females migrate downstream to areas of higher salinity near the mouths of estuaries where the eggs are laid and hatched, whereas the males tend to remain in the low-salinity areas for the remainder of their lives. For this reason, samples of adult crabs (or commercial catches) near the sea contain greater numbers of females, whereas those from the middle or upper reaches of bays contain larger percentages of males except at the breeding season. Once in the spawning areas, the females tend to remain for the duration of their lives or move a short way out to sea. Once hatched, the zoeae lead a planktonic existence until they transform to the megalopa stage. This stage also is planktonic, at least in part, for large numbers of megalopae enter estuaries in surface plankton, their abundance influenced to some degree by light, current or pressure (King 1971; More 1969; Naylor and Isaac 1973; Williams 1971). King (1971) found three waves of abundance in Texas, January-March, May-June, October, but there as elsewhere they occur all through the year. Migration either as megalopae or first crab stage leads up the estuary to the maturing grounds. Early recruits may reach these areas in their first summer, but the remainder may not reach them until early in the second year of life. In areas smaller than Chesapeake Bay, there may be a certain amount of overlap in mating and spawning grounds but the two areas tend to be distinct. In Chesapeake Bay, the spawning grounds are near the mouth of the Bay; in North Carolina and Louisiana, near the inlets and passes. In Texas, most females with eggs are found in the Gulf proper (Daugherty 1952; King 1971) but also in bays (More 1969).

In Chesapeake Bay, it has been demonstrated that crabs spawned in June of one year are mature about 14 months later and at that time mate. Most mating pairs are found in July, August, or September, though the mating season extends from May to October. At this time, females ready to molt into the mature stage (terminal molt) are carried about, cradled upright, under the males' bodies. Such pairs are called doublers. The male frees the female during the time she is actually casting the old exoskeleton, but when this is shed he grasps her again, this time with the ventral surfaces together, and completes the breeding act by introducing sperm via the copulatory stylets into the spermathecae. Copulation may last for several hours. When sperm transfer is complete, the female is allowed to resume an upright posture and is again carried under the male for a time until her shell hardens. Males may mate more than once and at any time during their last three intermolts (Van Engel 1958); females usually mate once, but the sperm supply may serve to fertilize more than one mass of eggs. However, Abbe (1974) reported an already mature and mated female, carapace width 140 mm, caught in upper Chesapeake Bay doubled with a male; the female was undergoing a second terminal molt. Usually, a female mated in late summer casts the first batch of eggs the following spring at an age of approximately two years, but egg laying may be at any time from two to nine months after mating. A second spawning has been observed to occur later in summer among some individuals, and it is possible that a third may occur, possibly as late as the succeeding spring or at an age of three years. Three years is judged to be about the normal maximum age for this species and the animals are estimated to undergo some 18 to 20 or more molts before reaching maturity (Van Engel 1958).

Although most spawning occurs in spring and early summer, warm water helping to assure survival of larvae, females with egg masses have been found in North Carolina from mid-March to late November. Northward the season is somewhat shorter and to the south (United States) it is longer (Williams 1965).

Five stages in the reproductive cycle of mature females have been described (Hard 1942), and a number of authors have estimated the number of eggs per spawning at 700,000 to more than 2 million. Rare records of ovigerous females in museum collections suggest that at least some spawning occurs almost year round in the tropics, for example in the Golfo de Venezuela where ovigerous females are most abundant between April and September, reaching a sample maximum of 75% in July and August (Taissoun 1969). Also, in the northern part of Bahia del Tablazo, Venezuela, ovigerous females occur during all the year except between August and November, reaching a sample maximum of 95% in May. Absence of ovigerous females there in late summer and fall occurs because heavy rainfall and increasing river flow freshen the area, driving females downstream to areas of higher salinity, where increases of ovigerous females occur in the Golfo de Venezuela during August and September.

Churchill (1919) found that eggs hatch in about 15 days at 26.1°C and slightly faster at higher temperatures.

