. Stout eyestalk with conspicuous, enlarged, club-shaped cornea; chelipeds of both sexes well developed and somewhat unequal . . . *Ocypode quadrata*  
Slender eyestalk with cornea not conspicuously enlarged; chelipeds of male very unequal, of female equal and quite small. . . . [*Uca*; for males, include cheliped characters in rest of key; for females, ignore them] . . . 2
2. Major palm with oblique tuberculate ridge on inner surface extending from lower margin to carpal cavity (males); merus of last legs with upper margin curved; 75 or fewer spoon-tipped hairs on inner meral surface of second maxilliped. . . . . 3  
Major palm without oblique tuberculate ridge on inner surface extending from lower margin to carpal cavity (males); merus of last legs with upper margin straight; more than 100 spoon-tipped hairs on inner meral surface of second maxilliped. . . . . *U. pugilator*
3. Joints of major cheliped bordered by red patches, especially near condyles of carpus and merus (fresh male specimens); merus of second and third walking legs with sparse ventral rows of stiff hairs or bristles, as long as on carpus and propodus; 0–20 (usually 0–15) spoon-tipped hairs on inner meral surface of second maxilliped . . . . . *U. minax*  
Joints of major cheliped bordered by yellow or yellow-brown color (fresh male specimens); merus of second and third walking legs ventrally with patch, row, or paired rows of dense velvety pubescence as well as sparse rows of stiff hairs on ventral edge (mainly distal half); 0–75, (usually 15–60) spoon-tipped hairs on inner meral surface of second maxilliped . . . . . *U. pugnax*

Genus *Ocypode* Weber 1795

*Ocypode quadrata* (Fabricius)

(Ghost crab; sand crab)

Rathbun 1918b:366.—Monod 1956:390.—China  
1966:256.

Fig. 375

*Cancer quadratus* Fabricius 1787:315.

*Ocytode albicans*.—Rathbun 1918b:367, pls. 127–128.—Hay and Shore 1918:450, pl. 37, fig. 1.—Guinot-Dumortier 1960:515, figs. 16a-c.

*Ocytode quadrata*.—Holthuis 1959:259.—Williams 1965:225, fig. 208.—Chace and Hobbs 1969:204, figs. 68–69.—Coelho and Ramos 1972:198.—Felder 1973:82, pl. 12, figs. 5, 8.—Powers 1977:140.

**Recognition characters.**—Carapace quadrilateral, convex above from front to back, sides nearly vertical; dorsal region finely granulate on middle and posterior parts, coarsely granulate toward sides, center of carapace with well-marked H-shaped depression. Front and side margins raised, beaded, or serrulate, lateral margin continued into prominent, acute angle at outer corner of orbit; similar but lower ridge extending upward and forward from base of third walking leg. Orbits large and open, extending all along anterior margin on either side of narrow front, both upper and lower margins crested and dentate. Eystalks large, club-shaped, cornea covering over half of distal article. Front narrow, deflexed; antennules and antennae much reduced, flagellum of antennules hidden beneath front.

Chelipeds in both sexes, and in young, unequal, well developed, rough; merus serrulate above, toothed on lower margins; carpus with sharp spines at inner angle; hands coarsely scabrotuberculate, margins of palm and fingers dentate, fingers pointed. Large hand with vertical stridulating ridge of tubercles on inner surface near base of dactyl that plays against smooth, distal, anteroventral ridge of ischium. Walking legs almost smooth, fringed with long, stiff, yellow hair, third pair longest, fourth shortest; meri of first 3 pairs broadened; propodi of these legs with longitudinal brushes of hair on anterior surface; dactyls of all legs fluted, depressions hairy. A hair-fringed breathing slit on ventral surface between basal articles of third and fourth walking legs.

**Measurements in mm.**—Carapace: male, length 44, width 50.

**Color.**—Gray, pepper-and-salt, grayish white, pale yellow, straw color, or yellowish white imitating color of beaches; sometimes light amber and often iridescent; yellow markings below and on legs; young mottled gray and brown (various authors). A brown phase was reported from black beaches of Dominica (Chace and Hobbs 1969). Cowles (1908) noticed that the ghost crab exhibits color changes. The crabs are generally dark in subdued light and in direct sunlight if temperature is not above 35°C. Above 35°C, the crabs are light colored regardless of light intensity. In absence of light, the crabs are

light colored regardless of temperature.

**Habitat.**—This species, the most terrestrial of the decapod crustaceans in the region, lives in abundance along the ocean beaches and sometimes on harbor beaches. The crabs construct burrows 0.6 to 1.2 m (2 to 4 ft) in depth from near the high-tide line to distances up to ¼ mi from the ocean.

**Type-locality.**—Jamaica.

**Known range.**—Block Island, R. I., to Santa Catarina, Brazil (megalopae have been taken at Woods Hole); Bermuda; Fernando de Noronha.

**Remarks.**—Perhaps because of their mode of life, ghost crabs have left a fragmentary fossil record. Rathbun (1935) recorded *O. quadrata* questionably from the Pleistocene of Florida, but Glaessner (1969) listed it only by genus. Hayasaka (1935) compared the “sandstone pipes” commonly found in certain Tertiary sandstones of Formosa to plaster casts of burrows made by the Formosan *O. ceratophthalma* and found them to be much alike. Burrows of the modern Formosan and eastern North America species are similar.

Habitats of *O. quadrata* have been treated in a number of scholarly and popular works, but the serious student is referred especially to Cowles (1908), Milne and Milne (1946), and Haley (1969, 1972). A popular account of some value, except for the concluding conjectures, was given by Phillips (1940). Only a brief summary from various authors can be given here.

Mating and spawning seasons of the species are correlated with temperature, hence vary in length to some degree with latitude. Early accounts state that spawning in the Carolinas appears to extend from April to July (Coues 1871), agreeing with that

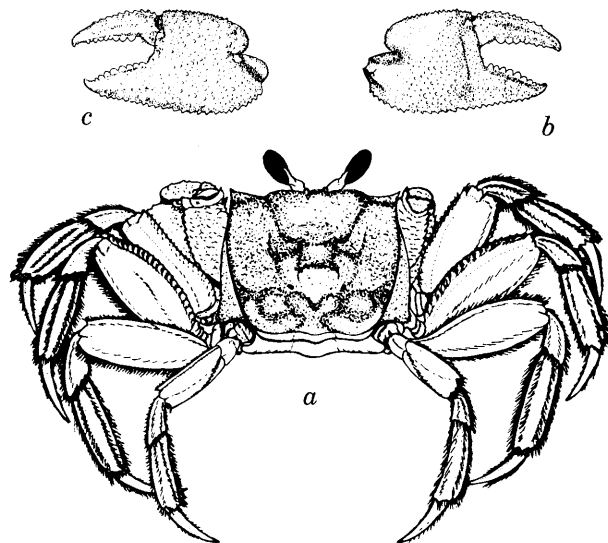


Fig. 375. *Ocytode quadrata* (Fabricius). a, Female in dorsal view, reduced (from Gmitter and Wotton 1953); major chela of male, b, outer view, c, inner view, reduced (from Crane 1941).



seen in New Jersey (Milne and Milne 1946) and at Tortugas, Fla. (Cowles 1908), but Haley (1972) stated that the crabs are inactive in Texas for only about three months a year when temperature is below 16°C. Mated females with ripening eggs found even before the active spring period indicate initiation of oogenesis in winter and retention of sperm during winter. Copulation probably occurs throughout the year, but in two peaks in spring and summer. Hughes (1973) stated that although mated pairs were occasionally dug from burrows in Costa Rica, burrows are not essential for mating nor do all matings occur at night (Henning and Klaassen 1973). Males in captivity usually rush females on sight; when mating occurs the pair have ventral sides juxtaposed for about 25 min, the male in vertical position with eyes pointed up and the passive female with eyes mostly retracted, a contrast to mating of most hard shell brachyurans in which the female is uppermost. Males in Texas enter puberty at about 24 mm carapace width (Haley 1969); first pleopods show puberty-related changes (also Hartnoll 1974), having grown at a constantly changing rate until the animal reaches about 25 mm width after which growth is isometric. Females maintain isometric growth except for a distinct change in the abdomen in which the fifth segment becomes widest; they enter puberty at 26 mm carapace width and are incapable of copulation below that size.

Ovigerous females differ in behavior from other individuals in that they wade in water more freely, run along on the bottom, and at intervals when the water is quiet open the abdomen out, flip upside down, extend the mouthparts, rotate the legs, and, thus, force water through the egg mass. Such females will run quickly to water when disturbed (Milne and Milne 1946).

From ovigerous females collected in evening or at night on the beach near the waterline, Diaz and Costlow (1972) obtained eggs that hatched and developed through larval stages. The eggs usually hatched on the night of collection, frequently on the way to the laboratory. Five zoeal stages were identified and described from rearing in water of 35‰ salinity at 25°C in a photoperiod of 12 light–12 dark h. The megalopa appeared in a minimum of 34 days following hatching. Prezoeae observed in a few broods lived only a few hours and did not molt to succeeding stages. There was high mortality in zoeal stages IV and V; less than 10% of all reared larvae reached the megalopa. The megalopa was first described by Say (1817) as *Monolepis inermis*. Smith (1873a, 1873b, 1880b) recognized the true status of the form and pointed out that though it is carried as far north as Vineyard Sound by the

Gulf Stream, that area is apparently too cold to support an adult population.

Haley (1972) outlined the life history, assuming that in a development time of 60 days the first crab stage should appear on the beach in July and late October (two Texas broods). A May brood could attain puberty in March of the following year with an instar period of 35 days for each of 7 molts. An August brood could attain puberty by the following July at the same rate. These two groups could thus represent the influx of new females in spring and summer. A female spawned in May develops to first crab in June and matures by April of the following year; in August these females make up the younger part of the spawning postpubertal females, the older ones spawning a second time after spring ovulation. By April of the third year these are the older part of the spawning females. They may or may not ovulate that summer and probably do not survive the following winter. A summer brood that reaches 7 mm carapace width in October overwinters as juveniles, mates in July, and spawns in August. These comprise the younger postpubertal females in spring and are the older postpubertal females spawning a second time that summer. A female probably ovulates no more than four times during a life span of nearly three years.

Burrows of *O. quadrata* show conspicuous zonation. The young crabs are found close to shore. Burrows of the young are near the water, extend to water level and are covered by high tides for a time, whereas older crabs burrow farther from water; the latter seldom are deep enough to reach water level. Hill and Hunter (1973) and Frey and Mayou (1970, 1971) observed that variation in shape, diameter, length, density and orientation of burrows could be used to differentiate subenvironments of beach-foredune areas. Burrows are of three general types: (1) a short vertical burrow made by young crabs, (2) a burrow sloped downward at about 45° away from the shoreline, often with branches, one of which may extend upward almost to the surface (or open to form a U-shaped tube), and (3) burrows higher on the beach or in dunes, much like the second type but without the vertical side branch. In fall in New Jersey the burrows have been found farther from water and far deeper than any studied earlier in the year, and it is presumed that various sizes of crabs hibernate in these. Hill and Hunter (1973) pointed out that burrows have different form in different latitudes.

Fisher and Tevesz (1979) observed that carapace width is approximately equal to burrow diameter. Adults along North Carolina outer banks were found to be more evenly spaced than would be expected under a Poisson distribution, but juveniles

had clumped distribution. The authors felt that the difference may reflect territorial behavior, adults defending larger areas of the stable beach environment than juveniles limited to a small area near the swash zone. The latter are poorer burrowers, and more subject to predation and desiccation than adults. Beach disturbances reduce adult to juvenile ratios and abundance of adult crabs.

Burrow making is primarily an occupation of daylight hours. The crabs cease feeding on the wet beach toward dawn. Those feeding on a fish carcass often burrow within an inch or two of the carcass. Young crabs near water make new burrows, older ones range inland and build burrows or occupy old holes, renovation perhaps being more common than new construction (Hill and Hunter 1973). Sand is brought to the mouth of the burrow and dropped or spread near the opening in a fan-shaped area. Toward noon, openings to burrows are plugged with damp sand, thus concealing the burrow. Toward evening, the crabs begin to emerge again, and by 10 p.m. the whole population is usually on the beach.

Ghost crabs traditionally have been considered as scavengers and predators (or cannibals) that tend to feed most actively along the drift line, looking for beached fish or refuse and small bits of food buried in the top layer of sand. Wolcott (1978), however, showed that scavenged material accounted for less than 10% of their food on North Carolina beaches. More than 90% of the diet was live prey, the mole crab, *Emerita talpoida*, and coquina clam, *Donax variabilis*, in equal weights making up most of this. Because of higher caloric content, the mole crab provides about 60% of the energy, the clam only 25%. Estimates indicated that the crabs consumed most of the production of the two prey species. The ghost crabs are the top carnivores on the beaches, having little competition. Fales (1976) also reported their feeding on mole crabs, and Sprunt (1948) considered them to be a major predator on tern chicks at Dry Tortugas, Fla.

The crabs go into the water at intervals to moisten the gills, retaining a small amount of water in the branchial chamber (Edney 1960), and the young do this more frequently than adults. When undisturbed, individuals do not actually enter water but will stop a few inches from the waterline with one side presented to the water, the legs of the other side anchored in sand, and wait for a wave to wash over them, after which they return to the higher parts of the beach. If disturbed, the crabs will run into the water, then leave it as soon as possible. These crabs do not swim but walk on the bottom or are rolled about by waves; they can survive for a limited time if forced to remain submerged.

The crabs also take up moisture from damp substrate through setae at the base of the second and third walking legs which conduct it into the branchial chambers (Bliss 1963). *Ocypode quadrata* will die in 20 h in an atmosphere of 30°C at 78% relative humidity if water lost by transpiration is not replaced (Bliss 1968).

Flemister and Flemister (1951) and Flemister (1958) showed that when *O. quadrata* is confined in water, oxygen consumption is elevated, but elevated least when chloride ion concentration of the water equals that of the blood. Lower or higher ion concentration of the water raises the respiration rate. They demonstrated that the animals normally have blood hypotonic to sea water. In sea water containing less than 120 or more than 160 millimoles of chloride per liter, the internal concentration is not maintained but tends to rise or fall depending on which end of this range the animal experiences. The antennal gland, aided by the gill membranes, functions in regulation of internal chloride ion concentration. Gifford (1962) found that *O. quadrata* can regulate major ions in its body fluid in all salinities tested (14–197‰ seawater) at temperatures between 12 and 25°C but that this ability is lowered above that temperature range, especially in high salinity.

The general relationship of habitat to oxygen consumption and general activity among certain decapods has been a subject of study of Ayers (1938), Pearse (1929), Vernberg (1956), and Gray (1957) in the Beaufort, N. C., area *Ocypode quadrata* was of prime interest because of its terrestrial adaptation combined with great activity. Of all the crabs studied there, the ghost crab possesses the highest rate of oxygen consumption both for the whole animal and for gill tissue alone. This is more striking when it is emphasized that *O. quadrata* has a reduced number of gills (though it has accessory respiratory tissues in the gill cavity) and the gill area per gram of weight in this species is by far the lowest among 16 species studied in near-shore, intertidal, and above-tide zones. However, air contains proportionately more oxygen than does water (Bliss 1968).

The eyes of *O. quadrata* are so large and prominent that it seems as if the crab can see exceptionally well. Experiment has shown that the eyes are primarily sensitive to large changes in intensity of light. The crabs do not tend to avoid strong light, but try to hide if lights are suddenly shut off or if an object on the beach is suddenly moved (Wolcott 1978). The eyes apparently aid in the search for food, but actual detection of food is by taste or smell.

Locomotion is accomplished by all eight walking

legs. Usually the crabs walk sideways or obliquely. If hotly pursued, they will run in another manner, holding the last pair of legs clear of the ground. Usually the crabs walk or run toward the side with the small chela, but they can also walk forward, or sometimes approach food by walking slowly backward.

When two crabs meet, they raise themselves on their legs, facing each other, chelipeds held apart with the tips pointing downward or downward and forward (Schöne 1968). After standing for a time, the encounter may end with one of the pair lowering or flattening itself; this sometimes happens when the "winner" is in a more elevated position. Fights are usually formalized; wild fights are rarely observed.

*Ocypode quadrata* produces three sounds: bubbling, rapping and rasping. These were detected in the burrow in early morning after the night's foraging (Horch and Salmon 1964, Salmon and Horch 1972). Rapping is done by animals when disturbed alone; rasping [stridulation] has been detected after one crab was thrust into the burrow of another; bubbling is produced by lone animals in burrows. The species responds to both airborne and substrate-borne sound through a single receptor (Barth's myochordotonal organ), but is most sensitive to substrate vibration.

### Genus *Uca* Leach 1814

(Fiddler crabs or calling crabs)

Rathbun 1918b:374.—Monod 1956:399.—Crane 1975:15.

Differing from all other brachyuran genera in enormous size of male major cheliped without stridulating ridge on ischium; minor cheliped of male and both chelipeds of female minute.

In her exhaustive monograph on fiddler crabs of the world, Crane (1975) distilled years of study into a compendium of information on systematics, zoogeography, ecology, functional morphology, behavior, phylogeny, and evolution of the group. She recognized 79 species, clustering them into a number of subgenera and subdividing many into subspecies, but while this monograph was in press for years Bott (1973a, b) published two short papers on *Uca* that produced a profound effect on taxonomy of the group. His first paper created a nomenclatural problem (questioning the type-species of *Uca*) still unresolved by the Commission on Zoological Nomenclature, and the second, by erection of 10 new genera, preoccupied most of Crane's subgenera. Von Hagen (1976, 1980) recognized that

attempts to follow either Bott's new set of genera or Crane's subgeneric system might result in chaos. Since evolutionary patterns in the group are only beginning to be understood, he recommended that workers "adhere to the familiar use of plain *Uca*" until expert opinion resolves the systematic problems. I gladly follow his simplification. The three species treated here are so universally recognized in the biological literature as *Uca minax* (LeConte 1855), *U. pugilator* (Bosc 1801 or 1802), and *U. pugnax* (Smith 1870) that no confusion should result from ignoring the rules of nomenclature in this case.

The following summary and species accounts are intended only as a convenient abstract of Crane's work, with a few notes on other papers. Any careful worker should refer to her masterful treatment. Moreover, fiddler crabs have been the subjects of a multitude of studies on general ecology, thermal relations, molting, reproduction, biochemistry and physiology, osmoregulation, radiation sensitivity, response to pollution, circadian activity, color change, etc., that are beyond the scope of this brief account. Much of the literature is listed by Powers (1977).

Much biological information on the three *Uca* species can be grouped as in Williams and Duke (1979), and I selectively quote or paraphrase their account here. *Uca* species live in an environmental borderland along the edges of estuaries, habitually staying away from the sea proper. The crabs are behaviorally terrestrial but physiologically aquatic (Herrnkind 1968b), orienting themselves within their narrow environment on the strand between water and land by means of visual cues, and able to return to it even if displaced several meters into either open water or to land beyond the beach. They exhibit endogenous rhythms in activity and color changes that are associated with local tidal schedule as well as diel cycles (Barnwell 1968). All are burrowers, some retreating into more or less impermanent burrows during periods of inundation and emerging during low water stands. Of species discussed here, *U. minax*, the largest, lives on muddy banks of marsh creeks and among *Spartina*, *Salicornia*, and freshwater herbs in marshes threaded by brackish to freshwater streams under tidal influence (Miller and Maurer 1973). *Uca pugnax*, medium sized, frequents salt marshes and sheltered shores on mud to sandy mud substrate. *Uca pugilator*, smallest of the three, lives on sheltered shores with sandy to sand-mud substrates more or less free from vegetation and often mixed with scattered shells and stones but with muddy surfaces for feeding nearby. The food of all consists largely of minute particulate matter, algae, bacteria, detritus, etc., from the surface of the substrate which is

scraped up by the small chelipeds and passed to the mouth for separation of accepted organic and rejected inorganic components by various mouthparts, the rejectamenta being left behind as trails of rounded pellets (Schwartz and Safir 1915; Miller 1961), but feeding underwater has been observed for *U. pugnax* and *minax*, and the latter will kill and consume either of the other two species (Teal 1958). Males, having only one small chela, feed twice as long as females, animals of each sex otherwise having equal metabolic responses (Valiela, et al. 1974).

Life histories of the three species are similar. Crane (1975) discussed courtship and mating in great detail indicating that males attract females by waving display and sound production, i.e., drumming the major hand against the substrate either on the surface or in burrows (Salmon and Horch 1972), and that copulation in the hard condition (Hartnoll 1969) takes place in the burrow of the male, or, in *U. pugilator* and *pugnax*, on the surface at night, and even underwater in captivity (Herrnkind 1968a). Apparently the huge claw of males is reserved for display (threat, attraction, etc.), not for handling females. Both sexes show a periodicity in gametogenesis (Young 1974). Courtship and mating are influenced by temperature, with some evidence of latitudinal adaptation (Crane 1975). Near New York, for example, *U. minax* fed and moved above ground during low tide in mid-June but did not display when air temperature during the preceding night fell below 21°C even though daytime temperature then regularly reached above 29°C. On Cape Cod in early June, several *U. pugilator* waved at low intensities on a sunny day when air temperature was 19°C and the previous nighttime low had been 10°C. Maximum breeding activity for that population was in mid-June followed by notably less activity in July even though temperature was higher then. Never was the activity on Cape Cod equivalent to that seen in more southern populations. Spawning following mating, therefore, is most extended at low latitudes.