Among *Callinectes* species, larval development of only *C. sapidus* and *C. similis* has been described from hatching eggs and rearing in the laboratory. Costlow, Rees, and Bookhout (1959) and Costlow and Bookhout (1959) described seven zoeal stages, atypically an eighth, and a megalopa for *C. sapidus*. Larvae and megalopae of the two species are apparently almost identical, the stages being similar

to those of other portunids (Costlow and Bookhout, personal communication). The megalopae of *Callinectes* lack an internal carpal spine on the chelipeds whereas megalopae of *Portunus* have a well-developed spine on this member (Williams 1971), showing one of the generic distinctions at an early phase of development.

Costlow (1965, 1967) followed the early work on larvae with a series of experimental studies showing that development of *C. sapidus* is subject to variation both in staging and duration. Total development time of *C. sapidus* from hatching of egg to transformation of the megalopa to first crab stage has varied from 31 to 69 days in the laboratory in various combinations of salinity and temperature, but duration of individual stages is variable even in a single salinity-temperature combination. Development progresses at a comparable rate in salinities between 20.1 and 31.1‰ at 25°C. Above 31.1‰, development slows and below 20.1‰, larvae rarely complete the first molt. Larvae never went beyond the first zoeal stage when reared at 20°C and did not progress beyond the third zoeal stage when reared at 30°C.

The stages are constant enough that Cargo (1960), More (1969), Nichols and Keney (1963), King (1971), Pinschmidt (1964), Sandifer (1973d), Tagatz (1968), Van Engel (1958), and Williams (1971) were able to identify zoeae or megalopae from nearshore oceanic and estuarine plankton. Sandifer (1973d) found the first four larval stages and the megalopa, but mainly the stage I larva. In nature as in experiments, development time may be extended by environmental conditions. Kalber (1970) showed that the early zoeae are good osmoregulators but that the late zoeae lose this ability. The megalopa, a poor regulator at first, becomes a good one by the fifth day, overall physiological adaptations to salinity fitting distributional stresses encountered.

Investigators working with larval stages (reviewed in Sandifer 1973d; Williams 1971) suggest that larvae and megalopae can move considerable distances; zoeae have been found off St. Johns River, Fla., at stations up to 160 km, and megalopae in the same area up to 128 km from shore. In Chesapeake Bay and Pamlico Sound, N. C., megalopae have been found 170 and 100 km respectively from presumed points of entry to the estuarine systems. Most of this off- and onshore movement of larval stages appears to be a homeostatic developmental feature. Some dispersal of larvae at the fringes of *Callinectes* populations obviously occurs, but the wanderers are at competitive disadvantage in establishing temporary range extensions. Nevertheless, larval dispersal of *Callinectes* coupled with movement of adults, usually judged to be minor except within an estuarine system (Fischler and Walburg 1962; Tagatz 1968), seems to assure genetic continuity over broad areas. In some areas such as west Florida there is evidence of longshore movement of adults (Leahy 1975).

Often considered a scavenger, which it certainly is, the normal diet of *C. sapidus* includes a variety of materials including fishes, benthic invertebrates and plant material (Darnell 1959; 1961; Dunnington 1956; Menzel and Hopkins 1956; Tagatz 1968). Individuals 100 mm in carapace width may feed on jellyfishes (Phillips, et al. 1969; Farr 1978). Odum and Heald (1972) found mainly an abundance of small mussels in stomach contents of individuls in a marsh in southwest Florida. Hamilton (1976) described feeding on *Littorina littorea* adhering to plant stems near the water line at high tide level. Virstein (1977), with use of exclusion experiments, showed that *C. sapidus* is a major predator on infauna in a shallow subtidal sand community in Chesapeake Bay. There (Orth 1977) the crabs obtain food either by thrusting chelae into sediment to obtain shallow, surface-dwelling animals or by digging holes 6–12 cm deep with chelae and walking legs to gather deeper dwelling animals. In excavating, they scoop up mud and sand with chelae and walking legs, carry sediment in the crook of the chelae, and thus form an inclined excavation, moving up and down as they dig. Sediment is loosened with the chelae and fifth legs. The rhizome mat underlying *Zostera* beds was found to prevent digging below 2 cm, but experimental removal of the rhizomes permits penetration. The crabs were also found to feed on epibiota on *Zostera* leaves, grabbing the leaves at the bases with chelae and passing the leaves through the mandibles. There are numerous notes on feeding and predation in the literature, recording such habits as feeding on oysters, clams, and tunicates.

In a study of gill area correlated with degree of activity and habit of several species of crabs, Gray (1957) found that the blue crab has a larger gill area per gram of body weight than the other portunids studied (*Ovalipes, Arenaeus*, and *Portunus* spp.), exceeding that of any crab studied among aquatic, intertidal, and land crabs in the Beaufort, N. C., area. The blue crab is notorious for its vigorous and pugnacious nature, and this anatomical feature gives one reason for such temperament.

Callinectes sapidus is fairly long-lived following its last molt, and thus affords a lodging place for parasites and commensals. Its gills and gill chambers may become clogged with clusters of a small stalked barnacle, *Octolasmis mulleri* (=*lowei*) (Causey 1961). Walker (1974) showed that this barnacle is present on gills of many crab species (12 species

in 10 genera) in Beaufort Inlet, N. C., but not on *C. sapidus* further upriver, indicating that salinity is probably a factor controlling incidence of the barnacle. Distribution of the barnacle on individual gills of *C. sapidus* was analyzed and factors affecting distribution discussed, chiefly cleaning action of epipods and respiratory flow of the crab. The cyprid larvae attach to blue crab gills a short distance in from the gill margin. Orientation of the larvae at settlement is a response to respiratory flow of water through the crab branchial chamber resulting in cirral nets of the young barnacles facing into the current (mostly efferent whereas in *Ovalipes ocellatus* they are on the afferent side, evidence of the burrowing habit). The crab's main protection is molting. After spawning the female blue crab has fulfilled her role in propagation and individual survival becomes less important for the species. Molting terminated, she gradually becomes debilitated under epizootic attack.

The barnacles *Balanus amphitrite* and *Chelonibia patula* attach to the carapace. The sacculinid parasite, *Loxothylacus texanus*, lives beneath the abdomen (Wass 1955). Hopkins (1947) discussed infestations of the parasitic nemertean *Cacrinonemertes carcinophila* on female blue crabs showing that only light-colored worms are found on the gills of mature females which have never spawned. Large red worms are found only on the gills of mature female crabs which have spawned at least once, or in the gills and egg masses of ovigerous females. Presence of large red nemerteans in the gills is a sure sign that the crab has spawned some time in the past.

The marine leech *Myzobdella lugubris* has been found to cling to *C. sapidus*, as well as other decapod crustaceans, and to deposit egg capsules on the exoskeleton, though it is not known to be parasitic on crustaceans (Daniels and Sawyer 1975; Sawyer, et al. 1975).

Further review of literature on parasites is beyond the scope of this account but some noteworthy references are: Adkins 1972; Bridgeman 1969; Christmas 1969; Colwell, et al. 1975; Heard 1970; Pauley, et al. 1975; Pearse 1932b, 1952b; Reinhard 1950a, 1950b, 1951; Rosen 1967; Sinderman and Rosenfield 1967; Sprague 1970; Umphlitt and McCrary 1975.

Agonistic behavior was well reviewed by Jachowski (1974) from observation of blue crabs in both field and laboratory. Most agonistic acts employ chelipeds as organs of expression as well as weapons. Such acts as cheliped extending, shielding, leaning, fending, embracing, poking, striking, grasping, and crouching are described and illustrated. Responses in an encounter varied with orientation of the two individuals, the distance between them, their size and sex, as well as being influenced by presence of food. Vigorous combat was seen only when threats failed to deter crabs attracted to food, or among males when a sexually attractive female was held by another. Presentation of a model of an adult male to captives showed that responses differed with speed of approach, orientation, cheliped posture and distance of the model, and with size and sex of the crabs. Captives responded to the model more often when it approached rapidly, frontally, or with extended chelipeds than when it approached slowly, laterally, or with folded chelipeds. Females responded to the model more often than did males, and smaller crabs more often than larger ones. More frequent responders typically extended their chelipeds, crouched in the apparently submissive gesture or withdrew from the model. Teytaud (1971) found that pre-pubertal "red-sign" females showed a significantly greater intensity of response to visual stimulus (male or female model) combined with male odor than with either olfactory or visual stimuli alone, or visual stimuli in combination with odor from mature females. Male models in display postures elicited significantly greater responses than nondisplaying models when each was presented with male odor. Dunham (1978), in a review, felt that Teytaud's studies were among the better designed of their kind but that most available evidence for a sex pheromone in Crustacea remains doubtful. Jachowski (1963) also noted young blue crabs clinging to the umbrellas of *Chrysaora quinquecirrha* but not feeding on them.