### *Uca minax* (LeConte)

(Red-jointed fiddler; brackish water fiddler)

Fig. 377a

*Gelasimus minax* Le Conte 1855:403.

*Uca minax*.—Rathbun 1918b:389, pl. 137.—Hay and Shore 1918:451, pl. 37, fig. 3.—Williams 1965:227, figs. 209A, 210B.—Felder 1973:85, pl. 12, fig. 12.—Powers 1977:143.

*Uca (Minuca) minax*.—Crane 1975:176, pl. 25, figs. E-H; text-figs. 67D, 81K, 100.

*Recognition characters*.—Carapace subquadrilateral, approximately 1.3 times as wide as long, widest behind outer orbital angles, convex in both directions, finely granulate, except somewhat coarsely so near anterolateral angles; shallow H-shaped depression near center of carapace, and horizontal depression behind orbit. Lateral margins nearly vertical; anterolateral angles slightly produced, continued backward and inward as low, well-defined ridge, and above orbits as low revolute ridge. Front greater than  $\frac{1}{3}$  frontoorbital width, broadly convex. Orbits large, open, eyebrow 5 times as wide as deep, lower margin dentate eyestalks long, slender. Antennules and antennae small, flagellum of antennules hardly visible. Merus of second maxilliped with usually 0–15 exceedingly slender spoon-shaped hairs on inner surface of merus.

Chelipeds in male very unequal, in female equal and of small size. Large chela with upper surface of merus sparingly granulate, inner edge denticulate, outer edge granulate; carpus tuberculate. Upper and outer face of large hand in male with tubercles diminishing to granules on lower face, ridged above; inner surface with oblique row of granules from lower margin to carpal cavity, short curved row leading down from ridge on upper margin, area between ridges tuberculate and with tuberculate ridge running along fixed finger from tip to internal distal border of palm. Fingers strong, widely gaping, cutting edges tuberculate; fixed finger with few larger teeth at irregular intervals, truncate at tip; dactyl longer and curving downward past tip of opposed finger. Walking legs strong, sparsely hairy, meri slightly wrinkled.

*Measurements in mm.*—Carapace: male, length 25, width 38; female, length 22, width 30.

*Color*.—Chestnut brown, becoming gray in front; chelipeds with red spots at articulations; hands ivory white; legs olive or grayish brown. Crane (1975) gave color as: lightest color of carapace grayish white to dull yellowish white, frontal and eyebrow regions sometimes dull orange; middle of cardiac region sometimes with red spot, major cheliped grayish orange to dull yellowish orange except narrow edging of red usually near articulations of articles, especially between carpus and hand.

*Habitat*.—This species occurs in marshes at some distance from water of high salinity. It is usually found on muddy substrates where flooding with freshwater occurs (Teal 1958), or on mud and sand substrate (Gray 1942), is often found in association with marsh phanerogams (Kerwin 1971), and has also been observed at the edge of low woodlands (Teal 1959). Whiting and Morshiri (1974) found that *U. minax* prefers substrates with high organic content, hence high energy value, but low oxygen

content, which explains the species' adaptation to withstanding low oxygen tensions. Experiments indicated that at high population densities the crabs reduce intraspecific encounters and competition by burrowing and subsequently covering their burrows. The crabs dig 2–5 cm diameter burrows (Allen and Curran 1974) to various depths, but the maximum is about 60 cm (2 ft); the openings are often considerably above high-tide level, and the bottoms reach to ground-water level. The burrows are only wide enough to accommodate the occupant. Usually only one crab lives in a burrow, though at times two females may occupy a single burrow, and burrows of females sometimes communicate with those of males, the connection being made by the female (Gray 1942). Young crabs are sometimes found in the burrows of females, never in those of males.

*Type-locality*.—Beesleys Point, N. J.

*Known range*.—Buzzards Bay (Wareham and southwestern Cape Cod), Mass., to northeast Florida, and from the area of Yankeetown, northwest Fla., to Louisiana, and on to Matagorda Bay, Tex., if Von Hagen's (1976) analysis treating *U. rapax longisignalis* Salmon and Atsides 1968 as a synonym is accepted. Heard (1977) agreed with the latter authors that the Gulf coast form is distinct.

*Remarks*.—The red-jointed fiddler has lived in freshwater for more than three weeks under experimental conditions (Teal 1958), and when offered choice of fresh or seawater chose freshwater. In choice of substrate experiments (mud or sand) it chose mud either above or underwater, but dug few burrows when competitive *Uca* species were present, an observation not confirmed by Whiting and Moshiri (1974).

Miller (1961) compared the mouthparts of *U. minax* to those of the more specialized Carolinian *Ucas*. He found that it prefers to feed in low areas of the *Spartina* marshes well up in estuaries where mud is fluid.

Teal (1959) found *U. minax* to have the lowest rate of oxygen consumption among a number of marsh crab species (*U. pugnax* and *pugilator*, *Sesarma cinereum* and *reticulatum*, *Eurytium limosum*, and *Panopeus herbstii*). He (also Vernberg 1959) showed that this species in all probability does not acclimate respiratory rate to change in temperature. Temperatures experienced in nature had no effect on survival (Teal 1958), but below 20°C the crabs are inactive (Gray 1942; Teal 1959). Gray found that *U. minax* overwinters in burrows just below the frost line. Gill area/g body weight in *U. minax* is lowest among the U. S. east coast *Uca* species (Gray 1957).

Sexual display of males is discussed by Crane (1975). In display, the males rear back on the last two or three walking legs so that the carapace is vertical. The major cheliped is extended diagonally up to about half of maximum extension. This position may be held for minutes, then the cheliped may be fully extended swiftly and smoothly, and finally brought back to the half-extended position in a series of jerks. This movement may be repeated about four times rather slowly. The small cheliped is moved asynchronously in similar motions.

Spawning occurs in summer. In Chesapeake Bay, ovigerous females are most abundant in July; none are known to occur before July or after the first week in September, and about the same length of breeding season is found in the Beaufort, N. C., area. Gray (1942) presented evidence for two spawnings per season. The act of egg laying has not been studied in minute detail, but Gray (1942) observed egg deposition among captive females held in aquaria. Completion of spawning was usually accomplished in a day but sometimes took as long as three days, depending on temperature. Hyman (1920) and others have dug ovigerous females from burrows. Freshly laid eggs were yellow or pale orange in color, but the color changed with development through purplish-black to an ashy gray color, at which stage the larvae emerged (see also Hyman 1920). Estimated egg counts on a number of ovigerous females ranged from 10,000 to 300,000, depending on size of the individual. Newly laid eggs measured about 0.09 mm in diameter but increased to about 0.27 mm at the time of hatching. Both Hyman (1920) and Gray (1942) observed that the females entered water in order to let the eggs hatch. Time of hatching extended from about 7:00 to 10:00 p.m., and the hatching of an egg mass required slightly less than an hour.

The first zoeal stage of *U. minax* is the smallest among these three species of *Uca*. (Larval stages are discussed in the remarks on *U. pugilator*). Sandifer (1975) found larvae of what was presumed to be this species mostly far upstream in the York River, Va., in an area inhabited almost exclusively by *U. minax*. It seemed to him unlikely that these early larvae would develop in such low salinity, but that they would be swept downstream to develop in marsh habitats (zoea I was abundant at the surface, II–IV were somewhat more abundant near bottom, V and the megalopa were abundant near bottom (bearing out Hyman's [1920] findings near Beaufort, N. C.) where the later stages concentrated in bottom strata would be brought back upstream by retention and migration.

*Uca pugilator* (Bosc [1802])

(Sand fiddler)

Figs. 376, 377c

*Ocypoda pugilator* Bosc [1802]:197.*Uca pugilator*.—Rathbun 1918b:400, pl. 141; pl. 160, fig. 2.—Hay and Shore 1918:452, pl. 37, fig. 2.—Williams 1965:232, figs. 209C, D; 211.—Felder 1973:83, 85).—Powers 1977:145.*Uca (Celuca) pugilator*.—Crane 1975:223, pl. 29, figs. E-H; text figs. 37K, 69F, 101.

*Recognition characters*.—Carapace subquadrilateral, up to 1.5 times as wide as long, widest behind outer orbital angles, very convex, smooth; shallow H-shaped depression near center of carapace and narrow, flattened shelf behind orbit. Lateral margin strongly curved outward behind orbit, continued backward and inward as low, well-defined ridge across entire fronto-orbital width. Front more than  $\frac{1}{3}$  of fronto-orbital width, broadly rounded below. Orbits large, open, upper margin slightly sinuous, lower margin dentate. Eyestalks long, slender. Antennule and antenna small. Merus of second maxillipeds with 150 to 200 spoon-tipped hairs arranged in about 10 rows on inner side.

Chelipeds in male very unequal, in females equal and small. Merus of large chela with short, granulated, rugose lines above and isolated dark hairs proximally, nearly smooth outside, lower margins granulate; merus of small chelipeds with scattered hairs. Carpus and outer surface of large hand with tubercles diminishing to granules on lower face of hand. Inner surface of palm without oblique tuberculate ridge as in *U. minax* and *U. pugnax*, but with tuberculate ridge running along fixed finger from tip proximally on internal distal border; surface granulate, granules coarser on thickest part of palm. Fingers strong, gaping; fixed finger with largest tubercles just behind middle and near truncate tip, inferior surface convex; dactyl evenly

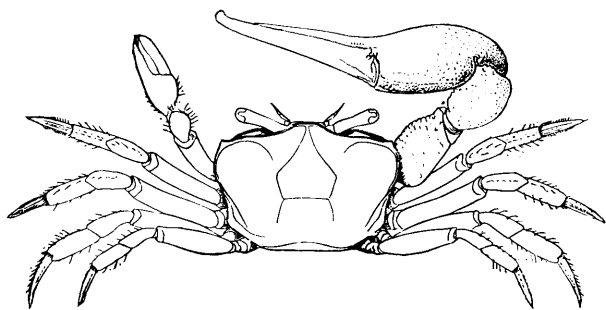


Fig. 376. *Uca pugilator* (Bosc). Male in dorsal view, about natural size (from Rathbun 1884).

denticulate and with irregularly placed large tubercles, strongly curving downward past tip of opposed finger. Walking legs narrow, last pair with upper surface of merus straight.

*Measurements in mm.*—Carapace: male, length 17, width 26; female, length 14, width 19.

*Color*.—Display whitening conspicuously present but fleeting in both sexes, usually yellowish white. Displaying males with fleeting purplish violet patch on cardiac region, sometimes pink and confined to gastric region in southern populations; major cheliped buff to yellowish white, base of chela often pale orange. Carapace in non-displaying phases variously marked in semi-reticular patterns of brown, or completely brown with small gold or light brown spots. Eyestalks buff or grayish white. Third maxillipeds white. Minor cheliped with hand white; walking legs white but anterior side of merus of first sometimes purplish brown or reddish purple (Crane 1975).

*Habitat*.—This species occurs in countless numbers on sandy and muddy beaches bordering marshes and along banks of tidal creeks. The crabs also occur farther from water in sandy situations of the *Salicornia-Distichlis* marsh and at times in *Juncus* marsh where the soil is sandy (Teal 1958). They burrow much as does *U. pugnax*, and populations of the two are often intermingled (Pearse 1914), though *U. pugilator* prefers sandier situations (Hyman 1922). Dembowski (1926) found that choice of a place to burrow depends upon many factors, among them phototaxis and thigmotaxis. Burrows may have any shape but are unbranched and usually dug at an angle to the surface of the ground, length of the burrow depending in part on amount of moisture in the ground. Digging by males is done with legs on the side opposite the large claw. The crabs plug the opening as soon as they feel the water level rising in the burrow with the tide, and do this by pulling in the edges of the burrows and by ramming sand up from below.

*Type-locality*.—"Caroline."

*Known range*.—Cape Cod, Mass.; (rare on the north shore) southward around the tip of peninsular Florida to near Pensacola (Heard 1982); single occurrences are on record from Old Providence Island, the Bahamas, and Santo Domingo (Crane 1975). Heard (1977, 1982) stated that another species whose range overlaps *U. pugilator*, *U. panacea* Novak and Salmon 1974, is distributed from west Florida to Texas.

*Remarks*.—Ovigerous female *U. pugilator* have been reported from early July to mid-August on Long Island (Schwartz and Safir 1915), March to midsummer in Virginia (Williams 1965), April to

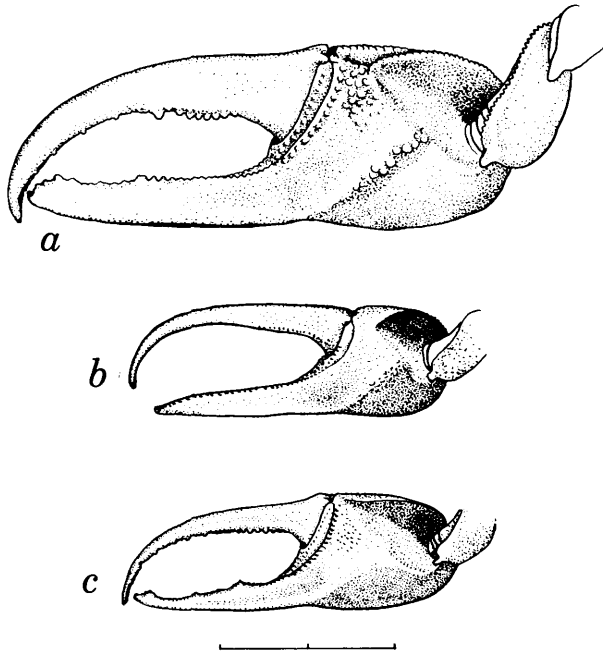


Fig. 377. Major chela of male, view of inner side: *a*, *Uca minax* (LeConte); *b*, *U. pugnax* (Smith); *c*, *U. pugilator* (Bosc); 1 cm indicated.

October near Miami, Fla. (Herrnkind 1968a), and Hedgpeth (1950) reported zoeae taken in a plankton net on May 20 at Long Lake, Tex. Females enter the water to let eggs hatch.

Representative of all *Uca* species discussed here, *U. pugilator* has five zoeal stages and a megalopa, each major subdivision of larval life lasting 3–4 weeks for a total development time of 6–8 weeks (Hyman 1920; Herrnkind 1968a). Gray (1942) described a transitory prezoal stage. The larvae are predatory, capturing prey (*Artemia* nauplii, etc.) on or between the telson spines by violent flapping of the abdomen, whereupon flexure of the body brings food to the mouth. The megalopa swims at first but gradually adopts a benthic existence. Zoeae of the three species have not been distinguished in plankton, but Sandifer (1973d) found zoeae of *Uca* sp. to be the most commonly collected and abundant decapod larvae in lower Chesapeake Bay, concentrations of  $> 100/m$  not being unusual. The zoeae were taken over a salinity range of 0.06 to 32.34‰ at temperatures of 19.4° to 30.8°C, but most numerous in the York and Pamunkey rivers tributary to the Bay, mainly at salinities  $< 5‰$  at 26° to 30°C. Larvae first appeared in June, peaked in July and disappeared in October. All of the zoeal stages were collected but stage I was most numerous, predominantly at the surface. Stage V was more numerous in bottom than in surface samples. Hyman (1920, 1922) found the first two zoeal stages most abundant at the surface, the third probably at in-

termediate depths, and the fourth and fifth zoeae usually on the bottom. Sandifer (1973d) found that the work of others (reviewed) reflected his findings with allowance for latitudinal variation, although workers in the Beaufort, N. C., area found larvae at higher salinities (Pinschmidt 1963, Dudley and Judy 1971). DeCoursey (1976) demonstrated that stage I zoeae have a distinct tidal rhythm of vertical movement.

Christy (1978) proposed that mating, incubation, hatching, and larval development in *U. pugilator* are so synchronized that male display reaches peaks at spring tides, and mating occurs in male burrows where females remain during the entire incubation period of about two weeks, emerging to release hatching larvae at neap tides. Ensuing larval development is so timed that the megalopae will be ready to metamorphose when they are swept into the estuary on spring tides. There are thus two breeding populations allied with new and full moon tidal phases. Non-breeding males and females, or displaying males, constitute the feeding droves that emerge at each low tide. DeCoursey (1979) extended this concept of periodicity by demonstrating that clutches of 1,500 to 94,000 eggs of *U. pugilator*, *pugnax* and *minax* hatch over the course of about two hours (ca. 104, 108, 104 min. respectively) in phase with time of nocturnal high tide. Females aid hatching by vigorous abdominal contractions. Ovigerous females isolated in laboratory aquaria for several days release zoeae synchronously with those in the wild. DeCoursey thought that such timing may minimize exposure of females to predation at time of releasing their young as well as placing early zoeae in favorable tidal currents.

The first two crab stages following metamorphosis are relatively weak and adapted to clinging, but following them the crab starts to assume the familiar structural and behavioral characteristics of the species, burrowing during high tides first in the wet intertidal area and later along the strand near or above the high-tide line (Herrnkind 1972). From that refuge the population emerges between high tides to carry on its activities in droves on the exposed intertidal surfaces. Rhythmic activities in such an environment follow naturally, but their behavioral complexities lie mainly beyond the purview of this paper (see Crane 1975). An example of internal rhythms is that of blood glucose level tied to the diurnal cycle, high in late afternoon, low in early morning. Example levels measured in mg % are: 5:30 a.m., 7.86; 1:30 p.m., 8.06; 5:30 p.m., 15.41 (Dean and Vernberg 1965).

Testing salinity tolerance, Teal (1958) found that 50% of *U. pugilator* died after 3.5 days in freshwa-

ter, but over 50% survived more than 10 days in seawater of 7‰ salinity. Given a choice of freshwater or seawater of 30‰ salinity, the crabs chose seawater but preferences of females were less strong than males, as was true of *U. pugnax*. He concluded that this species lies between *U. minax* and *U. pugnax* in its tolerance of freshwater and can survive soakings of the *Salicornia* marsh with rain between spring tides. Regulation of water and salt enables both *U. pugilator* and *pugnax* to maintain serum hypotonic to external media in 100% and 175% seawater under experimental conditions (Green, et al. 1959). Gill fluids in such crabs are more concentrated than the sera, and stomach fluid and urine are more concentrated than the external medium. Chief sites of water and electrolyte entrance are the stomach and gills. Chief sites of regulation are the antennary glands and gills, with some regulation by the stomach and probably the mid-gut gland.

Teal (1958) also concluded that *U. pugilator* cannot feed properly where sand is absent because in choice of substrate experiments (sand or mud above or underwater) it burrowed in sand above water and when restricted to an unfavorable low muddy marsh did not survive. In company of either of the other species, *U. pugilator* reduced its burrows in sand above water by 50%. Miller (1961) considered *U. pugilator* to have the most specialized mouthparts among Carolinian *Uca* species.

Respiration rates are higher underwater than in air (Teal 1959), probably due to increased activity necessary to aerate the gills. Like *Sesarma*, this species and *U. pugnax* can regulate their metabolism in air under experimental conditions down to 1% or 2% atmospheres (8–15 mm Hg), but low oxygen pressures are encountered in nature only in burrows in water and there the crabs, like *Sesarma*, can go into oxygen debt until emergence at the next low tide.

Latitudinal effects of temperature are manifest in metabolic response. Rate of metabolism in a Massachusetts population was higher at 1.4°C than in a Florida population, but at 15°C the difference was not significant. The northern population was less sensitive to temperature change and more resistant to low temperature than the Florida population (Démusy 1957). Edwards (1950) earlier had shown metabolic differences in the populations at 20°C. Teal (1959) found that crabs from Georgia showed no adjustment to respiration for temperature acclimation above 25°C, but that below 20°C there was some evidence of acclimation though not so well developed as in *U. pugnax*. Summer temperatures of 45°C on open *Distichlis-Salicornia* flats in Georgia prevent *U. pugilator* from permanently occupying these areas (Teal 1958). Metabolic activ-

ity in *Uca* of the temperate zone exhibits a seasonal cycle and this cyclic change must be taken into account in comparing physiologic activity of relatives at different latitudes. Metabolic response of fiddler crabs has real significance in their distribution (Vernberg 1959), manifesting itself to some degree even in the larval stages (Vernberg and Costlow 1966a).

Beyond respiratory responses, there is a significantly larger number of cells per unit volume and a higher titer of blood protein in *U. pugilator* at 30°C than at 10°C. Clotting times significantly lengthened in the 10°C crabs (Dean and Vernberg 1966). These physiological effects are associated with activity levels mediated by temperature.