The swimming behavior of *C. sapidus* has been studied by analysis of high-speed cinematographs (Spirito 1972).

Callinectes sapidus exhibits the usual cheliped laterality of brachyurans, having a crushing pincer on one side (usually right) and a cutting pincer on the other. Variations in this pattern were the subject of recent study (Hamilton, et al. 1976) in field and laboratory showing that the proportion of crabs with a right crusher decreases with size (age) from 100% in smallest crabs to 74% in largest crabs. Crabs with two cutters are not uncommon and apparently result from regeneration of a cutter regardless of which cheliped is autotomized. Only 0.4% of all crabs possessed two crushers. The authors discussed theories that account for these proportions, tending to agree with Przibram's (1931) idea that a cutter is always regenerated so the crab can attain a full-sized crusher in the least amount of time, the original cutter having to grow only a little and undergo change in dentition to become a crusher, while the regenerating crusher has to grow

only moderately before it becomes a normal-sized cutter. Learning adaptations to the new laterality would be necessary.

No attempt has been made to update review of early work on rhythm of color changes (Williams 1965).

Callinectes similis Williams

(Lesser blue crab, Gulf crab)

Figs. 293*b*, 300

Callinectes similis Williams 1966:87, figs. 3, 4E, F.—1974b:731, figs. 4, 18*a*, 20*c*, 22*a*.—Felder 1973:58, pl. 8, fig. 1.—Powers 1977:81.

Recognition characters.—Carapace with 4 frontal teeth, submesial pair small but definitely formed. Central trapezoidal (metagastric) area short and wide, anterior width about 2.75 times, posterior width about 1.6–1.7 times length. Anterolateral margins broadly arched; anterolateral teeth exclusive of outer orbital and lateral spine short and broad, tips of first 5 nearly rectangular, sixth and especially seventh acuminate; first 5 teeth with anterior margins shorter than posterior and separated by narrow based rounded notches. Lateral spine strong, slender, and curved forward. Surface of carapace even, lightly and quite uniformly granulate except smooth along posterolateral and posterior slopes, and nearly smooth along anterolateral and anterior margins, especially between teeth and along orbits; smooth areas with tendency to iridescence.

Chelipeds with very fine granulations on ridges; carpus bearing 2 obsolescent granulate ridges and suggestion of others, inferior lateral ridge terminating anteriorly in low tooth occasionally followed by low flattened eminence; chelae strong, not greatly dissimilar in size.

Male telson longer than wide; sixth segment of abdomen slightly sinuous-sided but broader at all levels than telson, proximal half slightly constricted laterally and less indurated than other parts, flush with sternum in retracted position. Mature female telson slightly wider than long. First pleopods of male reaching anteriorly ⅔ length of sternite VII, or beyond; distal portion slender, extending straight to tips curved slightly mesad, armed with scattered minute reflexed spinules, most dense distally and laterally and largest distally. Gonopores of female narrowly ellipsoid with long axis in transverse plane; aperture of each with simple rounded borders except at mesial end where it slopes from surface laterad under superior anterior margin.

Measurements in mm.—Largest male: carapace length 55, width at base of lateral spines 97, including lateral spines 122. Largest female: length 45, width at base of lateral spines 76, including lateral spines 95. Franks, et al. (1972) reported an individual with carapace width 171.

Variation.—Williams (1974b) discussed variation in this species.

Color.—Adult male: "Carapace green dorsally, irregular areas of iridescence at bases of and between anterolateral teeth, and on posterior and posterolateral borders. Chelipeds and portions of legs similar in color or more tannish green dorsally, with iridescent areas on outer and upper edges of carpus and hands; chelae white on outer face, blue to fuchsia on inner surface, with fuchsia on tips of fingers and teeth of opposed edges. Lateral spines and some anterolateral teeth, as well as spines on chelipeds, white tipped. Walking legs grading from fuchsia distally through violet blue to light blue mottled with white proximally, pubescence on legs beige. Swimming legs variably mottled with white; all legs with stellate fuchsia markings at articulations. Underparts white and blue" (Williams 1965).