The subject of intersexuality and relative growth was reopened by Darby (1935) as a result of examination of some 9,000 specimens of *U. pugilator* collected at Beaufort, N. C. Among these, 12 females were obtained with two fiddles, but no female was found with one large chela. These 12 specimens had fully widened, typically female abdomens and were always found feeding with the males in contrast to the other small-clawed females which stayed close to their holes. Darby termed these female-to-male intersexes. A male-to-female intersex, that is, a crab with a typical male abdomen and normal reproductive appendages, yet with small claws, was found only once at Charleston, S. C. Because feeding is accomplished with the small claw, it is not surprising that perfectly symmetrical large-clawed adults do not, or rarely, occur. Darby, thus, refuted the arguments of Huxley (1924) and Rathbun (1921) that females with narrow abdomens represented merely extremes in the normal variation curve for female abdomen growth, and supported the contention of Morgan (1921) that these were truly intersexes.

Vernberg and Costlow (1966b) demonstrated, from laboratory studies of *U. pugilator* and *rapax*, that young crabs with two large chelae are not uncommon (presumably males). Removal of one chela during the symmetrical period of development did not appear to influence subsequent formation of the large chela. Once asymmetry was established, differentiation of the chelae appeared to be fixed and removal of the large chela did not influence future development of handedness. At no time did the remaining small cheliped develop into large cheliped in absence of the large hand, which agreed with the findings of Morgan (1923). Miller (1973) contended that developing gonopods and enlargement of one chela in males occurs at the same time in an early postlarval stage, that growth of the major propodus is initially greatest in the palm but that a shift to an approximate doubling of the



growth rate of the fixed finger leads to elongation of the fingers while the rate for the palm remains constant. The resulting asymmetry also involves the first and second pair of walking legs on the major side.

Waving display (Crane 1975) in male *U. pugilator* is lateral circular but reverse in direction to that in other species. The cheliped is raised in front, still partly flexed, then extended outward, brought down and folded inward. There is a slight pause at the wave's highest point. In northern populations there is a jerk midway to the highest reach. The minor chela makes weak corresponding gestures and fingers of both chelae are nearly closed throughout. Waves are made at the rate of about one per second. The carapace is raised and lowered during each wave. At moments of extreme excitement, the major cheliped may be rapped against the substrate (Salmon 1971) or vibrated in the flexed position without touching the ground (Dembowski 1926, Burkenroad 1947b). Salmon, et al. (1977) demonstrated that *U. pugilator* and *minax* can detect both airborne (sound) and vibrational stimuli in substrate but are more sensitive to the latter, apparently detecting it through myochordotonal organs in the walking legs. Only sound carried through substrate was judged of importance for intraspecific communication. The female follows the male down the burrow after the drumming (Crane 1975).

Salmon, et al. (1978) studied display and burrow construction of *U. pugilator* and *panacea* in a mixed population in western Florida. There, *U. pugilator* is more abundant on clean sand whereas the latter is more abundant on wet muddy sand. Males of *U. panacea* display from burrows which descend 90 from a raised sand lip, whereas those of *pugilator* display to one side of funnel-shaped domes constructed to one side of openings to gently sloping burrows. No conspecific copulations were ever observed outside burrows at the surface in daytime, but five such interspecific matings that lasted about one hour were observed. Experiment and observation showed that the male courts the female with waving (visual) and rapping (acoustic) displays. Interspecific differences in these behaviors are statistically significant and geographic variations in the patterns are not a function of environmental factors such as temperature. Experimental hybrid matings (males of both species occasionally succeed in forced mating with females of the other species) result in fewer clutches of eggs than conspecific matings under the same conditions, and the larvae are less viable.

Intraspecific aggressive encounters between males of *U. pugilator* and *pugnax* were studied near Beau-

fort, N. C. (Hyatt and Salmon 1978). Most fights are between Residents (owning burrows) and Wanderers seeking to displace them; less commonly fighting occurs between Residents occupying adjacent burrows. In over 400 fights observed in each species, Wanderers were rarely successful in displacing Residents of the same size or larger, but they won a small percentage of fights when they were larger than the Residents. *Uca pugilator* Wanderers challenge Residents that are slightly smaller than themselves, but there was no evidence for size selection in *U. pugnax*. Combat duration and number of acts were not related to temperature, time of day, or time in relation to low tide, but incidence of fighting increases in early afternoon, most occurring within 1–3 h after low tide. The authors defined a series of 11 combat-act protocols and three fight categories. Differences between species were observed in length of fights and temperature. It was thought that the energy expended in reconstruction of impermanent burrows in sand near water at each change of the tide tends to engender strong defense of newly constructed shelters in *U. pugilator*, whereas more permanent burrows in mud banks where secondary choices are abundant and loss is not great lead to more passive defense in *U. pugnax*.

### *Uca pugnax* (Smith)

(Mud fiddler)

Fig. 377b

*Gelasimus pugnax* Smith 1870:131, pl. 2, fig. 1; pl. 4, figs. 2–2d.

*Uca pugnax*.—Rathbun 1918b:395, pl. 139.—Hay and Shore 1918:451, pl. 37, fig. 4.—Tashian and Vernberg 1958:89.—Williams 1965:229, figs. 209B, 210A.

*Uca (Minuca) pugnax pugnax*.—Crane 1975:200, 203, pl. 27, figs. E–H, text-figs. 39H, 46J, 67E, 81J, 100.

*Recognition characters*.—Carapace subquadrilateral, approximately 1.5 to 1.75 times as wide as long, widest behind outer orbital angles, very convex anteroposteriorly, lower edge of front and upper margin of orbit invisible in dorsal view, smooth. A shallow H-shaped depression near center of carapace, pit on branchial region in line with gastrocardiac sulcus, and pit behind middle of orbit. Anterolateral angles slightly produced, each continued backward and inward as low, well-defined ridge, and across entire fronto-orbital width. Front about  $\frac{2}{3}$  of fronto-orbital width, margin regularly arched. Or-

bits large, open, upper margin sinuous and oblique, lower margin dentate. Eyestalks long, slender. Antennule and antenna small. Merus of second maxilliped with 0–75 spoon-tipped hairs.

Chelipeds in male very unequal, in female equal and of small size. Large cheliped of male rough; merus with granulate rugose lines outside, lower margins granulated. Carpus and palm tuberculate outside; inner surface of palm with oblique row of granules leading from lower margin to carpal cavity; short row leading down from ridge on proximal half of upper margin; area between crests coarsely granulate or tuberculate and with tuberculate ridge running along finger from tip to internal distal border of palm. Fingers long, slender, widely gaping; fixed finger usually with 1 large tooth near middle, inferior border nearly straight, tip sometimes depressed, truncate; dactyl evenly denticulate and with irregularly placed large tubercles, strongly curving downward past tip of opposed finger. Walking legs with carpal and propodal articles hairy.

*Measurements in mm.*—Carapace: male, length 15, width 23; female, length 13, width 18.

*Variation.*—There is a tendency toward decrease in size in the southern extremity of the range (Tashian and Vernberg 1958).

*Color.*—Males usually brown, sometimes whitening to pale gray at least on branchial regions, but display whitening poorly or not at all developed; anterior part of carapace, eyestalks and anterior parts of third maxillipeds often blue to blue-green (turquoise), but often slight in southern extreme of range. Major cheliped dull yellowish orange to yellowish white, sometimes light brownish or yellowish, fingers white or nearly so; minor chela white; walking legs dark and banded. Females similar (Crane 1975).

*Habitat.*—The mud fiddler's name derives from its preference for a muddy marsh environment, often well shaded (Schwartz and Safir 1915), but it is perhaps somewhat excluded from areas where there is an abundance of halophyte roots or where substrate is too fluid to support burrows (Kraeuter and Wolf 1974). Results of salinity tolerance experiments are consistent with this type of distribution (Teal 1958): 50% of *U. pugnax* placed in freshwater died within 1.5 days, whereas 50% mortality occurred after three days in seawater of 7‰ salinity. Given a choice of freshwater or seawater of 30‰ salinity, the crabs chose seawater.

Given a choice of sand or mud substrate above or under water, *U. pugnax* burrowed only in mud without any reference to water level, and competitive species of *Uca* had no significant effect on numbers of burrows dug. When restricted to the

relatively high *Salicornia-Distichlis* marsh, *U. pugnax* survived less well than *U. pugilator*.

Burrows can extend to depths of 60 cm; the crabs dig most actively when the tide is falling, and often hasten to plug burrows when the tide is rising to cover the burrow mouths (Pearse 1914). Pearse found the maximum number of burrows about 60 cm below high-tide mark, and often the burrows had mud towers at the mouths when the beach was littered with debris. Crane (1943, 1975) observed "shelter building" in this species to be in its most rudimentary form among the *Ucas*. She found that in a mixed population of *U. pugnax* and *pugilator*, *U. pugnax* always chose the side of any surface irregularity for a hole entrance in preference to flat ground. Teal (1958) reported burrows on Georgia Sea Islands to be in situations similar to those observed by Pearse, on low levees bordering tidal creeks or farther from creeks in firm, marshy ground sometimes covered only at spring tides. Extreme variation in the number of crabs within the same general habitat (short, medium or tall *Spartina*) indicates that a clumped distribution is characteristic of crab populations there (Wolf, et al. 1975), a condition perhaps related to several factors as suggested by Teal. Where mixed populations of *U. pugnax* occur in Georgia, the number of burrows dug by each is less than would be predicted for populations of either alone (Aspey 1978).

*Type-locality.*—New Haven, [Conn.].

*Known range.*—Provincetown, Mass., to Daytona Beach, Fla. *Uca longisignalis* Salmon and Atsaides 1968 is now recognized as the Gulf of Mexico counterpart (Heard 1982).

*Remarks.*—According to Rathbun (1935), the fossil record for *U. pugnax* extends into the Pleistocene of New Jersey and Delaware, but Glaessner (1969) did not list it.

Waving display of male *U. pugnax* is weakly circular, almost straight at low intensity (Crane 1975). Jerks are almost always distinguishable but weak, 3 to 14 on rise of the cheliped and 1 to 7 on its descent. There is a variable pause at the highest point of the wave. The minor cheliped makes roughly corresponding motions. The body is held raised throughout a series of waves, with one or more walking legs kicked out during display. At times of high intensity, males will bob or curtsey between waves, with the major cheliped held flexed during this movement which is usually accompanied by stamping of the walking legs. Salmon and Atsaides (1968) found that males produce sounds at night by movements of the walking legs. Females attracted by waving, stamping or sounds follow the males into their burrows for mating.

Ovigerous females have been observed near

Woods Hole, Mass., from July 4 to July 15 (Pearse 1914). Farther south the spawning season is more extended, from early July to mid-August in New Jersey (Crane 1943), as early as May 21 at Long Lake, Tex. (Hedgpeth 1950), and in April in northeastern Florida (USNM records). On Long Island, N. Y., the peak of spawning occurs in August (Schwartz and Safir 1915). Crane (1943) thought it likely that in the region near New York two breeding times occur, one in July and the other in August.

The larval and postlarval stages are discussed in the remarks on *U. pugilator*. Hyman (1920) secured ovigerous females for hatching of eggs by digging them from burrows. He found the first zoea of *U. pugnax* to resemble closely that of *U. pugilator* except for smaller size of the former.

*Uca pugnax* exhibits one of the most highly developed thermal adaptabilities among marsh crabs tested (Teal 1959), and its abundance may be explained in part by its ability to regulate its metabolism over a wide range of temperature. At normal habitat temperatures, *U. pugnax* (= *rapax*) from Trinidad showed a higher metabolic rate than *U. pugnax* from localities in the United States (Tashian 1956). Tashian found that there is a decrease in sensitivity to temperature change from southern to northern populations, along with an increase in tolerance to low temperature. Teal (1958) found that temperatures experienced in nature are not limiting factors in distribution of *U. pugnax* in Georgia, though high temperatures near a lethal level occur at times in summer. Vernberg (1959), Vernberg and Tashian (1959), and Miller and Vernberg (1968) reinforced this conclusion, showing that *U. pugnax* exhibits a marked tendency to demonstrate seasonal thermal acclimation. Brett (1960) showed that the daily oxygen-consumption cycle is considerably modified by locomotion of the crabs. Gray (1957) found gill area per gram of weight in *U. pugnax* to be the lowest among *Uca* species along the U. S. east coast.

Crane (1943) observed hibernating *U. pugnax* in New Jersey, where the burrows were weathered open along the muddy banks of small creeks and could only have been submerged at spring tides. In March at air temperatures of 1.7° to 5.5°C, the immobile crabs were found from the burrow mouths to about 10 cm below the surface. Slight warming in the hand or in the sun elicited fairly rapid movement. Respiration rates for *U. pugnax* are higher underwater than in air (Teal 1959), probably because of increased activity necessary to ventilate the gills.

In another vein, Passano (1960) found an inverse correlation between temperature and proec-

dysis duration in *U. pugnax*. Surprisingly, at some temperature between 15° and 22°C proecydysis fails to proceed normally, though these animals experience much lower temperatures throughout their range. It was suggested that the northern limits of the species are influenced by the inability of larvae to molt in cold water; hence, adults cannot appear there.

Rhythmic cycles have received much attention in experiments with *Uca* species that are well summarized in studies by Barnwell (1966, especially 1968, and 1968a) and can only be touched upon here. Fiddler crabs inhabiting the intertidal zone must adapt activity to both day-night and tidal cycles. The tidal cycle imposes on them a rhythmic alternation between terrestrial and marine periods of existence. At the same time they are influenced by the day-night cycle, since they exhibit specific diurnal and nocturnal habits. Moreover, the interaction of daily and tidal rhythms may give rise to semimonthly variation in activity. It is now well established that persistent daily and tidal rhythms in physiological processes underlie rhythmic variations in behavior of crabs in the field. Rhythmic patterns recorded in the laboratory are found to be closely correlated with tidal conditions in the field. Persistent patterns can be modified by transplanting crabs to intertidal zones of other coasts where they are exposed to tidal cycles which differ from those in the original habitat. Experiments which have established these generalizations have involved not only *U. pugnax*, but also *U. pugilator* and *minax*.

Wheeler (1978) linked rhythmic patterns to larval development of *U. pugnax*, showing that larvae in Delaware are normally hatched in synchrony with the lunar cycle, with peaks at 15-day intervals at new and full moon. Zoel stages were passed through in 15 days at 25°C in water of 25‰ salinity. Megalopae lived a mean of 12.5 days before metamorphosing to first crab. It was concluded that zoeae hatched on new or full moon would develop into megalopae during the next spring tide and metamorphose to first crab in approximately one lunar month. The pattern was thought to facilitate substrate selection at high spring tides.

Primarily because of the tremendous asymmetry in chelipeds of male fiddler crabs, *Uca* became an object of studies on relative growth. (In some of these papers no clear species designation was made.) In fiddler crabs [*Uca pugnax*] the percentage weight of the chela alters throughout life from 2% (the value retained by the female) to 65% (Huxley 1927). In the related larger species, *U. minax*, since allometric growth continues longer, the chela may weigh over ¾ of the remainder of the body (77%). In-

creasing relative size of the chela is associated with an increasing asymmetry of the central nervous system. Thus, such animals have no fixed form, for the proportions of parts are changing throughout postlarval life. On this basis, Huxley challenged Morgan's (1923) statement that females with intermediate-width abdomens (subject also to allometric growth, Huxley 1924) were actually intersexual female types. Tazelaar (1933) explored the subtleties of relative growth in *U. pugnax* in detail, finding that walking legs near the great chela and near the wide abdomen of females also reflect relative growth influences.

Miller (1961) in his well-illustrated study considered *U. pugnax* to be intermediate in development of spoon-shaped hairs on the mouthparts and, therefore, more ubiquitous in choice of feeding substrates than its congeners in the Carolinas. Great detail is given in this study.

Heard (1970) reported trematodes and cestodes from the three U. S. east coast *Uca* species, and (1975) showed that *U. minax* is a major food item of the white catfish, *Ictalurus catus*.

### Superfamily Uncertain

#### Family Palicidae

Carapace broadly transverse, subquadrilateral. Anterolateral margins dentate. Frontoorbital width great, front dentate. Orbits and eyes large. Buccal cavity quadrate, outer maxillipeds not covering it; ischium of third maxillipeds strongly produced forward on inner side; merus small, subtriangular, with notch on inner distal side for articulation of palp. Afferent channels to gills opening at bases of chelipeds, efferent channels at anteroexternal angles of buccal cavity.

Chelipeds of moderate size, often unequal in male, usually tuberculate or granulate. Next 3 pairs of legs long, slender, and rough; last pair either very short and slender, subdorsal, smooth, or similar in position and ornamentation to other legs, and near size of first walking leg. Abdomen of male much narrower than sternum. Genital ducts of female

opening sternally, apparently near mesial end of fifth sternite (near second legs). (Rathbun 1918b.)

Because position of the family Palicidae in a superfamily is uncertain, Glaessner (1969) placed the group at the end of the list, as here. Placement by Faxon (1895) and Bouvier (1898) was near the Dorippidae, and near the Pinnotheridae (as Cymopoliidae) by Monod (1956) and Rathbun (1918b) who followed Alcock and Borradaile.

#### Genus *Palicus* Phillipi 1838

Rathbun 1918b:183.—Holthuis and Gottlieb 1958:104.

Carapace more or less depressed, broader than long, subquadrate to heptagonal, more or less covered with granules and symmetrical tubercles or rugosities with tendency to arrangement in transverse series. Front broadly triangular, horizontal, usually lobed or toothed. Anterolateral border straight or slightly curved, and lobed or toothed. Eyes large, constricted in middle, bearing 2 or more lobiform protuberances. Orbits deep, upper border cut by 2 or 3 clefts, lower border usually with 2 clefts. Antennules folding transversely; interantennular septum narrow; enlarged basal antennal article in orbital hiatus, flagellum well developed. Epistome ill defined. Buccal cavity square, lobelike prolongation of pterygostomial region at its anterolateral corner overlapping inner lobe of orbit and sometimes horizontal, sometimes bent down in vertical plane, and, in some species, deflexed in young but horizontal in adults. External maxillipeds often not meeting in middle, oblique merus much smaller and narrower than ischium; distomesial corner of ischium; and distolateral corner of merus produced; palp articulating in distal marginal concavity of merus.

Chelipeds short, usually slender in female, right often greatly enlarged in male. Second and third ambulatory legs largest, second usually longer than third, first similar but smaller, fourth weak, sometimes filiform and elevated above third. Abdominal segments free in both sexes. (Rathbun 1918b.)

#### Key to Species

1. Last sternal segment without posterolateral laminate crest conspicuous in dorsal view . . . . . 2  
    Last sternal segment bearing posterolateral laminate crest conspicuous in dorsal view . . . . . *P. sica*
2. First 2 anterolateral teeth with rounded tips, teeth set apart by rounded sinuses; frontal margin almost straight or shallowly notched between low, rounded, submesial frontal lobes and inner orbital lobe . . . *P. alternatus*  
    First 2 anterolateral teeth with acute tips and somewhat serrated sides, teeth

set apart by V-shaped sinuses; frontal margin conspicuously sinuous between somewhat prominent submesial frontal lobes and inner orbital lobe, notch for antennal article rather broad . . . . . *P. faxoni*

***Palicus alternatus* Rathbun**

Fig. 378

*Palicus alternatus* Rathbun 1897a:95.—Williams 1965:215, fig. 200.—Powers 1977:118.

*Cymopolia alternata*.—Rathbun 1918b:188, text-fig. 117, pls. 42–43.

*Recognition characters*.—Elevations of carapace covered with small tubercles composed of single or a few granules. Front broadly triangular, notched at middle, with 4 submesial lobes or teeth, outer teeth less advanced than inner and broadly rounded. Orbits deep with upper border cut into teeth; middle tooth broad, obliquely truncate, bounded on each side by a V-shaped fissure; next tooth separated from outer tooth by shallow sinus; outer tooth directed forward or a little outward, tip curved inward. First 2 anterolateral teeth broad, dentiform with rounded tips, well separated; third tooth close to second, rudimentary or in form of small tubercle. Outer suborbital lobe nearly straight; inner lobe divided into 2 parts with inner angle produced in acute tooth beneath obtusely and often downturned pterygostomial lobe. Posterior margin bordered above by thin, sinuous, elevated ridge broken into variable number of unequal transverse tubercles with usually some granules interspersed.

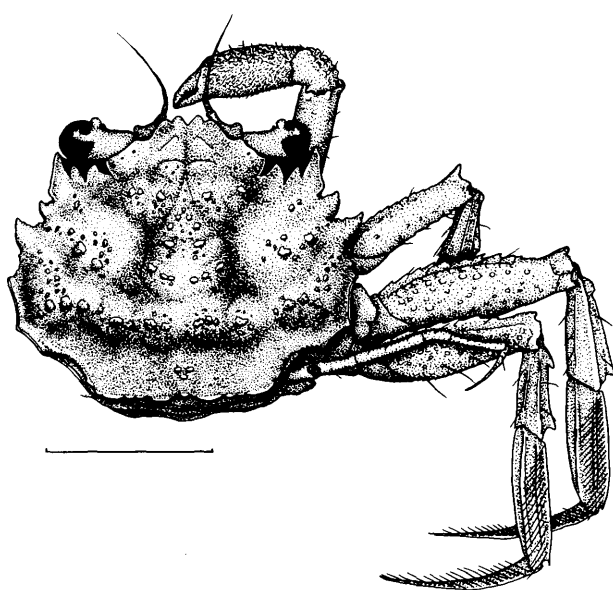


Fig. 378. *Palicus alternatus* Rathbun. Animal in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

Chelipeds of male occurring in 2 forms. In one form, chelipeds very unequal; on right side large and heavy, on left, slender and weak, both tuberculate and pubescent; carpus with outer, laminate, lobed crest; hand surmounted by less pronounced double crest. Right hand very thick, width at distal end often equaling  $\frac{1}{2}$  length of carapace; fixed finger short, wide; dactyl strongly bent down, overlapping opposed finger and leaving narrow gape. Left hand somewhat over  $\frac{1}{3}$  width of right, fingers long and narrow. In second, weaker form males, right hand about twice depth of left; fingers long and slender. Females with chelipeds more nearly equal.

First 3 walking legs flattened, second longer than others. First reaching middle of propodus of second, with posterior margin of propodus and proximal half of dactyl hairy in male; third reaching middle of dactyl of second, fourth slender, much shorter than third. Meri rough with squamous tubercles; with shallow, single longitudinal groove on anterior surface, 2 on upper surface; first 3 meri with superodistal lobe, subtriangular on first, subrectangular on second and third, lobe exceeding article on first, equal to article on second, not reaching end of article on third. Carpus with rounded, anterior proximal lobe; anterior subdistal lobe low and rounded on first leg, triangular on second and third legs. Propodus with anterior margin convex, posterior margin straight.

Abdominal appendages of first form of male stout and twisted, tip bilobed, inner lobe thinner and longer than outer; second form of male with appendages weaker, not twisted, and tip less spreading.

*Measurements in mm*.—Carapace: male, length 7.1, width 11.9; female, length 13.1, width 16.2, but ovigerous at much smaller size.

*Variation*.—The species shows great variation in structure. In some individuals the carapace is wider behind in proportion to its length than in typical individuals, and the sides are less parallel. There is no consistency in relative size of the anterolateral teeth, for in some the first is largest and all teeth point forward, but in others the second tooth is largest and points slightly outward. In some individuals the anterodistal tooth on the merus of the second and third legs is more produced than in typical specimens, and there is variation in the length-width proportions of the propodus of the second leg. Details of lobulation on the front and

lower margin of the eye are also subject to variation.

*Habitat*.—The species has been taken from a variety of fine and coarse bottoms (Rathbun 1918b); 7.3 to 285 m (SCMRRRI).

*Type-locality*.—29°11'30"N, 85°29'00"W, 47.6 m (south of Cape San Blas, Fla.).

*Known range*.—Cape Hatteras to SE Cape Fear, N. C.; Gulf of Mexico along west coast of Florida from Cape San Blas to Key West.

*Remarks*.—Ovigerous females have been reported in Florida from January to August, and from North Carolina in October (Rathbun 1918b, USNM.).

### *Palicus faxoni* Rathbun

Fig. 379

*Palicus faxoni* Rathbun 1897a:96.—Williams 1965:216, fig. 201.—Coelho and Ramos 1972:198.—Powers 1977:118.

*Cymopolia faxoni*.—Rathbun 1918b:194, text-fig. 120, pl. 45, figs. 2–3.

*Recognition characters*.—Carapace broader than long, sides converging anteriorly; adult female quite convex, surface hairy, and with numerous tubercles and granules. Front broadly triangular; 4 submesial frontal lobes well marked, outer pair not much wider than inner, median emargination deeper than wide with end often rounded, lateral emargination shallow. Eyes large; orbits deep, with upper border cut into teeth by V-shaped sinuses, middle and outer teeth triangular, subacute, middle one equilateral, outer one narrow and separated from outer orbital tooth by shallower sinus; outer orbital tooth directed forward, tip oblique, its lateral margin nearly straight. Lateral border with 2 sharp-pointed, slightly serrated teeth, second smaller, outer borders convex, inner concave. Lower margin of orbit oblique, bilobed; inner lobe in advance of outer, obscurely divided, outer part rounded, inner part a small acute tooth somewhat obscured by ventrally bent, pterygostomial lobe, sharp pointed at tip; outer lobe slightly convex. Posterior margin preceded by tuberculate ridge.

Chelipeds in both sexes somewhat unequal, right hand approximately twice as wide as left. Walking legs short and broad; first 3 meral articles with large, flat, acute distal spine, posterior distal tooth of merus sharp; carpal lobes prominent, distal one of second and third legs acute; propodus of second and third legs widening distally, dactyls wide, posterior margin sinuous.

*Measurements in mm*.—Carapace: male, length

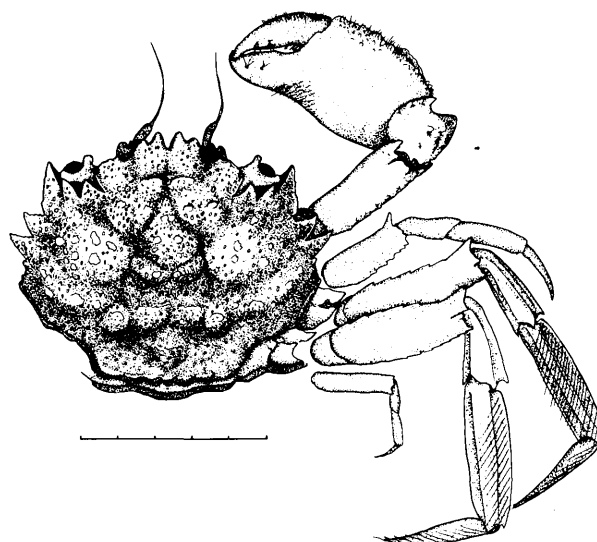


Fig. 379. *Palicus faxoni* Rathbun. Male in dorsal view, legs of left side not shown; cheliped, second and third walking legs detached; first and fourth walking legs from female in Rathbun (1918b); 5 mm indicated (from Williams 1965).

12.5, width 15.1; female, length 10, width 11.

*Habitat*.—Sand; 59 to 190 m.

*Type-locality*.—Off Cape Hatteras, N. C., 89.6 m.

*Known range*.—Off Cape Hatteras, N. C., to near Cape Canaveral, Fla.; off Yucatan, Mexico; near Quita Sueño Banks; SW St. Christopher; off Cabo Frio, Rio de Janeiro.

*Remarks*.—Individuals collected from a reef SE of Cape Lookout, N. C., in September and October withstood experimental exposure to temperature of 4°C for 7 h but were dead after 17-h exposure (F. J. and W. B. Vernberg 1970).

### *Palicus sica* (A. Milne Edwards)

Fig. 380

*Cymopolia sica* A. Milne Edwards 1880:29 (part).—Chace 1940:49.

*Palicus sicus*.—A. Milne Edwards and Bouvier 1902:56, pl. 10, figs. 7–11; pl. 11, fig. 9.—W. E. Pequegnat 1970:198.

*Palicus sica*.—Powers 1977:119.

*Recognition characters*.—Carapace rather evenly but not strikingly convex, regions not deeply marked, granules of different sizes, sometimes clustered to form tubercles. Front broad, moderately prominent, submesial teeth small, median sinus a narrow V, sinuses between submesial teeth shallow, rounded and wider. Orbit with upper marginal lobes shallow, rounded, separated by rather shallow V-shaped sinuses, outer lobe nar-

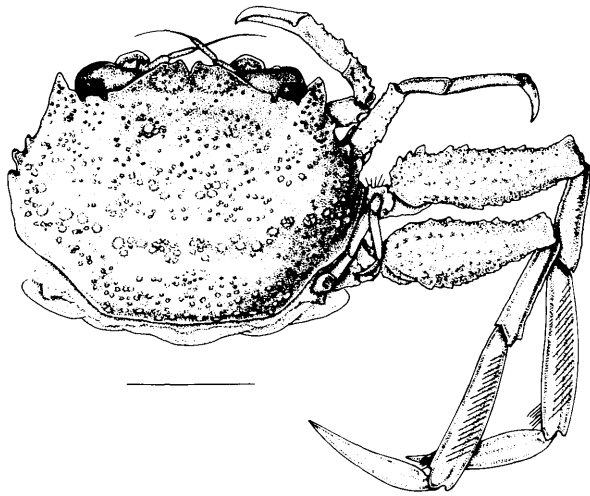


Fig. 380. *Palicus sica* (A. Milne Edwards). Female in dorsal view, legs of left side not shown, 5 mm indicated (USNM 17892).

row, outer orbital tooth projecting forward. Three anterolateral teeth small, second and third largest. Sinuous line of tubercles above posterior margin. Lower orbital margin oblique; outer lobe somewhat rectangular, inner lobe with 3 distal crenulations, inner angle subacute. Pterygostomian lobe broad, obtuse, covering all but tip of inner orbital lobe in ventral view.

Chelipeds slender and equal in both sexes. Second and third walking legs with rounded, dorsal plates on coxae; merus coarsely spinulose, especially along anterior margins, anterodistal angle subacute, almost rectangular; carpus long and narrow, anterior lobes low; propodus widening distally; dactyl with flexor margin sinuous, feathered setae along both margins of propodus and extensor margin of dactyl; first legs short, slender, merus slightly roughened, distal angle obtuse.

Last sternal segment with laminate crest projecting behind third and fourth walking legs. Abdominal segments of female carinate, first with shallow, granulate, posterolateral lobes, second with prominent median lobe, third invisible from dorsal view; abdomen of male wide, sides of third to fifth segments nearly straight.

*Measurements in mm.*—Carapace: male, length 6.8, width 10 (Milne Edwards and Bouvier 1902); female, length 9.8, width 13.5 (Rathbun 1918b).

*Color.*—Carapace light brown with slightly bluish cast; eyestalks reddish-brown; walking legs with some tubercles on meri salmon, sides of carpi and upper edge of propodi with faint dashes of brownish or salmon (Rathbun 1918b).

*Habitat.*—Sand, mud, shell and coral bottoms; 12.8 to 391 (481 + ?) m (W. E. Pequegnat 1970 in part).

*Type-locality.*—Barbados, 150 m, Blake Stn. 293.

*Known range.*—Off Charleston, S. C., to NNE Cape Canaveral, Fla; west coast of Florida through West Indies to Barbados and Grenada.

*Remarks.*—The specific name (*sica*) is a noun in apposition (Powell 1977). Oviparous females are known from the Gulf of Mexico in March (USNM) and July (W. E. Pequegnat 1970), near Quita Sueño Bank in June, and north of Cuba in November (USNM).

### Extralimital Species

The following list includes species having doubtful position in the regional fauna. Some range primarily in deep water, occurring incidentally on the continental shelf. Others have a range limited to shallow waters from beyond the immediate region. Species listed by name only have range limits given by Williams and Wigley (1977).

#### Family Penaeidae

*Hymenopenaeus robustus* Smith.

#### Family Hippolytidae

*Bythocaris nana* Smith.

*Caridion gordonii* (Bate).

#### Family Pandalidae

*Parapandalus willisi* L. H. Pequegnat.

*Plesionika martia* (A. Milne Edwards).

*Plesionika tenuipes* (Smith). Western Atlantic from Rhode Island to southern Florida; Gulf of Mexico. 159 to 476 m (L. H. Pequegnat 1970).

#### Family Paguridae

*Catapagurus gracilis* (Smith).

*Catapagurus sharreri* A. Milne Edwards.

#### Family Majidae

*Mithrax (Mithrax) cornutus* Saussure. Off Cape Canaveral, Fla.; Mississippi Delta through Florida Straits to Bahia, Brazil; shallow reef flats to 600 m.

*Notolopas lamellatus* Stimpson. A single female was erroneously recorded by Rathbun (1925) from "Off Beaufort, N. C., Fish Hawk." This eastern Pacific species was included with Atlantic material through a mistake in cataloguing.

#### Family Portunidae

*Bathynectes longispina* Stimpson. Martha's Vineyard, Mass., to off Mississippi Delta, southward to off Goajara Peninsula, Colombia; Bermuda; usually beyond edge of continental shelf; rarely as shallow as 7.3 m (Lewis 1976, 1977; Manning and Holthuis 1981; Roberts 1969).

### Family Geryonidae

*Geryon quinquedens* Smith. Red crab. Gulf of Maine southward in western Atlantic, possibly to Argentina (Scelzo and Valentini 1974). Continental slope except for marginal occurrences at outer edge of continental shelf (Haefner 1977a; Rathbun 1937; Schroeder 1959; Wigley, et al. 1975).

### Family Pinnotheridae

*Parapinnixa beaufortensis* Rathbun. Williams (1965) listed this form among extralimital and indeterminate species. The only specimen known is the holotype from fishing grounds, 20 mi. off Beaufort Inlet, N. C. Rathbun (1918b) doubtfully referred this form to the genus *Parapinnixa* and believed that it was a postlarval stage of an unknown species because of small size, relatively large eyes, hairiness of legs and carapace, and thin gripping edges of the fingers, suggesting that in another molt or two, gaping fingers might emerge. Williams thought that it might be a young *Palicus*, but shape of the external maxillipeds as well as the successively diminished ambulatory legs with hairy fringes strongly suggest pinnixid affinities.

### Family Palicidae

*Palicus gracilis* (Smith).

A large amount of unidentified material is in existing collections and some of this contains undescribed species. It is expected that oceanographic research in the eastern United States will soon add to knowledge of decapod crustaceans in the region.

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## Literature Cited

- Abbe, G. R.  
1974. Second terminal molt in an adult female blue crab, *Callinectes sapidus* Rathbun. Transactions of the American Fisheries Society, 103(3):643–644.
- Abele, L. G.  
1972. A reevaluation of the *Neopanope texana-sayi* complex with notes on *N. packardii* (Crustacea: Decapoda: Xanthidae) in the northwestern Atlantic. Chesapeake Science, 13(4):263–271.  
1973. Taxonomy, distribution and ecology of the genus *Sesarma* (Crustacea, Decapoda, Grapsidae) in eastern North America, with special reference to Florida. American Midland Naturalist, 90(2):375–386.
- Abramowitz, A. A.  
1935. Color changes in cancrivora crabs of Bermuda. Proceedings of the National Academy of Sciences, 21(12):677–681.
- Adams, A. E.  
1979. The life history of the snow crab *Chionoecetes opilio*: a literature review. Alaska Sea Grant Program, Sea Grant Report 78–13, 141 pages.
- Adams, S. M., and J. W. Angelovic.  
1970. Assimilation of detritus and its associated bacteria by three species of estuarine animals. Chesapeake Science, 11(4):249–254.
- Adkins, G.  
1972. Notes on the occurrence and distribution of the rhizocephalan parasite (*Loxothylacus texanus* Boschma) of blue crabs (*Callinectes sapidus* Rathbun) in Louisiana estuaries. Louisiana Wild Life and Fisheries Commission, Technical Bulletin 2, 13 pages.
- Adkison, D. L., and R. W. Heard.  
1978. Description of a new genus and species of Pseudioninae (Isopoda: Bopyridae) parasite of the hermit crab *Pagurus annulipes* (Stimpson) from North Carolina. Proceedings of the Biological Society of Washington, 91(2):408–817.
- Alcock, A.  
1895. Materials for a carcinological fauna of India. No. 1. The Brachyura Oxyrhyncha. Journal of the Asiatic Society of Bengal, 64:157–291, plates 3–5.  
1896. Materials for a carcinological fauna of India. No. 2. Brachyura Oxyrhyncha. Journal of the Asiatic Society of Bengal, 65, part 2(2):134–296.  
1905. Catalogue of the Indian decapod Crustacea in the collection of the Indian Museum. Part II. Anomura. Fascicle I, Pagurides. Calcutta, xi + 197 pages.
- Aldrich, J. C.  
1974. Allometric studies on energy relationships in the spider crab *Libinia emarginata* (Leach). Biological Bulletin, 147(2):257–273.  
1976. The spider crab *Libinia emarginata* Leach, 1815 (Decapoda Brachyura), and the starfish, an unsuitable predator but a cooperative prey. Crustaceana, 31(2):151–156.
- Allee, W. C.  
1923. Studies in marine ecology: III, Some physical factors related to the distribution of littoral invertebrates. Biological Bulletin, 44(5):205–253.
- Allee, W. C., and M. B. Douglis.  
1945. A dominance order in the hermit crab, *Pagurus longicarpus* Say. Ecology, 26:411–412.
- Allen, E. A., and H. A. Curran.  
1974. Biogenic sedimentary structures produced by crabs in lagoon margin and salt marsh environments near Beaufort, North Carolina. Journal of Sedimentary Petrology, 44(2):538–548.
- Allen, J. A.  
1959. On the biology of *Pandalus borealis* Krøyer, with reference to a population off the Northumberland coast. Journal of the Marine Biological Association of the United Kingdom, 38(1):189–220.  
1962. Observations on *Spirontocaris* from Northumberland waters. Crustaceana, 3(3):227–238.  
1963. Observations on the biology of *Pandalus montagui* [Crustacea Decapoda]. Journal of the Marine Biological Association of the United Kingdom, 43(3): 665–682.  
1966. The dynamics and interrelationships of mixed populations of caridea found off the north-east coast of England. Pages 45–66 in H. Barnes (ed.), Some contemporary studies in marine science. Hafner Publishing Co., New York, 716 pages.  
1966a. Notes on the relationship of the bopyrid parasite *Hemiarthrus abdominalis* (Krøyer) with its hosts. Crustaceana, 10(1):1–6.
- Almaça, C.  
1960. Variabilidade de alguns caracteres usados na taxonomiada gen. *Carcinus* Leach. Revista da Faculdade de Ciências, Universidade de Lisboa, series 2<sup>a</sup>, C, 8(2): 137–156.  
1962. Sur la distribution géographique du genre *Carcinus* Leach (Crust. Dec. Brach.). Revista da Faculdade de Ciências, Universidade de Lisboa, series 2<sup>a</sup>, C, 10(1):109–113.  
1963. Sur le probleme de l'origine de *Carcinus maenas* (L.) du littoral Americain. Revista da Facul-