Ovigerous female: "Similar to male except with more violet blue on inner surface of chelae; fingers either with white teeth or fuchsia colored teeth. Legs with dactyls reddish orange grading abruptly to blue on propodi, pubescence brown to beige. Abdomen with iridescent areas" (Williams 1965).

Carapace of juveniles sometimes with a maculate light olive pattern.

Gore (1977a) gave great detail on color, pointing out that the dactyls of the swimming legs are a pale translucent blue and the propodi are olive drab on each end and banded with translucent blue mesially.

Habitat.—The species occurs in the oceanic littoral where it has been taken in salinities of 24.9–37.4‰ in temperatures of 13.2°–29.0°C at depths as great as 92 m (rarely to depths of 379 m off eastern Florida). It has usually been found most abundantly in salinities greater than 15‰. In all areas studied the species is associated with *C. sapidus*, often in large numbers (Williams 1974b, summary).

Type-locality.—2–3 mi. off beach between St. Johns River jetties and Jacksonville Beach, Fla.

Known range.—Off Delaware Bay to Key West, Fla.; northwestern Florida around Gulf of Mexico to off Campeche, Yucatan; also Isla de Providencia, Colombia (USNM); reported from northern Jamaica (Norse 1978).

Remarks.—This species closely resembles *C. danae* and *C. ornatus* with which it has often been confused. So far as known, only *C. sapidus* occurs with regularity in the same range along the Carolina-

Florida coast. Small to medium-sized individuals of these species are exceedingly difficult to distinguish.

Callinectes similis seems to be the Carolinian member of the complex. The few specimens from off Delaware Bay are all juveniles, suggesting that northern limits for this species, as for many others from the Carolinian Province, vary seasonally and are extended northward during favorable warm years.

Callinectes similis has the smoothest and most uniformly granulated carapace among these three, and the shortest, broadest anterolateral teeth. These teeth are not equilaterally triangular, having shorter anterior than posterior borders, and are directed more forward in the anterior portion than in the remainder of the row. Central teeth in the row have the anterior border extending almost straight laterad. The carapace of mature females has very little sculpture and remarkably uniform granulation