- dade de Ciências, Universidade de Lisboa, series 2<sup>a</sup>, C, 11(2):121–136.
- Alves, M. I. M., and M. P. Paiva.  
1976. Frequência de acasalamentos em lagostas do genero *Panulirus* White (Decapoda, Palinuridae). Arquivos de Ciências do Mar, 16(2):61–63.
- Anderson, W. D., Jr., J. K. Dias, R. K. Dias, D. M. Cupka, and N.A. Chamberlain.  
1977. The macrofauna of the surf zone off Folly Beach, South Carolina. NOAA Technical Report NMFS SSRF-704, 23 pages.
- Anderson, W. W.  
1970. Contributions to the life histories of several penaeid shrimps (Penaeidae) along the South Atlantic Coast of the United States. Fish and Wildlife Service Special Scientific Report—Fisheries, 605, iii + 24 pages.
- Anderson, W. W., J. E. King, and M. J. Lindner.  
1949. Early stages in the life history of the common marine shrimp, *Penaeus setiferus* (Linnaeus). Biological Bulletin, 96(2):168–172.
- Andrews, E. A.  
1883. On the anatomy of *Libinia emarginata* Leach, the spider crab. Transactions of the Connecticut Academy of Arts and Sciences, 6(1):99–121, plates 25–27.  
1911. Color differences in the sexes of a crab. Zoologischen Anzeiger, 37(19/20):401–403.
- Anonymous.  
1950. Truly a blue crab. Maryland Tidewater News, 7(4):5.  
1965. Invasion. Desperation as blue crabs swamp Nile delta. Fishing News International, 4(1):56–57.  
1975. Gulf Specimen Company, Inc. Catalog No. 5. Panacea, Florida. 32346, 118 pages.  
1975a. Photos of crabs with by-line. The Northumberland Echo, Heathsville, Virginia, 74(30):July 31.  
1979. Shrimp Landings, December 1978. Current Fisheries Statistics, 7727. NOAA, NMFS, May 3.
- Apollonio, S.  
1969. Breeding and fecundity of the glass shrimp, (*Pasiphaea multidentata* (Decapoda, Caridea) in the Gulf of Maine. Journal of the Fisheries Research Board of Canada, 26(8):1969–1983.
- Armstrong, J. C.  
1940. New species of Caridea from the Bahamas. American Museum Novitates, 1096, 10 pages.  
1949. New Caridea from the Dominican Republic. American Museum Novitates, 1410, 27 pages.
- Aspey, W. P.  
1978. Fiddler crab behavioral ecology: burrow density in *Uca pugnax* (Smith) and *Uca pugilator* (Bosc) (Decapoda Brachyura). Crustaceana, 34(3):235–244.
- Ayers, J. C.  
1938. Relationship of habitat to oxygen consumption by certain estuarine crabs. Ecology, 19(4):523–527.
- Baba, K.  
1969. Four new genera with their representatives and six new species of the Galatheidae in the collection of the Zoological Laboratory, Kyushu University, with redefinition of the genus *Galathea*. Contributions from the Zoological Laboratory, Faculty of Agriculture, Kyushu University, 2(1):1–32.
- Bae, D. H.  
1963. A summary report on some major marine fisheries resources of Korea. Indo-Pacific Fisheries Council, Proceedings 10th Session, Seoul, Republic of Korea, 10–25 October, 1962, Section II:118–123.
- Balss, H.  
1929. Decapoden des Roten Meeres. IV. Oxyrhyncha und Schlussbetrachtungen. (Expedition S. M. Schiff "Pola" in das Rote Meer. Zoologische Ergebnisse 36). Denkschriften K. Akademie der Wissenschaften, Wien. Mathematisch-naturwissenschaftliche Klasse, 102:1–30, plate 1.  
1957. Decapoda. VIII. Systematik. Bronns Klassen und Ordnungen des Tierreichs. Band 5, Abteilung I, Buch 7, Lieferung 12:1505–1672.
- Banner, A. H.  
1953. The Crangonidae, or snapping shrimp, of Hawaii. Pacific Science, 7(1):3–144, 147.
- Banner, A. H., and D. M. Banner.  
1966a. Contributions to the knowledge of the alpheid shrimp of the Pacific Ocean. Part X. Collections from Fiji, and Samoa. Pacific Science, 20(2):145–188.  
1966b. The alpheid shrimp of Thailand. The Siam Society Monograph Series, 3, vi + 168 pages.
- Banoub, M. W.  
1963. Survey of the blue-crab *Callinectes sapidus* (Rath.), in Lake Edku in 1960. Hydrobiological Department, Alexandria Institute of Hydrobiology, Kayed Bey, Alexandria, Egypt, Notes and Memoirs, 69:1–18.
- Barnard, K. H.  
1950. Descriptive catalogue of South African decapod Crustacea (crabs and shrimps). Annals of the South African Museum, 38:1–837.
- Barnwell, F. H.  
1966. Daily and tidal patterns of activity in individual fiddler crabs (genus *Uca*) from the Woods Hole region. Biological Bulletin, 130(1):1–17.  
1968. The role of rhythmic systems in the adaptation of fiddler crabs to the intertidal zone. American Zoologist, 8(3):569–583.  
1968a. Comparative aspects of the chromatophoric responses to light and temperature in fiddler crabs of the genus *Uca*. Biological Bulletin, 134(2):221–234.
- Barr, L.  
1970. Alaska's fishery resources—the shrimps. U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries, Fishery Leaflet 631, 10 pages.  
1975. Observations on the biology of the arrow crab,

- Stenorhynchus seticornis* (Herbst) in Lameshur Bay, St. John, Virgin Islands. In Results of the Tektite Program. Natural History Museum of Los Angeles County Science Bulletin, 20:47–56.
- Bate, C. S.  
1888. Report on the Crustacea Macrura collected by H.M.S. Challenger during the years 1873–76. Report on the scientific results of the voyage of H.M.S. Challenger, Zoology, 24, xc + 942 pages, plates 1–150.
- Beach, N. W.  
1969. The oyster crab, *Pinnotheres ostreum* Say, in the vicinity of Beaufort, North Carolina. Crustaceana, 17(2):187–199.
- Bearden, C. M.  
1961. Notes on postlarvae of commercial shrimp (*Penaeus*) in South Carolina. Contributions from Bears Bluff Laboratories, 33, 8 pages.
- Beers, J. R.  
1958. An histological and histochemical study of the green gland of *Cancer borealis*. Anatomical Record, 131(3): 531–532.
- Beeston, M. D.  
1971. Decapod crustaceans and fish populations in experimental marine ponds receiving treated sewage waters. Pages 182–204 in E. J. Kuenzler and A. F. Chestnut, Structure and functioning of estuarine ecosystems exposed to treated sewage wastes. Annual Report for 1970–71, Sea Grant No. GH.103, Project 10, University of North Carolina, Chapel Hill, 345 pages.
- Behre, E. H.  
1950. Annotated list of the fauna of the Grand Isle region, 1928–1946. Occasional papers of the Marine Laboratory, Louisiana State University, Baton Rouge, 6, 66 pages.
- Bell, F. W., and R. F. Fullenbaum  
1973. The American lobster fishery: Economic analysis of alternative management strategies. Marine Fisheries Review, 35(8):7–12.
- Bell, T.  
1853. A history of the British stalk-eyed Crustacea. London, John van Voorst, 1 Paternoster Row, lxx + 386 pages.  
1855. Horae Carcinologicae, or notices of Crustacea. I. A monograph of the Leucosiadae, with observations on the relations, structure, habits and distribution of the family; a revision of the generic characters; and descriptions of new genera and species. Transactions of the Linnean Society of London, 21, pt. 4(31):277–314, plates 30–34.
- Bender, E. S.  
1971. Studies of the life history of the stone crab, *Menippe mercenaria* (Say), in the Cedar Key area. Master's Thesis, University of Florida, Gainesville, x + 110 pages.
- Benedict, J. E.  
1892. Preliminary descriptions of thirty-seven new species of hermit crabs of the genus *Eupagurus* in the U.S. National Museum. Proceedings of the United States National Museum, 15(887): 1–26.  
1896. A question concerning a British pagurid. Annals and Magazine of Natural History, series 6, 18(13):99–100.  
1901a. The hermit crabs of the *Pagurus bernhardus* type. Proceedings of the United States National Museum, 23(1216):451–466.  
1901b. Four new symmetrical hermit crabs (pagurids) from the West India region. Proceedings of the United States National Museum, 23(1236): 771–778.  
1901c. The anomuran collections made by the Fish Hawk Expedition to Porto Rico. United States Fish Commission Bulletin for 1900, 2(2):129–148, plates 3–6.  
1902. Description of a new genus and forty-six new species of crustaceans of the family Galatheiidae, with a list the known marine species. Proceedings of the United States National Museum, 26(1311):243–334.  
1903. Revision of the Crustacea of the genus *Lepidopa*. Proceedings of the United States National Museum, 26(1337):889–895.  
1904. A new genus and two new species of crustaceans of the family Albuneidae from the Pacific Ocean; with remarks on the probable use of the antennulae in *Albunea* and *Lepidopa*. Proceedings of the United States National Museum, 27(1367):621–625.
- Benedict, J. E., and M. J. Rathbun.  
1891. The genus *Panopeus*. Proceedings of the United States National Museum, 14(858):355–385, plates 19–24.
- Berkeley, A. A.  
1930. The postembryonic development of the common pandalids of British Columbia. Contributions to Canadian Biology and Fisheries (new series), 6(6):79–163.
- Berreur-Bonnenfant, J., and H. Charniaux-Cotton.  
1966. Hermaphroditisme proterandrique et fonctionnement de la zone germinative chez la crevette *Pandalus borealis* Krøyer. Bulletin de la Societe Zoologique de France, 90(2–3)(for 1965):243–259.
- Berrill, M.  
1975. Gregarious behavior of juveniles of the spiny lobster, *Panulirus argus* (Crustacea: Decapoda). Bulletin of Marine Science, 25(4):515–522.
- Bethe, A.  
1897. Das Nervensystem von *Carc. Maenas*. Archiv für Mikroskopische Anatomie und Entwicklungsgeschichte, 50:462–545, 589–639.
- Biffar, T. A.  
1971a. The genus *Callianassa* (Crustacea, Decapoda, Thalassinidea) in South Florida, with keys to the western Atlantic species. Bulletin of Marine Science, 21(3):637–715.  
1971b. New species of *Callianassa* (Decapoda, Thalassinidea) from the western Atlantic. Crusta-

- ceana, 21(3):225–236.
- Biffar, T. A., and A. J. Provenzano, Jr.  
1972. A reexamination of *Dardanus venosus* (H. Milne Edwards) and *D. imperator* (Miers), with a description of a new species of *Dardanus* from the western Atlantic (Crustacea, Decapoda, Diogenidae). *Bulletin of Marine Science*, 22(4):777–805.
- Bigelow, H. B., and M. Sears.  
1939. Studies of the waters of the continental shelf, Cape Cod to Chesapeake Bay. III. A volumetric study of the zooplankton. *Memoirs of the Museum of Comparative Zoology at Harvard College*, 54(4):183–378.
- Bigford, T. E.  
1978. Effects of several diets on survival, development time, and growth of laboratory-reared spider crab, *Libinia emarginata*, larvae. *Fishery Bulletin*, 76(1): 59–64.  
1979. Ontogeny of light and gravity responses in rock crab larvae (*Cancer irroratus*). *Marine Biology*, 52(1):69–76.  
1979a. Synopsis of biological data on the rock crab, *Cancer irroratus* Say. NOAA Technical Report NMFS Circular 426, 26 pages.
- Bill, R. G., and W. F. Herrnkind.  
1976. Drag reduction by formation movement in spiny lobsters. *Science*, 193(4258):1146–1148.
- Binford, R.  
1912. The germ cells and the process of fertilization in the crab, *Menippe mercenaria*. Dissertation, The Johns Hopkins University, 51 pages.
- Blacker, R. W.  
1957. Benthic animals as indicators of hydrographic conditions and climatic change in Svalbard waters. *Fishery Investigations*, series 2, 20(10): 1–49, 20 tables.
- Blake, S. F.  
1953. The Pleistocene fauna of Wailes Bluff and Langleys Bluff, Maryland. *Smithsonian Miscellaneous Collections*, 121(12):1–32, 1 plate.
- Bliss, D. E.  
1963. The pericardial sacs of terrestrial Brachyura. Pages 59–78 in H. B. Whittington and W. D. I. Rolfe (eds.), *Phylogeny and evolution of Crustacea*, Museum of Comparative Zoology, Special Publication, xii + 192 pages, Cambridge, Mass.  
1968. Transition from water to land in decapod crustaceans. *American Zoologist*, 8(3):355–392.
- Boeck, A.  
1864. Beskrivelse og fremlagde Tegninger af 4 norske Decapoder, undersøgte af Overlaege Danielssen og ham. *Forhandlinger Videnskabs-Selskabet, I Christiania* (for 1863):189–190.
- Boesch, D. F.  
1971. On the occurrence of *Pinnixa lunzi* Glassell (Decapoda Pinnotheridae) off Virginia, U. S. A. *Crustaceana*, 20(2):219–220.
- Boesch, D. F., and A. E. Smalley.  
1972. A new axiid (Decapoda, Thalassinidea) from the northern Gulf of Mexico and tropical Atlantic. *Bulletin of Marine Science*, 22(1):45–52.
- Bohnsack, J. A.  
1976. The spider crab, *Mithrax spinosissimus*: an investigation including commercial aspects. *Florida Scientist*, 39(4):259–266.
- Bonnelly de Calventi, I.  
1974. Pt. 1. Taxonomía de crustáceos y corales—Camarones de Rio de Republica Dominicana manual para su identificación. In *Estudios de biología pesquera dominicana*. Publicaciones de la Universidad Autonoma de Santo Domingo, 159, Coleccion Ciencia y Tecnologia (1):35–63.
- Bookhout, C. G., and J. D. Costlow, Jr.  
1974. Larval development of *Portunus spinicarpus* reared in the laboratory. *Bulletin of Marine Science*, 24(1):20–51.  
1977. Larval development of *Callinectes similis* reared in the laboratory. *Bulletin of Marine Science*, 27(4):704–728.  
1979. Larval development of *Pilumnus dasypodus* and *Pilumnus sayi* reared in the laboratory (Decapoda Brachyura, Xanthidae). *Crustaceana*, supplement 5:1–16.
- Boone, L.  
1927. Crustacea from tropical east American seas. Scientific results of the first oceanographic expedition of the “Pawnee,” 1925. *Bulletin of the Bingham Oceanographic Collection*, 1(2):1–147.  
1930. Crustacea: Anomura, Macrura, Schizopoda, Isopoda, Amphipoda, Mysidacea, Cirripedia, and Copepoda. Scientific results of the cruises of the yachts “Eagle” and “Ara,” 1921–1928, William K. Vanderbilt, Commanding. *Bulletin of the Vanderbilt Marine Museum*, 3:1–221, plates 1–83.
- Boothe, B. B., Jr.  
1977. New and additional records of *Pinnixa* (Brachyura: Pinnotheridae) from South Carolina, U.S.A. *Journal of the Elisha Mitchell Scientific Society*, 92(4)(for 1976):162–163.
- Borradaile, L. A.  
1903. On the classification of the Thalassinidea. *Annals and Magazine of Natural History*, series 7, 7(53):534–551.  
1907. On the classification of the decapod crustaceans. *Annals and Magazine of Natural History*, series 7, 19(114):457–486.  
1915. On the species of *Lucifer* and their distribution. *Annals and Magazine of Natural History*, series 8, 16(93):226–231.  
1916. Crustacea. Part I. Decapoda. In *British Antarctic (“Terra Nova”) Expedition, 1910*, *Natural History Reports*. London, British Museum (Natural History), *Zoology*, 3(2):75–110.  
1920. On a new commensal prawn. *Annals and Mag-*

- azine of Natural History, series 9, 5(25):132–133.
- Bosc, L. A. G.  
[1802]. Histoire naturelle des Crustacés, contenant leur description et leurs moeurs; avec figures dessinées d'après nature. Paris, 1:1–258, plates 1–8.
- Boschi, E. E.  
1963. Los camerones comerciales de la familia Penaeidae de la costa Atlántica de América del Sur. Clave para el reconocimiento de las especies y datos bioecológicos. Boletín del Instituto de Biología Marina, 3:1–39.
- Boschma, H.  
1968. *Loxothylacus engeli* nov. spec., a rhizocephalan parasite of the crab *Anasimus latus* Rathbun. Beaufortia, 15:21–26.  
1972. On the occurrence of *Carcinus maenas* (Linnaeus) and its parasite *Sacculina carcini* Thompson in Burma, with notes on the transport of crabs to new localities. Zoologische Mededelingen, 47:145–155.
- Boston, M. A., and A. J. Provenzano, Jr.  
1978. Interspecific infertility in three species of grass shrimp from Chesapeake Bay. American Zoologist, abstract 281, 18(3):621.
- Bott, R.  
1973a. Die Typus-Art der Gattung *Uca* Leach 1814 (Decapoda: Ocypodidae). Senckenbergiana Biologica, 54(4/6):311–314.  
1973b. Die verwandtschaftlichen Beziehungen der *Uca*-Arten (Decapoda: Ocypodidae). Senckenbergiana Biologica, 54(4/6):315–325.
- Bourne, G. C.  
1922. The Raninidae: a study in carcinology. Journal of the Linnean Society of London, Zoology, 35(231):25–79, plates 4–7.
- Bousfield, E. L.  
1955. Ecological control of the occurrence of barnacles in the Miramichi estuary. National Museum of Canada, Bulletin 137, iii + 69 pages.  
1956. Studies on the shore Crustacea collected in eastern Nova Scotia and Newfoundland, 1954. Annual Report of the National Museum of Canada for the Fiscal Year 1954–55, Bulletin 142:127–152.  
1958. Littoral marine arthropods and mollusks collected in western Nova Scotia, 1956. Proceedings of the Nova Scotian Institute of Science, 24(3)(1956–57):303–325.
- Bousfield, E. L., and D. R. Laubitz.  
1972. Station lists and new distributional records of littoral marine invertebrates of the Canadian Atlantic and New England regions. National Museum of Natural Sciences Publications in Biological Oceanography, 5, 51 pages.
- Bousfield, E. L., and A. H. Leim.  
1960. The fauna of Minas Basin and Minas Channel. National Museum of Canada, Bulletin 166:1–30.
- Bouvier, E. L.  
1896. Sur la classification des Lithodinés et sur leur distribution dans les océans. Annales des Sciences Naturelles, Zoologie et Paleontologie, series 8, 1:1–46.  
1898. Sur la classification, les origines et la distribution des crabes de la famille des Dorippidés. Bulletin de la Société Philomathique de Paris, series 8, 9(1896–1897):54–70.  
1905. Sur les Macroures nageurs (abstraction faites des Carides) recueillis par les expéditions américaines du *Hassler* et du *Blake*. Comptes Rendus Hebdomadaires de Séances de l'Académie des Sciences, Paris, 141:746–749.  
1906. Observations sur les Peneides du genre *Haliaporus* Sp. Bate. Bulletin du Muséum Océanographique, Monaco, 81:1–11.  
1915. Sur les formes adaptatives du *Scyllarus arctus* L. et sur le développement post-larvaire des Scyllares. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris, 160:288–291.  
1918. Sur une petite collection de Crustacés de Cuba offerte au Muséum par M. de Boury. Bulletin du Muséum National d'Histoire Naturelle, Paris, 24:6–15.  
1922. Observations complémentaires sur les Crustacés Décapodes (abstraction faite des Carides) provenant des campagnes de S.A.S. le Prince de Monaco. Résultats des Campagnes Scientifiques... Monaco, 62, 106 pages, 6 plates.  
1925. Les Macroures, Marcheurs. Memoirs of the Museum of Comparative Zoology at Harvard College, 47(5):397–472, plates 1–11.  
1940. Décapodes marcheurs. Faune de France, 37. Paul Lechevalier et Fils, Paris, 404 pages, 14 plates.
- Bowler, M. W., and A. J. Seidenberg.  
1971. Salinity tolerance of the prawns, *Palaemonetes vulgaris* and *P. pugio*, and its relationship to the distribution of these species in nature. Virginia Journal of Science, 22(3):94.
- Bowman, T. E.  
1967. The planktonic shrimp, *Lucifer chacei* sp. nov., (Sergestidae: Luciferinae), the Pacific twin of the Atlantic *Lucifer faxoni*. Pacific Science, 21(2):266–271.
- Bowman, T. E., and J. C. McCain.  
1967. Distribution of the planktonic shrimp, *Lucifer*, in the Western North Atlantic. Bulletin of Marine Science, 17(3):660–671.
- Branford, J. R.  
1978. Incubation period for the lobster *Homarus gammarus* at various temperatures. Marine Biology, 47(4):363–368.
- Bray, D. M.  
1976. A review of two western Australian shrimps of the genus *Palaemonetes*, *P. australis* Dakin 1915 and *P. atrinubes* sp. nov. (Decapoda, Palaemonidae). Records of the Western Australian Mu-

- seum, 4(1):65–84.
- Breen, P. A., and K. H. Mann.  
1976. Changing lobster abundance and the destruction of kelp beds by sea urchins. *Marine Biology*, 34(2):137–142.
- Brett, W. J.  
1960. Locomotion and oxygen-consumption rhythms in *Uca pugnax*. *Proceedings of the Indiana Academy of Science*, 69(for 1959):310–311.
- Bridgeman, J. F.  
1969. Life cycles of *Carneophilus choanophallus* n. sp. and *C. basodactylophallus* n. sp. (Trematoda: Microphallidae). *Tulane Studies in Zoology and Botany*, 15(3):81–105.
- Broad, A. C.  
1950. The North Carolina shrimp survey. University of North Carolina Institute of Fisheries Research Annual Report, 1950, 62 pages.  
1957. Larval development of *Palaemonetes pugio* Holthuis. *Biological Bulletin*, 112(2):144–161, plates 1–4.  
1957a. The relationship between diet and larval development of *Palaemonetes*. *Biological Bulletin*, 112(2):162–170.  
1957b. Larval development of the crustacean *Thor floridanus* Kingsley. *Journal of the Elisha Mitchell Scientific Society*, 73(2):317–328.
- Broekhuysen, G. J., Jr.  
1936. On development, growth and distribution of *Carcinides maenas* (L.). *Archives Neerlandaises de Zoologie*, 2(2 & 3):257–399.
- Brooks, W. K.  
1882. *Lucifer*, a study in development. *Philosophical Transactions of the Royal Society of London*, 173(1):57–137, plates 1–11.
- Brooks, W. K., and F. H. Herrick.  
1892. The embryology and metamorphosis of the Macrourea. *Memoirs, National Academy of Sciences*, 5(4):323–576, plates 1–57.
- Brooks, W. K., and E. B. Wilson.  
1883. The first zoea of *Porcellana*. *Studies from the Biological Laboratory, Johns Hopkins University*, 2:58–64, plates 6–7.
- Brown, A., Jr., and D. Patlan.  
1974. Color changes in the ovaries of penaeid shrimp as a determinant of their maturity. *Marine Fisheries Review*, 36(7):23–26, colored figures 1–12.
- Brown, F. A.  
1939. The coloration and colour changes of the Gulf-weed shrimp, *Latreutes fucorum*. *American Naturalist*, 73 (749):564–568.
- Bruce, A. J.  
1974. On *Lysmata grabhami* (Gordon), a widely distributed tropical hippolytid shrimp (Decapoda, Caridea). *Crustaceana* 27(1):107–109, 1 plate.  
1975. On the occurrence of *Discias atlanticus* Gurney, 1939 in the western Indian Ocean (Decapoda, Caridea). *Crustaceana*, 29(3):301–305.
- Brucks, J. T.  
1971. Currents of the Caribbean and adjacent regions as deduced from drift-bottle studies. *Bulletin of Marine Science*, 21(2):455–465.
- Brues, C. T.  
1927. Occurrence of the marine crab *Callinectes ornatus* in brackish and fresh water. *American Naturalist*, 6(677):566–568.
- Brunel, P.  
1961. Observations sur la biologie et la biométrie du crabe-araignée *Chionoecetes opilio* Fabr. *Station de Biologie Marine, Grande-Rivière, Rapport Annuel, 1960*, pages 59–67.  
1970. Catalogue d'invertébrés benthiques du Golfe Saint-Laurent recueillis de 1951 à 1966 par la Station de Biologie Marine de Grande-Rivière. *Travaux de Biologie de l'Université de Montréal*, 53, 54 pages.
- Brusher, H. A., W. C. Renfro, and R. A. Neal.  
1972. Notes on distribution, size, and ovarian development of some penaeid shrimps in the northwestern Gulf of Mexico, 1961–62. *Contributions in Marine Science, University of Texas Marine Science Institute*, 16:75–87.
- Bryce, G. W., Jr.  
1961. Larval development of *Tozeuma carolinense* Kingsley, including ecological notes on adults. *Master's Thesis, University of North Carolina, Chapel Hill*, 59 pages.
- Buchanan, J. B.  
1963. The biology of *Calocaris macandreae* (Crustacea: Thalassinidea). *Journal of the Marine Biological Association of the United Kingdom*, 43(3):729–747.
- Buesa Mas, R. J.  
1961. Segunda pesca exploratoria y datos biológicos de la langosta *Panulirus argus* en Cuba. *Centro de Investigaciones Pesqueras, Contribucion*, 12:1–66.
- Buitendijk, A. M., and L. B. Holthuis.  
1949. Note on the Zuiderzee crab, *Rithropanopeus harrisi* (Gould) subspecies *tridentatus* (Maitland). *Zoologische Mededelingen*, 30(7):95–106.
- Bulgurkov, K.  
1968. Occurrence of *Callinectes sapidus* Rathbun (Crustacea Decapoda) in Black Sea. *Proceedings of the Research Institute of Fisheries and Oceanography, Varna*, 9:97–99. (In Russian with English summary.)
- Bullis, H. R., Jr., and J. R. Thompson.  
1965. Collections by the exploratory fishing vessels *Oregon*, *Silver Bay*, *Combat*, and *Pelican* made during 1956–1960 in the southwestern North Atlantic. *United States Fish and Wildlife Service Special Scientific Report—Fisheries*, 510, iv + 130 pages.
- Burkenroad, M. D.  
1934a. Littoral Penaeidea chiefly from the Bingham Oceanographic Collection. With a revision of *Penaeopsis* and description of two new genera

- and eleven new American species. *Bulletin of the Bingham Oceanographic Collection*, 4(7): 1–109.
- 1934b. The Penaeidea of Louisiana with a discussion of their world relationships. *Bulletin of the American Museum of Natural History*, 68(2):1–143.
1936. The Aristaeinae, Solenocerinae and pelagic Penaeinae of the Bingham Oceanographic Collection. *Bulletin of the Bingham Oceanographic Collection*, 5(2):1–151.
1939. Further observations on Penaeidae of the northern Gulf of Mexico. *Bulletin of the Bingham Oceanographic Collection*, 6(6):1–62.
1945. Status of the name *Sicyonia* H.M.E., with a note on *S. typica* (Boeck) and description of two new species. *Arkiv for Zoologi, K. Svenska Vetenskapsakademien, Stockholm*, 37A(9):1–10.
- 1947a. Reproductive activities of decapod Crustacea. *American Naturalist*, 81(800):392–398.
- 1947b. Production of sound by the fiddler crab, *Uca pugilator* Bosc, with remarks on its nocturnal and mating behaviour. *Ecology*, 28(4):458–462.
1949. Occurrence and life histories of commercial shrimp. *Science*, 110(2869):688–689.
1963. The evolution of the Eucarida, (Crustacea, Eumalacostraca), in relation to the fossil record. *Tulane Studies in Geology*, 2(1):2–17.
- Bursey, C. R.  
1978. Temperature and salinity tolerance of the mole crab, *Emerita talpoida* (Say) (Crustacea, Anomura). *Comparative Biochemistry and Physiology*, 61A(1):81–83.
- Bursey, C. R., and E. E. Bonner.  
1977. Osmotic regulation and salinity tolerance of the mole crab, *Emerita talpoida* (Say) (Crustacea, Anomura). *Comparative Biochemistry and Physiology*, 57A(2):207–210.
- Burukovskii, R. N.  
1972. Some problems of the taxonomy and distribution of prawns of the genus *Penaeus*. (Nekotorye voprosy sistematiki i rasprostraneniya krevetok roda *Penaeus*). *Trudy AtlantNIRO*, 42:3–19. From: *Rybokhozyaistvennye issledovaniya v Atlanticheskom okeane* (Fisheries Research in the Atlantic Ocean).
- Burukovsky, R. N.  
1974. *Opredelitel' krevetok langusutov i omarov*. (Determination of shrimps, spiny lobsters and lobsters.) Moscow. Food Industry, 128 pages. (In Russian.)
- Butler, T. H.  
1964. Record of shrimps (Order Decapoda) from British Columbia. *Journal of the Fisheries Research Board of Canada*, 21(2):419–421.
- 1964a. Growth, reproduction, and distribution of pandalid shrimps in British Columbia. *Journal of the Fisheries Research Board of Canada*, 21(6):1403–1452.
1971. A review of the biology of the pink shrimp, *Pandalus borealis* Krøyer 1838. *Biology of Canadian shrimp and review of research problems*. *Canadian Fisheries Reports*, 17:17–24.
1980. Shrimps of the Pacific coast of Canada. *Canadian Bulletin of Fisheries and Aquatic Sciences*, Bulletin 202, 280 pages, frontispiece and plates 1–8 (colored).
- Caddy J. F.  
1973. Underwater observations on tracks of dredges and trawls and some effects of dredging on a scallop ground. *Journal of the Fisheries Research Board of Canada*, 30(2):173–180.
- Cain, T. D.  
1972. Additional epifauna of a reef off North Carolina. *Journal of the Elisha Mitchell Scientific Society*, 88(2):79–82.
- Caine, E. A.  
1974. Feeding of *Ovalipes guadalupeensis* (Saussure) (Decapoda: Brachyura: Portunidae), and morphological adaptations to a burrowing existence. *Biological Bulletin*, 147(3):550–559.
1975. Feeding and masticatory structures of selected Anomura (Crustacea). *Journal of Experimental Marine Biology and Ecology*, 18(3):277–301.
- 1975a. Feeding of *Pinnotheres maculatus* Say (Brachyura: Pinnotheridae). *Forma et Functio*, 8(3/4):395–403.
1976. Relationship between diet and the gland filter of the gastric mill in hermit crabs (Decapoda, Paguridea). *Crustaceana*, 31(3):312–313.
- Calef, G. W., and G. D. Grice.  
1967. Influence of the Amazon River outflow on the ecology of the western tropical Atlantic. II. Zooplankton abundance, copepod distribution, with remarks on the fauna of low-salinity areas. *Journal of Marine Research*, 25(1):84–94.
- Calman, W. T.  
1899. On the British Pandalidae. *The Annals and Magazine of Natural History*, series 7, 3(13), article 2:27–29, plates 1–4.
1909. Crustacea. Part 7, Appendiculata, fascicle 3. In R. Lankester (ed.), *A treatise on zoology*. London, Adams and Charles Black, viii + 346 pages.
- Camp, D. K., N. H. Whiting, and R. E. Martin.  
1977. Nearshore marine ecology at Hutchinson Island, Florida: 1971–1974. V. Arthropods. *Florida Marine Research Publications*, 25:1–63.
- Cano, G.  
1893. Sviluppo dei dromidei. *Atti della Reale Accademia della Scienze Fisiche e Matematiche di Napoli*, series 2, 4(for 1894)(2):1–23, 2 plates.
- Capen, R. L.  
1972. Studies of water uptake in the euryhaline crab, *Rhithropanopeus harrisi*. *The Journal of Experimental Zoology*, 182(3):307–319.

- Cargo, D. G.  
1960. A megalops of the blue crab, *Callinectes sapidus*, in the Patuxent River, Maryland. Chesapeake Science, 1(2):110.
- Carlgren, O., and J. W. Hedgpeth.  
1952. Actiniaria, Zoantharia and Ceriantharia from shallow water in the northwestern Gulf of Mexico. Publications of the Institute of Marine Science, Texas, 2(2):140–172.
- Carlisle, D. B.  
1957. On the hormonal inhibition of moulting in decapod Crustacea. Journal of the Marine Biological Association of the United Kingdom, 36(2):291–307.  
1959. On the sexual biology of *Pandalus borealis* (Crustacea Decapoda). I. Histology of incretory elements. Journal of the Marine Biological Association of the United Kingdom, 38(2):381–394.  
1959a. On the sexual biology of *Pandalus borealis* (Crustacea Decapoda). II. The termination of the male phase. Journal of the Marine Biological Association of the United Kingdom, 38(3):481–491.  
1959b. On the sexual biology of *Pandalus borealis* (Crustacea Decapoda). III. The initiation of the female phase. Journal of the Marine Biological Association of the United Kingdom, 38(3):493–506.
- Carrillo, V. F.  
1968. Morfología de *Macrobrachium acanthurus* Wiegmann en el Estado de Veracruz, Mexico. F. A. O. Fisheries Reports (Food and Agriculture Organization of the United Nations), 57(2):415–425.
- Carvacho, A.  
1977. Sur le palpe mandibulaire dans the genre *Leander* Desmarest (Decapoda, Palaemonidae). Crustaceana, 33(1):100–101.  
1979. Les crevettes carides de la mangrove guadeloupéenne. Bulletin du Muséum National d'Histoire Naturelle, Paris, series 4, 1, section A(2):445–470.
- Catesby, M.  
1743. The Natural History of Carolina, Florida and the Bahama Islands: . . . II, pages 1–100, i-xliv, 7 pages, plates 1–100, 1–20. London.
- Caullery M.  
1896. Crustacés Schizopodes et Décapodes. In Résultats scientifiques de la campagne du *Caudan* dans le Golfe de Gascogne. Annales de l'Université de Lyon, fascicule 26:365–419, plates 13–17.
- Causey, D.  
1961. The barnacle genus *Octolasmis* in the Gulf of Mexico. Turtox News, 39(2):51–55.
- Cerame-Vivas, M. J., A. B. Williams, and I. E. Gray.  
1963. New decapod crustacean records for the coast of North Carolina. Crustaceana, 5(2):157–159.
- Cerame-Vivas, M. J., and I. E. Gray  
1966. The distributional pattern of benthic invertebrates of the continental shelf off North Carolina. Ecology, 47(2):260–270.
- Chace, F. A., Jr.  
1937. The Templeton Crocker Expedition. VII. Caridean decapod Crustacea from the Gulf of California and the west coast of Lower California. Zoologica, 22(2):109–138.  
1939a. Reports on the scientific results of the first Atlantis expedition to the West Indies, under the joint auspices of the University of Havana and Harvard University. Preliminary descriptions of one new genus and seventeen new species of decapod and stomatopod Crustacea. Memorias de la Sociedad Cubana de Historia Natural, 13(1):31–54.  
1939b. On the systematic status of the crustacean genera *Naushonia*, *Homoriscus*, and *Coralliocrangon*. Annals and Magazine of Natural History, series 11, 3:524–530.  
1940. Reports on the scientific results of the Atlantis expeditions to the West Indies, under the joint auspices of the University of Havana and Harvard University. The brachyuran crabs. Torreia, Havana, 4:1–67.  
1942. Reports on the scientific results of the Atlantis expeditions to the West Indies, under the joint auspices of the University of Havana and Harvard University. The Anomuran Crustacea. I. Galatheidae. Torreia, Havana, 11:1–106.  
1942a. Six new species of decapod and stomatopod Crustacea from the Gulf of Mexico. Proceedings of the New England Zoological Club, 19:79–92, plates 23–28.  
1951. The oceanic crabs of the genera *Planes* and *Pachygrapsus*. Proceedings of the United States National Museum, 101(3272):65–103.  
1955. Notes on shrimps from the Marshall Islands. Proceedings of the United States National Museum, 105(3349):1–22.  
1958. A new shrimp of the genus *Periclimenes* from the West Indies. Proceedings of the Biological Society of Washington, 71:125–132.  
1966. Decapod crustaceans from St. Helena Island, South Atlantic. Proceedings of the United States National Museum, 118(3536):623–661, 2 plates.  
1968. A new crab of the genus *Cycloes* (Crustacea; Brachyura; Calappidae) from Saint Helena, South Atlantic Ocean. Proceedings of the Biological Society of Washington, 81(55):605–612.  
1970. A new shrimp of the genus *Lysmata* (Decapoda, Hippolytidae) from the western Atlantic. Crustaceana, 19(1):59–66.  
1972. The shrimps of the Smithsonian-Bredin Caribbean Expeditions with a summary of the West Indian shallow-water species (Crustacea: De-



- capoda: Natantia). Smithsonian Contributions to Zoology, 98:i-x, 1-179.
- 1972a. *Palaemon debilis* from Hawaii and the status of the genus *Palaemonetes* (Decapoda, Palaemonidae). Crustaceana, 23(1):12-19.
1976. Shrimps of the pasiphaeid genus *Leptochela* with descriptions of three new species (Crustacea: Decapoda: Caridea). Smithsonian Contributions to Zoology, 222, iii + 51 pages.
- Chace, F. A., Jr., and D.E. Brown.
1978. A new polychelate shrimp from the Great Barrier Reef of Australia and its bearing on the family Bresiliidae (Crustacea: Decapoda: Caridea). Proceedings of the Biological Society of Washington, 91(3):756-766.
- Chace, F. A., Jr., and H. H. Hobbs, Jr.
1969. The freshwater and terrestrial decapod crustaceans of the West Indies with special reference to Dominica. Bredin-Archbold-Smithsonian Biological Survey of Dominica. United States National Museum Bulletin, 292, v + 258 pages, plates 1-5.
- Chace, F. A., Jr., and R. B. Manning.
1972. Two new caridean shrimps, one representing a new family, from marine pools on Ascension Island (Crustacea: Decapoda: Natantia). Smithsonian Contributions to Zoology, 131, 18 pages.
- Chamberlain, N. A.
1957. Larval development of *Neopanope texana sayi*. Biological Bulletin, 113(2):338.
1961. Studies on the larval development of *Neopanope texana sayi* (Smith) and other crabs of the family Xanthidae (Brachyura). Chesapeake Bay Institute, The Johns Hopkins University, Technical Report 22, 35 pages, 16 plates.
1962. Ecological studies of the larval development of *Rhithropanopeus harrisi* (Xanthidae, Brachyura). Chesapeake Bay Institute, The Johns Hopkins University, Technical Report 28, ii + 47 pages.
- Chapple, W. D.
- 1969a. Postural control of shell position by the abdomen of the hermit crab, *Pagurus pollicarus* [sic]. I. Morphology of the superficial muscles and their nerves. Journal of Experimental Zoology, 171:397-408.
- 1969b. Postural control of shell position by the abdomen of the hermit crab, *Pagurus pollicarus* [sic]. II. Reflex control of the ventral superficial muscle. Journal of Experimental Zoology, 171:409-416.
- 1969c. Postural control of shell position by the abdomen of the hermit crab, *Pagurus pollicarus* [sic]. III. Analysis of movements and calculations of forces exerted by the muscles. Journal of Experimental Zoology, 171:417-424.
- Cheung, T. S.
- 1966a. An observed act of copulation in the shore crab, *Carcinus maenas* (L.). Crustaceana, 11(1):107-108.
- 1966b. The development of egg membranes and egg attachment in the shore crab, *Carcinus maenas* and some related decapods. Journal of the Marine Biological Association of the United Kingdom, 46(2):373-400.
1968. Trans-molt retention of sperm in the female stone crab, *Menippe mercenaria* (Say). Crustaceana, 15(1):117-120.
1969. The environmental and hormonal control of growth and reproduction in the adult female stone crab, *Menippe mercenaria* (Say). Biological Bulletin, 36(3):327-346.
1973. Experiments on the simultaneous regeneration of claws in the aged male stone crab, *Menippe mercenaria* (Say), with special reference to the terminal molt. Bulletin of the Institute of Zoology, Academia Sinica (Taipei), 12(1):1-11.
1976. A biostatistical study of the functional consistency in the reversed claws of the adult male stone crabs, *Menippe mercenaria* (Say). Crustaceana, 31(2):137-144.
- Chin, E.
1960. The bait shrimp fishery of Galveston Bay, Texas. Transactions of the American Fisheries Society, 89(2):135-141.
- Chin, E., and D. M. Allen.
1959. List of references on the biology of shrimp. United States Fish and Wildlife Service, Special Scientific Report—Fisheries, 276:1-143.
- China, W. E. (editor).
1966. Official list of generic names in zoology. Second installment: Names 1257-1651. International Trust for Zoological Nomenclature, London, xli-xliii, 201-267 pages.
- Choudhury, P. C.
1970. Complete larval development of the palaemonid shrimp *Macrobrachium acanthurus* (Wiegmann, 1836), reared in the laboratory. Crustaceana, 18(2):113-132.
1971. Laboratory rearing of larvae of the palaemonid shrimp *Macrobrachium acanthurus* (Wiegmann, 1836). Crustaceana, 21(2):113-126.
- Christensen, A. M., and J. J. McDermott.
1958. Life-history and biology of the oyster crab, *Pinnotheres ostreum* Say. Biological Bulletin, 114(2):146-179.
- Christiansen, M. E.
1969. Crustacea Decapoda Brachyura. Marine Invertebrates of Scandinavia, Universitetsforlaget, Oslo, 143 pages.
1971. Larval development of *Hyas araneus* (Linnaeus) with and without antibiotics (Decapoda, Brachyura, Majidae). Crustaceana, 21(3):307-315.
1973. The complete larval development of *Hyas araneus* (Linnaeus) and *Hyas coarctatus* Leach (Decapoda, Brachyura, Majidae) reared in the laboratory. Norwegian Journal of Zoology, 21(2):63-89.
- Christiansen, M. E., and B. O. Christiansen.
1962. The Crustacea Decapoda of Isfjorden, a comparison with the Swedish Spitsbergen Expe-