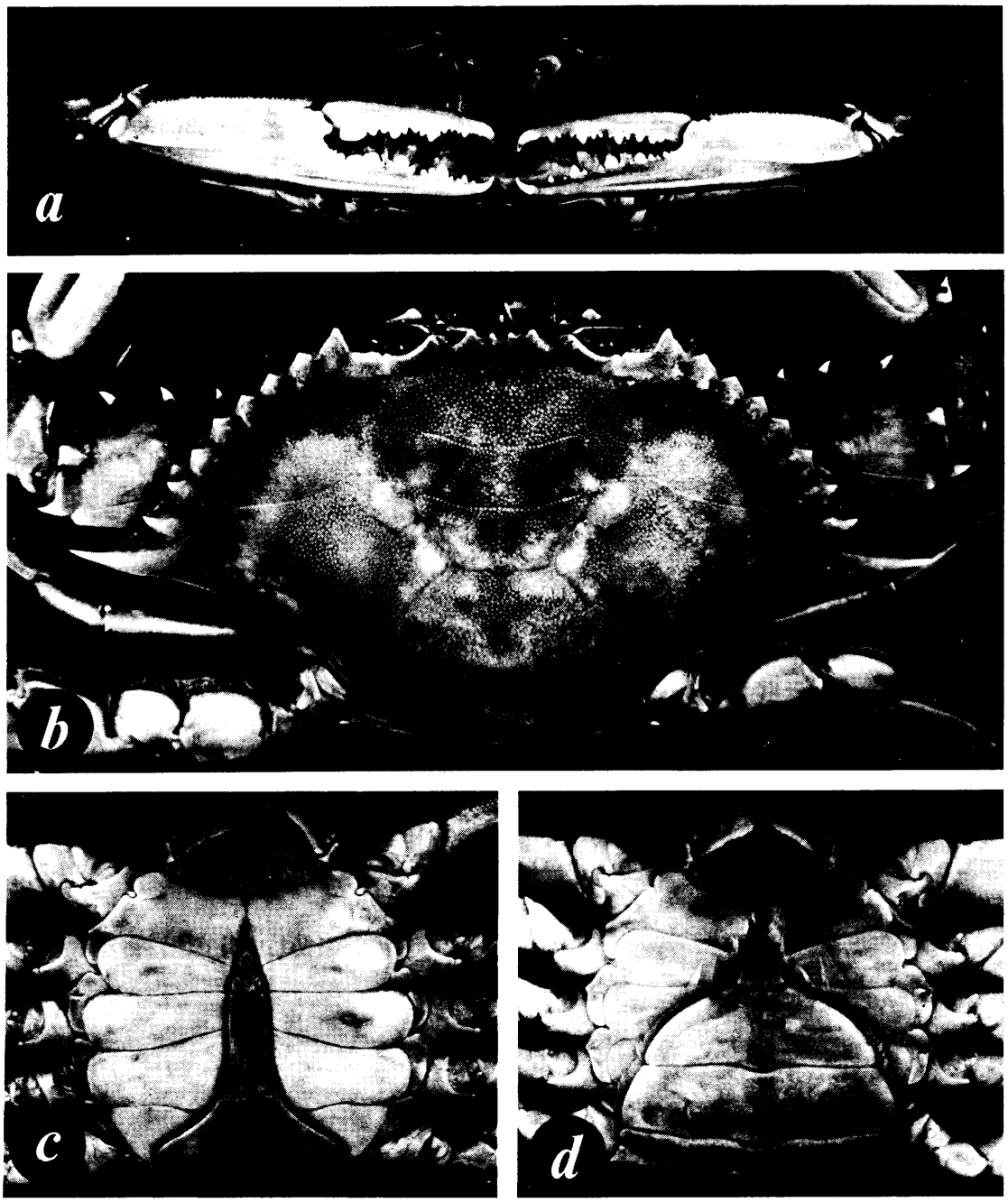

Fig. 300. *Callinectes similis* Williams. *a*, Male chelae in frontal view; *b*, carapace; abdomen and sternal area, *c* male, *d*, female; *a* × 1, *b* × 1.4, *c* × 1.2, *d* × 1.3 (from Williams 1974b).

overall. Granulations on the ridges of the chelipeds are among the finest of any species in the genus (Williams 1974b).

Published data on spawning in Texas and South and North Carolina summarized by Williams (1966) suggested a spring and fall spawning season for *C. similis*, and Tagatz (1967) found this true for northeastern Florida as well where females spawn in the ocean from March to July, peaking in May when 75% of them are ovigerous, and again from October to November. Ovigerous females in the collection of the USNM indicate that these limits are somewhat broader elsewhere and may be correlated with temperature, for there are representatives from Louisiana and Texas in February and Campeche Banks in December.

From ovigerous females trawled in the vicinity of Beaufort Inlet, N. C., Bookhout and Costlow (1977) reared freshly hatched larvae to the first crab stage in filtered sea water of 30‰ salinity. Eight zoeal stages and a megalopa were described and illustrated, with particular reference to types of setae on the appendages. Comparison was made to stages of the congener *C. sapidus*, with updated information on development of the latter.

In studies on osmoregulatory ability, Engel (1977) found that *C. similis* is a poorer osmoregulator at low salinities (tested in 5, 20, and 35‰) than *C. sapidus*, the difference in osmoregulatory capacity corresponding well with their distribution in estuaries.

Overstreet and Heard (1978) found that red drum, *Sciaenops ocellata*, in Mississippi Sound consume a diet dominated by crustaceans, especially *C. similis*, although the diet changes with season and locality and contains far too many organisms to be listed in detail in this manual.

Genus *Cronius* Stimpson 1860

Rathbun 1930a:138.

Cronius ruber (Lamarck)

Fig. 301

Portunus ruber Lamarck 1818:260.

Cronius ruber.—Rathbun 1930a:139, pls. 62–63.—Monod 1956:189, figs. 218, 221.—Guniot-Dumortier 1960:514, fig. 15*a,b*.—Williams 1965: 174, fig. 154.—Garth 1961:143.—1965:15.—Forest and Guinot 1966:61.—Jones 1968b:188.—Coelho and Ramos 1972:188.—Felder 1973:55, pl. 8, fig. 3.—Powers 1977:81.—Manning and Holthuis 1981:98, fig. 21*a-b*.