- dition in 1908. Tromsø Museum Biological Svalbard Expedition 1958. Acta Borealia, A. Scientia, 19, 53 pages.
- Christiansen, M. E., and J. D. Costlow, Jr.  
1975. The effect of salinity and cyclic temperature on larval development of the mud-crab *Rhithropanopeus harrisi* (Brachyura: Xanthidae) reared in the laboratory. Marine Biology, 32(3):215–221.
- Christiansen, M. E., J. D. Costlow, Jr., and R. J. Monroe.  
1977a. Effects of the juvenile hormone mimic ZR-515 (Altosid®) on larval development of the mud-crab *Rhithropanopeus harrisi* in various salinities and cyclic temperatures. Marine Biology, 39(3):269–279.  
1977b. Effects of the juvenile hormone mimic ZR-512 (Altozar®) on larval development of the mud-crab *Rhithropanopeus harrisi* at various cyclic temperatures. Marine Biology, 39(3):281–288.
- Christmas, J. Y.  
1969. Parasitic barnacles in Mississippi estuaries with special reference to *Loxothylacus texanus* Boschma in the blue crab (*Callinectes sapidus*). Proceedings of the 22nd Annual Conference, Southeastern Game and Fish Commissioners, pages 272–275.
- Christmas, J. Y., G. Gunter, and P. Musgrave.  
1966. Studies of annual abundance of postlarval penaeid shrimp in the estuarine waters of Mississippi as related to subsequent commercial catches. Gulf Research Reports, 2(2):177–212.
- Christoffersen, M. L.  
1979. Decapod Crustacea: Alpheoidea. Résultats Scientifiques des Campagnes de la *Calypso*, Fascicule 11. Campagne de la *Calypso* au large des Côtes Atlantiques de l'Amérique du Sud (1961–1962). I. Number 36. Annales de l'Institut Océanographique, new series 55, fascicule supplement: 297–377.
- Christy, J. H.  
1978. Adaptive significance of reproductive cycles in the fiddler crab *Uca pugilator*: a hypothesis. Science, 199(4327):453–455.
- Churchill, E. P., Jr.  
1919. Life history of the blue crab. Bulletin of the Bureau of Fisheries, 36 (for 1917–18):95–128, colored frontispiece, plates 47–55.
- Clark, E.  
1965. Parasitic stone crab? Sea Frontiers, 11(1):52–54.
- Clay, E.  
1965. Literature survey of the common fauna of estuaries. 16. *Carcinus maenas* L. Imperial Chemical Industries Ltd. Brixham Laboratory, PVM45/A/916, 16 pages.
- Clifton, H. E., C. V. W. Mahnken, J. C. Van Derwalker, and R. A. Waller.  
1970. Tektite 1, Man-in-the-sea-project: marine science program. Science, 168(3932):659–663.
- Cobb, J. S., and B. F. Phillips (eds.).  
1980. The biology and management of lobsters. Vol. I. Physiology and behavior, xv + 463 pages. Vol. II. Ecology and management, xiii + 390 pages, Academic Press, New York.
- Cobb, S. J. [sic].  
1976. The American lobster: the biology of *Homarus americanus*. Zoology/NOAA Sea Grant, University of Rhode Island, Marine Technical Report 49, 32 pages.
- Cobb, S. P.  
1971. A new species of *Sicyonia* (Decapoda, Penaeidae) from the Western Atlantic with notes on *S. stimpsoni* Bouvier. Crustaceana, 20(1):104–111.
- Cobb, S. P., C. R. Futch, and D. K. Camp.  
1973. The rock shrimp, *Sicyonia brevirostris* Stimpson, 1871 (Decapoda, Penaeidae). Memoirs of the Hourglass Cruises, 3(1):1–38.
- Coelho, P. A.  
1964. Alguns crustáceos decapodos novos para Pernambuco e Estados vizinhos na Coleção Carcinológica do Instituto Oceanográfico da 256. Universidade do Recife. Ciência e Cultura, 16(2):255–256.  
1966a. Lista dos Porcellanidae (Crustácea, Decápoda, Anomura) do litoral de Pernambuco e dos estados vizinhos. Trabalhos Instituto de Biologia Marítima e Oceanográficos, Universidade Recife, Brazil, 5/6 (for 1963–64):51–68.  
1966b. Distribuição dos Crustáceos decápodos na área de Barra das Jangadas. Trabalhos Instituto Oceanográficos, Universidade Recife, Brazil, 5/6 (for 1963–64):159–173.  
1966c. Nota sobre a abundância do Raninidae *Symethis variolosa* (Fabricius) no nordeste do Brasil. Ciência e Cultura, São Paulo, 18(2):252–253.  
1967. Os crustáceos decápodos de alguns manguezais Pernambucanos. Trabalhos Instituto Oceanográficos, Universidade de Recife, Brazil, 7/8: 71–90.  
1970. Estuários e lugunas do Nordeste. Pages 49–60, in J. Vasconcelos Sobrinho. As regiões naturais do Nordeste, o meio e a civilização. Recife, Conselho do Desenvolvimento de Pernambuco, 1970.  
1971. Nota previa sobre os Majidae do Norte e Nordeste do Brasil (Crustacea, Decapoda). Arquivos do Museu Nacional, 54:137–143.
- Coelho, P. A., and M. de A. Ramos.  
1972. A constituição e a distribuição da fauna de decápodos do litoral leste da América do Sul entre as latitudes de 5°N e 39°S. Trabalhos do Instituto Oceanográficos, Universidade Federal, Pernambuco, Recife, 13:133–236.
- Collins, J. S. H., and S. F. Morris.  
1976. Tertiary and Pleistocene crabs from Barbados and Trinidad. Palaeontology, 19(1):107–131, plates 17–20.
- Colwell, R. R., T. C. Wicks, and H. S. Tubiash.  
1975. A comparative study of the bacterial flora of the hemolymph of *Callinectes sapidus*. Marine Fisheries Review, 37(5–6):29–33.

- Connolly, C. J.  
1923. The larval stages and megalops of *Cancer amoenus*. Contributions to Canadian Biology, new series, 1(17):335–352.  
1925. The larval stages and megalops of *Rhithropanopeus harrisi* (Gould). Contributions to Canadian Biology, Toronto, new series, 2(15):327–333, 3 plates.
- Conover, M. R., and D. E. Miller.  
1978. The importance of the large chelae in the territorial and pairing behaviour of the snapping shrimp, *Alpheus heterochaelis*. Marine Behaviour and Physiology, 5(3):185–192.
- Cook, H. L.  
1966. A generic key to the protozoan, mysis and postlarval stages of the littoral penaeidae of the northwestern Gulf of Mexico. Fishery Bulletin, 65(2):437–447.
- Cook, H. L., and M. J. Lindner.  
1970. Synopsis of biological data on the brown shrimp *Penaeus aztecus aztecus* Ives, 1891. FAO Fisheries Reports, 57(4):1471–1497.
- Cook, H. L., and M. A. Murphy.  
1965. Early developmental stages of the rock shrimp, *Sicyonia brevirostris* Stimpson, reared in the laboratory. Tulane Studies in Zoology, 12(4):109–127.  
1971. Early developmental stages of the brown shrimp, *Penaeus aztecus* Ives, reared in the laboratory. Fishery Bulletin, 69(1):223–239.
- Cooley, N. R.  
1978. An inventory of the estuarine fauna in the vicinity of Pensacola Florida. Florida Marine Research Publications, 31:1–119.
- Coonfield, B. R.  
1940. The chromatophore system of the larvae of *Crangon armillatus*. Papers from Tortugas Laboratory, Carnegie Institution of Washington, 37(7):121–126, 1 plate.
- Cooper, G. M.  
1933. Dr. Clarence A. Shore. In Second General Session. Transactions of the Medical Society of the State of North Carolina, 80th Annual Session, Raleigh, N. C., April 17th, 18th and 19th, pages 117–122.  
1940. Dr. Clarence A. Shore and the State Laboratory of Hygiene. In Dedication Exercises State Laboratory of Hygiene, Raleigh, February 21, 1940. The Health Bulletin, 55(4):16–19.
- Cooper R. A., and J. R. Uzman.  
1971. Migrations and growth of deep-sea lobsters, *Homarus americanus*. Science, 171(3968):288–290.
- Copeland, B. J., and V. Truitt.  
1966. Fauna of the Aransas Pass Inlet, Texas. Texas Journal of Science, 18(1):65–74.
- Cornick, J. W., and J. E. Stewart.  
1968. Pathogenicity of *Gaffkya homari* for the crab *Cancer irroratus*. Journal of the Fisheries Research Board of Canada, 25(4):795–799.
- Corredor, L.  
1978. Notes on the behavior and ecology of the new fish cleaner shrimp *Brachycarpus biunguiculatus* (Lucas) (Decapoda, Natantia, Palaemonidae). Crustaceana, 35(1):35–40.
- Corrington, J. D.  
1927. Commensal association of a spider crab and a medusa. Biological Bulletin, 53(5):346–350.
- Costello, T. J., and D. M. Allen.  
1970. Synopsis of biological data on the pink shrimp *Penaeus duorarum duorarum* Burkenroad. F.A.O. Fisheries Reports, 57(4):1499–1537.
- Costello, T., T. M. Bert, D. G. Cartano, G. Davis, G. Lyon, C. Rockwood, J. Stevely, J. Tashiro, W. L. Trent, D. Turgeon, and J. Zuboy.  
1979. Fishery management plan for the stone crab fishery of the Gulf of Mexico. Pages 19450–19496 in Stone crab fishery; plan approval and proposed regulations. Federal Register, 44(65), book 1:19444–19496.
- Costlow, J. D., Jr.  
1965. Variability in larval stages of the blue crab, *Callinectes sapidus*. Biological Bulletin, 128(1):58–66.  
1966. The effect of eyestalk extirpation on larval development of the crab *Sesarma reticulatum* Say. Pages 209–224 in Harold Barnes (ed.), Some contemporary studies in marine science. Hafner Publishing Co., New York, 716 pages.  
1976. The effect of salinity and temperature on survival and metamorphosis of megalops of the blue crab *Callinectes sapidus*. Helgolander Wissenschaftliche Meeresuntersuchungen, 15:84–97.
- Costlow, J. D., Jr., and C. G. Bookhout.  
1959. The larval development of *Callinectes sapidus* Rathbun reared in the laboratory. Biological Bulletin, 116(3):373–396.  
1960. The complete larval development of *Sesarma cinereum* (Bosc) reared in the laboratory. Biological Bulletin, 118(2):203–214.  
1961a. The larval stages of *Panopeus herbstii* Milne-Edwards reared in the laboratory. Journal of the Elisha Mitchell Scientific Society, 77(1):33–42.  
1961b. The larval development of *Eurypanopeus depressus* (Smith) under laboratory conditions. Crustaceana, 2(1):6–15.  
1962a. The larval development of *Sesarma reticulatum* Say reared in the laboratory. Crustaceana, 4(4):281–294.  
1962b. The larval development of *Hepatus epheliticus* (L.) under laboratory conditions. Journal of the Elisha Mitchell Scientific Society, 78(2):113–125.  
1966a. The larval development of *Ovalipes ocellatus* (Herbst) under laboratory conditions. Journal of the Elisha Mitchell Scientific Society, 82(2):160–171.  
1966b. Larval stages of the crab, *Pinnotheres maculatus*, under laboratory conditions. Chesapeake Sci-

- ence, 7(3):157–163.
- 1966c. Larval development of the crab *Hexapanopeus angustifrons*. Chesapeake Science, 7(3):148–156.
1968. Larval development of the crab, *Leptodius agassizii* A. Milne Edwards in the laboratory (Brachyura, Xanthidae). Crustaceana, supplement 2, Studies on decapod larval development, pages 203–213.
- Costlow, J. D., and A. N. Sastry.
1966. Free amino acids in developing stages of two crabs, *Callinectes sapidus* and *Rhithropanopeus harrisi* (Gould). Acta Embryologiae et Morphologiae Experimentalis, 9:44–55.
- Costlow, J. D., Jr., C. G. Bookhout, and R. Monroe.
1960. The effect of salinity and temperature on larval development of *Sesarma cinereum* (Bosc) reared in the laboratory. Biological Bulletin, 118(2):183–202.
1962. Salinity-temperature effects on the larval development of the crab, *Panopeus herbstii* Milne-Edwards, reared in the laboratory. Physiological Zoology, 35(1):79–93.
1966. Studies on the larval development of the crab, *Rhithropanopeus harrisi* (Gould). 1. The effect of salinity and temperature on larval development. Physiological Zoology, 39(2):81–100.
- Costlow, J. D., Jr., G. H. Rees, and C. G. Bookhout.
1959. Preliminary note on the complete larval development of *Callinectes sapidus* Rathbun under laboratory conditions. Limnology and Oceanography, 4(2):222–223.
- Couch, J. A.
1978. Diseases, parasites, and toxic responses of commercial penaeid shrimps of the Gulf of Mexico and south Atlantic coasts of North America. Fishery Bulletin, 76(1):1–44.
- Coues, E.
1871. Notes on the natural history of Fort Macon, N. C., and vicinity. (No. 2). Proceedings of the Academy of Natural Sciences of Philadelphia, 23(1):120–148.
- Coutière, H.
1902. Sur quelques especes nouvelles du genre *Automate* de Man. Bulletin du Muséum d'Histoire Naturelle (Paris), 8(5):337–342.
1909. The American species of snapping shrimps of the genus *Synalpheus*. Proceedings of the United States National Museum, 36(1659):1–93.
- Couture, R.
1968. Ecologie d'*Argis dentata* Rathbun. (Rapport préliminaire des travaux en cours, été 1967.) Station de Biologie Marine, Grande-Rivière, Québec, Rapport Annuel, pages 57–59.
- Couture, R., and G. Filteau.
1971. Age, croissance et mortalité d'*Argis dentata* (Crustacea, Decapoda) dans de sud-ouest du golfe Saint-Laurent. Le Naturaliste Canadien, 98(5):837–850.
- Couture, R., and P. Trudel.
1968. Les crevettes des eaux côtières du Québec. Le Naturaliste Canadien, 95:857–885.
1969. Biologie et écologie de *Pandalus montagui* Leach (Decapoda Natantia). I. Distribution et migrations, à Grande-Rivière (Gaspé), Québec. Le Naturaliste Canadien, 96(3):283–299.
- 1969a. Biologie et écologie de *Pandalus montagui* Leach (Decapoda Natantia). II. Âge, croissance et reproduction. Le Naturaliste Canadien, 96(3):301–315.
- Cowles, R. P.
1908. I. Habits, reactions, and associations in *Ocypoda arenaria*. Papers from the Tortugas Laboratory of the Carnegie Institution of Washington, 2(1):1–41.
1930. A biological study of the offshore waters of Chesapeake Bay. Bulletin of the United States Bureau of Fisheries, 46:277–381.
- Craig, W. J., Jr.
1974. Physiological ecology of the commensal crabs, *Polyonyx gibbesi* Haig and *Pinnixa chaetoptera* Stimpson. Oecologia, 15(3):235–244.
- Crane, J.
1941. On the growth and ecology of brachyuran crabs of the genus *Ocypode*. (Eastern Pacific Expeditions of the New York Zoological Society. XXIX.) Zoologica 26, pt. 4(29):297–310, 2 plates.
1943. Display, breeding and relationships of fiddler crabs (Brachyura, Genus *Uca*) in the northeastern United States. Zoologica, 28, pt. 4(23):217–223.
1975. Fiddler crabs of the world. Ocypodidae: genus *Uca*. Princeton University Press, Princeton, N.J., xxiv + 736 pages, 21 maps, 50 plates.
- Crawford, D. R., and W. J. J. deSmidt.
1922. The spiny lobster, *Panulirus argus*, of southern Florida: its natural history and utilization. Bulletin of the United States Bureau of Fisheries, 38(for 1921–22):281–310.
- Creaser, E. P.
1950. Repetition of egg laying and number of eggs of the Bermuda spiny lobster. Proceedings of the Gulf and Caribbean Fisheries Institute, November 1949, pages 30–31.
1952. Sexual dimorphism in weight and length relationships of the Bermuda spiny lobster. Proceedings of the Gulf and Caribbean Fisheries Institute, Fourth Annual Session, November 1951, pages 59–63.
- Creaser, E. P., and D. Travis.
1950. Evidence of a homing instinct in the Bermuda spiny lobster. Science, 112(2902):169–170.
- Criales, M.-M.
1980. Commensal caridean shrimps of Octocorallia and Antipatharia in Curaçao and Bonaire. Studies Fauna Curaçao, 61:68–85.
- Crichton, O. W.
1960. Marsh crab, intertidal tunnel-maker and grass-eater. Estuarine Bulletin, University of Dela-

- ware, 5(4):3–10.
1974. Caloric studies of *Spartina* and the marsh crab *Sesarma reticulatum* (Say). Pages 142–144 in F. C. Daiber, Tidal marshes of Delaware, pages 99–149 in H. T. Odum, B. J. Copeland and E. A. McMahan (eds.), Coastal ecological systems of the United States, Vol. II. The Coastal Conservation Foundation, Washington, D.C., 521 pages.
- Cronin, E. T., and T. W. Johnson, Jr.  
1958. A halophilic *Enterobryus* in the mole crab *Emerita talpoida* Say. *Journal of the Elisha Mitchell Scientific Society*, 74:167–172.
- Cronin, L. E., J. C. Daiber, and E. M. Hulbert.  
1962. Quantitative seasonal aspects of zooplankton in the Delaware River estuary. *Chesapeake Science*, 3(2):63–93.
- Cronin, T. W.  
1979. Factors contributing to the retention of larvae of the crab *Rhithropanopeus harrisi* in the Newport River estuary, North Carolina. Dissertation Abstracts International, 40(10):4690-B. Ph.D., Duke University, 1979, 218 pages.
- Crosnier, A.  
1965. Faune de Madagascar. XVIII. Crustacés Décapodes. Grapsidae et Ocypodidae. Office de la Recherche Scientifique et Technique Outre-Mer (O.R.S.T.O.M.), Paris, 143 pages, plates 1–11.
- Crosnier, A., and J. Forest.  
1966. Campagne de la *Calypso* dans le golfe de Guinée et aux îles Principe, São Tomé et Annobon (1956), et campagne aux îles du Cap Vert (1959). (Suite). 19. Crustacés Décapodes: Alpheidae. Résultats Scientifiques des Campagnes de la "Calypso," fascicule 7:199–314.
- Crothers, J. H.  
1967. The biology of the shore crab *Carcinus maenas* (L.). 1. The background-anatomy, growth and life history. *Field Studies*, 2:407–434.  
1968. The biology of the shore crab *Carcinus maenas* (L.): 2. The life of the adult crab. *Field Studies*, 2:579–614.  
1969. The distribution of crabs in Dale Roads (Milford Haven, Pembrokeshire) during summer. *Field Studies*, 3(1):109–124, 10 maps.  
1970. The distribution of crabs on rocky shores around the Dale Peninsula. *Field Studies*, 3(2):263–274.
- Crozier, W. J.  
1918. Note on the coloration of *Planes minutus*. *American Naturalist*, 52(615):262–263.
- Cummings, W. C.  
1961. Maturation and spawning of the pink shrimp *Penaeus duorarum* Burkenroad. *Transactions of the American Fisheries Society*, 90(4):462–468.
- Cutress, C. E., and D. M. Ross.  
1969. The sea anemone *Calliactis tricolor* and its association with the hermit crab *Dardanus venosus*. *Journal of Zoology*, 158(2):225–241, 6 plates.
- Cutress, C., D. M. Ross, and L. Sutton.  
1970. The association of *Calliactis tricolor* with its pagurid calappid, and majid partners in the Caribbean. *Canadian Journal of Zoology*, 48(2):371–376.
- Dahl, E.  
1944. On an unexpected occurrence of *Sylon hippolytes* M. Sars (Cirripedia, Rhizocephala). *Kungl. Fysiografiska Sällskapet I Lund Förhandlingar*, 13(4)(for 1943):38–40.
- Dall, W.  
1968. Food and feeding of some Australian penaeid shrimp. *Proceedings of the World Scientific Conference on the Biology and Culture of Shrimps and Prawns*. FAO Fisheries Reports, 57(2):251–258.
- Dana, J. D.  
1852. On the classifications of the Corystoidea, Paguridea, etc. *American Journal of Science and Arts*, series 2, 13(37):119–124.
- Daniels, B. A., and R. T. Sawyer.  
1975. The biology of the leech *Myzodbella lugubris* infesting blue crabs and catfish. *Biological Bulletin*, 143(2):193–198.
- Danielssen, D. C.  
1859. Beretning om en zoologisk Reise foretagen i Sommeren 1857. *Nyt Magazin for Naturvidenskaberne*, Christiania, 11(1):1–58.
- Danielssen, D. C., and A. Boeck.  
1872. Beskrivelse af nogle til Crustacea Decapoda henhorendenorske Arter. *Nyt Magazin for Naturvidenskaberne*, Christiania, 19:189–199, 1 plate.
- Darby, H. H.  
1934. The mechanism of asymmetry in the Alpheidae. *Papers of the Tortugas Laboratory, Carnegie Institution of Washington*, 28(17):347–361, plates 1–3.  
1935. Intersexuality in the Crustacea. *Papers of the Tortugas Laboratory, Carnegie Institution of Washington*, 29:147–149, 1 plate.
- Dardeau, M.  
1980. A new species of *Pontophilus* (Crustacea: Natantia: Crangonidae) from the Gulf of Mexico and the western Atlantic. *Proceedings of the Biological Society of Washington*, 93(3):563–572.
- Darnell, R. M.  
1958. Food habits of fishes and larger invertebrates of Lake Pontchartrain, Louisiana, an estuarine community. *Publications of the Institute of Marine Science, Texas*, 5:353–416.  
1959. Studies of the life history of the blue crab (*Callinectes sapidus* Rathbun) in Louisiana waters. *Transactions of the American Fisheries Society*, 88:294–304.  
1961. Trophic spectrum of an estuarine community, based on studies of Lake Pontchartrain, Louisiana. *Ecology*, 42(3):553–568.
- Daugherty, F. M., Jr.  
1952. Notes on *Callinectes danae* Smith in Aransas Bay, Texas, and adjacent waters. *Texas Journal of*

- Science, 4(2):264–267.
- Davenport, D. G. C., and J. F. Hickok.  
1960. Analyses of the behaviour of commensals in host-factor, I. A hesioned polychaete and a pinnotherid crab. *Animal Behaviour*, 8(3–4):209–218.
- Davis, Gary E.  
1975. Minimum size of mature spiny lobsters, *Panulirus argus* at Dry Tortugas, Florida. *Transactions of the American Fisheries Society*, 104(4):675–676.
- Dawson, C. E.  
1949. Florida crawfish research. *Proceedings of the Gulf and Caribbean Fisheries Institute. Inaugural Session, August 1948*, pages 21–28.  
1954. A bibliography of the lobster and the spiny lobster, Families Homaridae and Palinuridae. Florida State Board of Conservation, 86 pages.  
1963. Notes on *Stenopus scutellatus* Rankin and *Neopontonides beaufortensis* (Borradaile) from the northern Gulf of Mexico. *Crustaceana*, 5(2):155–157.  
1967. Notice of the occurrence of the alpheid shrimp *Leptalpheus forceps* Williams in the northern Gulf of Mexico. *Crustaceana*, 12(2):224.
- Dawson, C. E., Jr., and C. P. Idyll.  
1951. Investigations on the Florida spiny lobster, *Panulirus argus* (Latreille). Florida State Board of Conservation, Technical Series, 2:5–39.
- Day, J. W., Jr., W. G. Smith, P. R. Wagner, and W. C. Stowe.  
1973. Community structure and carbon budget of a salt marsh and shallow bay estuarine system in Louisiana. Center for Wetland Resources, Louisiana State University, Publication LSU-SG-72-04, iv + 180 pages.
- Dean, J. M., and F. J. Vernberg.  
1965. Variations in the blood glucose level of Crustacea. *Comparative Biochemistry and Physiology*, 14(1):29–34.  
1966. Hypothermia and blood of crabs. *Comparative Biochemistry and Physiology*, 17(1):19–22.
- DeCoursey, P. J.  
1976. Vertical migration of larval *Uca* in a shallow estuary. *American Zoologist*, 16(2), abstract 362:244.  
1979. Egg-hatching rhythms in three species of fiddler crabs. Pages 399–406 in E. Naylor and R. G. Hartnoll (eds.), *Cyclic phenomena in marine plants and animals*. Pergamon Press, Oxford, New York, xxiv + 477 pages.
- Deevey, G. B.  
1960. The zooplankton of the surface waters of the Delaware Bay region. *Bulletin of the Bingham Oceanographic Collection*, 17(2):5–53.
- Deichmann, E.  
1954. The “Texas longhorn shells” from the Florida waters. *The Nautilus*, 67(3):76–80.
- DeKay, J. E.  
1844. *Zoology of New-York, or the New-York fauna; comprising detailed descriptions of all the animals hitherto observed within the state of New-York, with brief notices of those occasionally found near its borders, and accompanied by appropriate illustrations*. 6, Crustacea, pages 1–70, plates 1–13. Carroll and Cook, Albany.
- Dembowski, J. B.  
1926. Notes on the behavior of the fiddler crab. *Biological Bulletin*, 50(3):179–201.
- Démeusy, N.  
1957. Respiratory metabolism of the fiddler crab *Uca pugilator* from two different latitudinal populations. *Biological Bulletin*, 113(2):245–253.
- Desbonne, I.  
1867. In I. Desbonne and A. Schramm, *Crustacés de la Guadeloupe d’après un manuscrit du . . . I. Desbonne comparé avec les échantillons de Crustacés de sa collection et les dernières publications de MM. H. de Saussure et W. Stimpson. I. Partie. Brachyures*. [Edited, with a preface, by A. Schramm.] Pages 1–60, plates 1–8.
- Deveau, L. B., and J. W. Aucoin.  
1966. Spider crab explorations, Gulf of St. Lawrence, December 1965 to February 1966. Industrial Development Service, Department of Fisheries of Canada, Project Report 10, 38 pages.
- Dexter, R. W.  
1952. The lobster and its conservation in Connecticut. *Turtlox News*, 30(9):162–165.
- Diaz, H.  
1974. Life history pattern and population growth of the mole crab, *Emerita talpoida* Say. Ph.D. dissertation, Duke University, 148 pages.
- Diaz, H., and J. D. Costlow.  
1972. Larval development of *Ocyropsis quadrata* (Brachyura: Crustacea) under laboratory conditions. *Marine Biology*, 15(2):120–131.
- Dobkin, S.  
1961. Early developmental stages of pink shrimp, *Penaeus duorarum*, from Florida waters. *United States Fish and Wildlife Service Fishery Bulletin*, 190, 61:i-iii, 321–349.  
1962. Abbreviated larval development in a species of *Thor* (Decapoda: Caridea). *American Zoologist*, 2(3):404–405.  
1968. The larval development of a species of *Thor* (Caridea, Hippolytidae) from South Florida, U.S.A.). *Crustaceana*, supplement 2, *Studies on decapod larval development*, pages 1–18.  
1971. A contribution to knowledge of the larval development of *Macrobrachium acanthurus* (Wiegmann, 1836) reared in the laboratory (Decapoda, Palaemonidae). *Crustaceana*, 21(3):294–297.
- Dobkin, S., and R. B. Manning.  
1964. Osmoregulation in two species of *Palaemonetes* (Crustacea: Decapoda) from Florida. *Bulletin of Marine Science of the Gulf and Caribbean*, 14(1):149–157.
- Dons, C.  
1915. Nord-Norges decapoder. *Tromsø Museums Aarshefter*, 37 (for 1914):15–153, plates 1–2.

- Döriges, J.  
1977. Marine macrobenthic communities of the Sapelo Island, Georgia region. Pages 399–421 in Bruce C. Coull (ed.), *Ecology of marine benthos*. The Belle W. Baruch Library in Marine Science 6, University of South Carolina Press, Columbia, xx + 467 pages.
- Dow, R. L.  
1967. Temperature limitations on the supply of northern shrimp (*Pandalus borealis*) in Maine (U.S.A.) waters. *Marine Biology Association of India, Symposium on Crustacea*, 4(2):1301–1304.  
1977. Relationships of sea surface temperature to American and European lobster landings. *Journal du Conseil International pour l'Exploration de la Mer*, 37(2):186–191.
- Dragovich, A. J., and J. A. Kelly, Jr.  
1964. Ecological observations of macro-invertebrates in Tampa Bay, Florida. *Bulletin of Marine Science of the Gulf and Caribbean*, 14(1):74–102.
- Dries, M., and D. Adelung.  
1976. Neue Ergebnisse über Afzucht von *Carcinus maenas* im Laboratorium. *Marine Biology*, 38(1):17–24.
- Dudley, D. L., and M. H. Judy.  
1971. Occurrence of larval, juvenile, and mature crabs in the vicinity of Beaufort Inlet, North Carolina. NOAA Technical Report, NMFS Special Scientific Report—Fisheries, 637, 10 pages.
- Dugger, D. M., and S. Dobkin.  
1975. A contribution to knowledge of the larval development of *Macrobrachium olfersii* (Wiegmann, 1836) (Decapoda, Palaemonidae). *Crustaceana*, 29(1):1–30.
- Duncker, G.  
1934. Gefangenschaftsbeobachtungen an *Sesarma cinerea* Milne-Edw. *Zoologische Jahrbücher, Abt. für Systematik Geographie und Biologie der Tiere, Jena*, 66:285–290.
- Dunham, P. J.  
1978. Sex pheromones in Crustacea. *Biological Reviews*, 53(4):555–583.
- Dunnington, E. A.  
1956. Blue crabs observed to dig soft shell clams for food. *Maryland Tidewater News*, 12:1–4.
- Duronslet, M. J., J. M. Lyon, and F. Marullo.  
1972. Vertical distribution of postlarval brown, *Penaeus aztecus*, and white, *P. setiferus*, shrimp during immigration through a tidal pass. *Transactions of the American Fisheries Society*, 101(4):748–752.
- Easton, W. H.  
1940. A Pleistocene occurrence of *Libinia dubia*, a brachyuran. *Journal of Paleontology*, 14(5):519–520.
- Edmondson, C. H.  
1962. Xanthidae of Hawaii. *Occasional Papers of Bernice P. Bishop Museum, Honolulu, Hawaii*, 22(13):215–309.
- Edney, E. B.  
1960. Terrestrial adaptations. Pages 367–393 in T. H. Waterman (ed.), *The physiology of Crustacea*, Vol. 1. Academic Press, New York and London, xviii + 670 pages.
- Edwards, G. A.  
1950. The influence of eyestalk removal on the metabolism of the fiddler crab. *Physiologia Comparata et Oecologia*, 2(1):34–50.
- Edwards, G. A., and L. Irving.  
1943. The influence of temperature and season upon the oxygen consumption of the sand crab, *Emerita talpoida* Say and *Talorchestia megalophthalma*. *Journal of Cellular and Comparative Physiology*, 21(2):169–189.
- Efford, I. E.  
1966. Feeding in the sand crab, *Emerita analoga* (Stimpson) (Decapoda, Anomura). *Crustaceana*, 10(2):167–182, plate 13.  
1967. Neoteny in sand crabs of the genus *Emerita* (Anomura, Hippidae). *Crustaceana*, 13(1):81–93.  
1969. *Leucolepidopa sunda* gen. nov., sp. nov. (Decapoda, Albuneidae), a new Indo-Pacific sand crab. *Breviora*, 318, 9 pages.  
1970. Recruitment to sedentary marine populations as exemplified by the sand crab *Emerita analoga* (Decapoda, Hippidae). *Crustaceana*, 18(3):293–308.  
1971. The species of sand crabs in the genus *Lepidopa* (Decapoda: Albuneidae). *Zoologischer Anzeiger*, 186(1,2):59–102.  
1976. Distribution of the sand crabs in the genus *Emerita* (Decapoda, Hippidae). *Crustaceana*, 30(2):169–183.
- Eidemiller, A.  
1969. Entry behavior of the crab *Pinnotheres maculatus* Say. *Quarterly Journal of the Florida Academy of Sciences*, 32(4):266–274.
- Ekman, S.  
1953. *Zoogeography of the sea*. Sidgwick and Jackson Ltd., London, xiv + 417 pages.
- Eldred, B.  
1959. A report on the shrimps (Penaeidae) collected from the Tortugas controlled area. Florida State Board of Conservation, Special Scientific Report 2, 6 pages.  
1962. The attachment of the barnacle, *Balanus amphitrite niveus* Darwin, and other fouling organisms to the rock shrimp, *Sicyonia dorsalis* Kingsley. *Crustaceana*, 3(3):203–206.
- Eldred, B., J. Williams, G. T. Martin, and E. A. Joyce, Jr.  
1965. Seasonal distribution of penaeid larvae and postlarvae of the Tampa Bay area, Florida. Florida State Board of Conservation Marine Laboratory, Technical Series, 44, 47 pages.
- Eldred, B., R. M. Ingle, K. D. Woodburn, R. F. Hutton, and H. Jones.  
1961. Biological observations on the commercial

- shrimp, *Penaeus duorarum* Burkenroad, in Florida waters. Florida State Board of Conservation Marine Laboratory, Professional Paper Series, 3, 139 pages.
- Elnor, R. W., and A. B. Stasko.  
1978. Mating behavior of the rock crab, *Cancer irroratus*. Journal of the Fisheries Research Board of Canada, 35(10):1385–1388.
- Elofsson, R.  
1961. The larvae of *Pasiphaea multidentata* (Esmark) and *Pasiphaea tarda* (Krøyer). Sarsia, 4:43–53.
- Enders, H. E.  
1905. Notes on the commensals found in the tubes of *Chaetopterus pergamentaceus*. American Naturalist, 39(457):37–40.
- Engel, D. W.  
1977. Comparison of the osmoregulatory capabilities of two portunid crabs, *Callinectes sapidus* and *C. similis*. Marine Biology, 41(3):275–279.
- Esmark, L.  
1866. Carcinologiske Bidrag til den skandinaviske Fauna. Forhandlinger Videnskabs-Selskabet, Christiania, Aar 1865, pages 258–260, 314–316.
- Evans, P. D., and K. H. Mann.  
1977. Selection of prey by American lobsters (*Homarus americanus*) when offered a choice between sea urchins and crabs. Journal of the Fisheries Research Board of Canada, 34(11):2203–2207.
- Everett, J. T.  
1972. Inshore lobster fishing. Fishery Facts–4, NMFS, 26 pages.
- Ewald, J. J.  
1965. The laboratory rearing of pink shrimp, *Penaeus duorarum* Burkenroad. Bulletin of Marine Science, 15(2):436–449.  
1969. Observations on the biology of *Tozeuma carolinense* (Decapoda, Hippolytidae) from Florida, with special reference to larval development. Bulletin of Marine Science, 19(3):510–549.
- Fabricius, J. C.  
1775. Systema entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus, 832 pages. Flensburgi & Lipsiae.  
1781. Species insectorum exhibentes eorum differentias specificas, synonyma auctorum, loca natalia, metamorphosin adiectis observationibus, descriptionibus, vol. 1, viii + 552 pages.  
1787. Mantissa insectorum sistens eorum species nuper detectas adiectis characteribus genericis, differentiis specificis, emendationibus, observationibus, vol. 1, xx + 348 pages. Hafniae.  
1793. Entomologia systematica emendata et aucta secundum classes, ordines, genera, species adiectis synonymis, locis, observationibus, descriptionibus, vol 2, viii + 519 pages. Hafniae.  
1798. Supplementum entomologiae systematicae, 572 pages. Hafniae.
- Fabricius, O.  
1780. Fauna Groenlandica, systematice sistens animalia Groenlandiae occidentalis hactenus indagata . . . maximaque parte secundum proprias observationes Othonis Fabricii, xvi + 452 pages, 1 plate. Hafniae et Lipsiae.  
1788. Beskrivelse over den store Grønlandske krabbe. Nye samling af det Knogelige Dansk Videnskabs Selskabs Skrifter, 3:181–190, 1 plate.
- Factor, J. R.  
1978. Morphology of the mouthparts of larval lobsters, *Homarus americanus* (Decapoda: Nephropidae), with special emphasis on their setae. Biological Bulletin, 154(3):383–408.
- Fales, R. R.  
1976. Apparent predation on the mole crab *Emerita talpoida* (Say) by the ghost crab *Ocyroide quadrata* (Fabricius). Chesapeake Science, 17(1):1–65.
- Farr, J. A.  
1978. Blue crab predation on jellyfish. Florida Scientist, 41(4):217–219.
- Fausto-Filho, J.  
1966a. Primeira contribuição ao inventário dos crustáceos decápodos marinhos do nordeste Brasileiro. Arquivos da Estação de Biologia Marinha da Universidade Federal do Ceará, 6(1):31–37.  
1966b. Sobre os peneideos do nordeste Brasileiro. Arquivos da Estação de Biologia Marinha da Universidade Federal do Ceará, 6(1):47–50.  
1967a. Segunda contribuição ao inventário dos crustáceos decápodos marinhos do nordeste Brasileiro. Arquivos da Estação de Biologia Marinha da Universidade Federal do Ceará, 7(1):11–14.  
1967b. Sobre os calapídeos do norte e nordeste do Brasil. Arquivos da Estação de Biologia Marinha da Universidade Federal do Ceará, 7(1):41–62, 4 plates.  
1968. Terceira contribuição ao inventário dos crustáceos decápodos marinhos do nordeste Brasileiro. Arquivos da Estação de Biologia Marinha da Universidade Federal do Ceará, 8(1):43–45.  
1974. Stomatopod and decapod crustaceans of the Archipelago of Fernando de Noronha, north-east Brazil. Arquivos de Ciências do Mar, Universidade Federal do Ceará, Fortaleza, 14(1):1–35.  
1975. Quinta contribuição ao inventário dos crustáceos decápodos marinhos do nordeste Brasileiro. Arquivos de Ciências do Mar, 15(2):79–84.
- Fausto-Filho, J., and J. B. S. Sampaio Neto.  
1976. Observações sobre alguns crustáceos estomatópodos e decápodos do norte do Brasil. Arquivos de Ciências do Mar, 16(2):65–71.
- Faxon, W.  
1879. On some young stages in the development of *Hippa*, *Porcellana*, and *Pinnixa*. Bulletin of the Museum of Comparative Zoology at Harvard College, 5(11):253–268, 5 plates.  
1895. Reports on an exploration off the west coasts



- of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U. S. Fish Commission steamer "Albatross", during 1891.... XV. The stalk-eyed Crustacea. Memoirs of the Museum of Comparative Zoology, 18, 292 pages, 67 plates (10 colored).
- Felder, D. L.  
1973. An annotated key to crabs and lobsters (Decapoda, Reptantia) from coastal waters of the northwestern Gulf of Mexico. Center for Wetland Resources, Louisiana State University, Sea Grant Publication LSU-SG-73-02, vii + 103 pages, 1 page addenda and errata, 12 plates.
- 1973a. A record of *Pinnixa lunzi* Glassell (Decapoda, Pinnotheridae) from off the coast of Texas, U.S.A. Crustaceana, 24(1):148-149.
1978. Osmotic and ionic regulation in several western Atlantic Callinassidae (Crustacea, Decapoda, Thalassinidea). Biological Bulletin, 154(3):409-429.
- Felder, D. L., and A. H. Chaney.  
1979. Decapod crustacean fauna of Seven and One-half Fathom Reef, Texas: Species composition, abundance, and species diversity. Contributions in Marine Science, 22:1-29.
- Feliciano, C.  
1956. A prenaupliosoma stage in the larval development of the spiny lobster, *Panulirus argus* (Latreille), from Puerto Rico. Bulletin of Marine Science of the Gulf and Caribbean, 6(4):341-345.
- Fenucci, J. L.  
1975. Los cangrejos de la Familia Pinnotheridae del litoral Argentino (Crustacea, Decapoda, Brachyura). Physis, section A, 34(88):165-184, 4 plates.
- Ferreira, P. F., Jr., K. A. Simon, and A. J. McCusker.  
1979. Epibenthic invertebrates. Chapter 8, pages i-iii, 8-1-8-49, in New Haven Harbor Ecological Studies 1979. Normandeau Associates, Inc., Bedford, New Hampshire, Chapters 1-13 (separately paged).
- Filice, F. P.  
1958. Invertebrates from the estuarine portion of San Francisco Bay and some factors influencing their distributions. The Wasmann Journal of Biology, 16(2):159-211.
- Fingerman, M.  
1968. Crustacean color changes with emphasis on the fiddler crab. Scientia (Revista di Scienza), 103(671-672):136-151.
- Fink, H. K.  
1941. Deconditioning the "fright reflex" in the hermit crab, *Pagurus longicarpus*. Journal of Comparative Psychology, 32(1):33-39.
- Fischler, K. J., and C. H. Walburg.  
1962. Blue crab movement in coastal South Carolina, 1958-59. Transactions of the American Fisheries Society, 91(3):275-278.
- Fish, C. J.  
1925. Seasonal distribution of the plankton of the Woods Hole region. Bulletin of the United States Bureau of Fisheries, 41:91-178, 81 graphs.
- Fisher, J. B., and M. J. S. Tevesz.  
1979. Within-habitat spatial patterns of *Ocypode quadrata* (Fabricius) (Decapoda Brachyura). Crustaceana, supplement 5:31-36.
- Fleming, L. E.  
1969. Use of male external genitalic details as taxonomic characters in some species of Palaemonetes (Decapoda, Palaemonidae). Proceedings of the Biological Society of Washington, 82:443-452.
- Flemister, L. J.  
1958. Salt and water anatomy, constancy and regulation in related crabs from marine and terrestrial habitats. Biological Bulletin, 115(2):180-200.
- Flemister, L. J., and S. C. Flemister.  
1951. Chloride ion regulation and oxygen consumption in the crab *Ocypode albicans* (Bosq.). Biological Bulletin, 101(3):259-273.
- Fontaine, B.  
1977a. Fixation d'une ponte de gasteropode sur des crevettes de la famille des Crangonidées. Revue des Travaux de l'Institut des Pêches Maritimes, 41(3):301-307.
- 1977b. Note sur la présence d'une crevette tropicale et de l'un de ses stades post-larvaires dans l'Atlantique du nord-ouest. Revue des Travaux de l'Institut des Pêches Maritimes, 41(3):309-314.
- Fontaine, C. T., and D. V. Lightner.  
1975. Cellular response to injury in penaeid shrimp. Marine Fisheries Review, 37(5-6):4-10.
- Fontaine, C. T., and R. A. Neal.  
1968. Relation between tail length and total length for three commercially important species of penaeid shrimp. Fishery Bulletin, 67(1):125-126.
- Forest, J.  
1965. Campagnes du "Professeur Lacaze-Duthiers" aux Belears: Juin 1953 et Aout 1954 Crustacés Décapodes. Vie et Milieu, series B, 16(1):325-413, 6 plates.
1974. Les dromies de l'Atlantique Oriental. Description de *Sternodromia* gen. nov. et de deux espèces nouvelles du genre *Dromia* Weber (Crustacea Decapoda Dromiidae). Annales de l'Institut Océanographique, new series, 50(1):71-123, 8 plates.
- Forest, J., and D. Guinot.  
1961. Crustacés Décapodes Brachyours de Tahiti et des Tuamotu. Expédition Française sur les Récifs Coralliens de la Nouvelle-Calédonie. Éditions de la Fondation Singer-Polignac, Paris, vol 1, ix + 195 pages, 18 plates.
1966. Résultats Scientifiques des Campagnes de la "Calypso," fascicule 7. Campagne de la "Calypso" dans le Golfe de Guinée et aux Îles Prin-