Recognition characters.—Carapace somewhat hexagonal, smooth but pubescent; sinuous transverse ridge extending between lateral spines, and another shorter, transverse, biarcuate ridge about halfway between this ridge and front. Front with 4 prominent teeth, not including inner orbitals; submesial pair of teeth most advanced; second pair more pointed and directed slightly laterad, separated from notched inner orbitals by deep cut. Orbit nearly circular, basal fixed article of antenna with spine below insertion of movable part. Anterolateral teeth unequal, alternating large and small; lateral spine not strikingly enlarged.

Chelipeds heavy; merus with 4 to 6 spines in front, and with small distal spine behind; carpus with granulate ridges on all surfaces, armed with 4 spines on superior surface, 2 on inner and 2 on outer border; fingers strongly ribbed.

Measurements in mm.—Carapace: male, length 50, width 79; female, length 59, width 92.

Color.—"Violet red or deep purple red more or less marbled with a lighter shade or white. Extremity of all spines black" (Rathbun 1930a).

Habitat.—Siebenaler (1952) reported *C. ruber* as a "trash" form on the Tortugas shrimping grounds, and Park (1969; 1978) judged it to be primarily resident on rocky or coral bottoms. Below low tide mark to 73 m; Fausto-Filho and Neto (1976) reported a maximum depth of 105 m. Manning and Holthuis (1981) summarized the findings of West African zoologists, characterizing *C. ruber* as a shallow-water species occurring on a variety of bottom types.

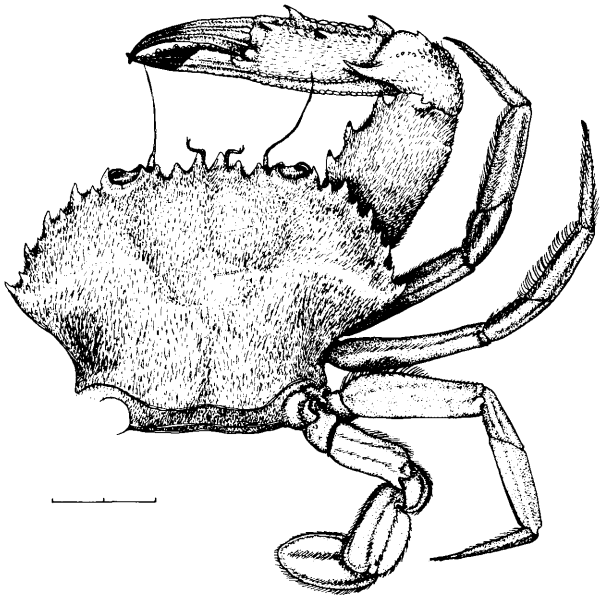

Fig. 301. *Cronius ruber* (Lamarck). Male in dorsal view, legs of left side not shown, 2 cm indicated (redrawn from Monod 1956 *in* Williams 1965).

Type-locality.—Brazil.

Known range.—Vicinity of Little Egg Inlet, N. J. (Milstein, et al. 1977); Rehoboth Bay, Del. (USNM); Virginia (rare, Van Engel and Sandifer 1972); South Carolina to Santa Catarina, Brazil; Baja California to Peru; Clipperton Is., Galapagos Is.; West Africa from Mauritania to Angola; Cape Verde, Principe, São Tome and Annobon I.

Remarks.—Rathbun (1930a) reported ovigerous females from Panama in March; Park (1978) found them mainly in March but a few in June-July; along West Africa they are reported in January, March, and September (Manning and Holthuis 1981).

The New Jersey record is based on a male (50 mm cl, USNM) taken 27 September 1974 from an engine block used as an anchor for an offshore epifauna study during the period January 1972 through December 1974. Depth of the anchor at time of collection was 12.2 m, water temperature 19.5°C, salinity 31‰ (C. B. Milstein, personal communication, and Milstein, et al. 1977).

Randall (1967) reported *C. ruber* from stomach contents of the Nassau grouper, *Epinephelus striatus*, and mutton snapper, *Lutjanus analis*.

Genus *Portunus* Weber 1795

Rathbun 1930a:33.—Hemming 1958b:133.—Stephenson and Campbell 1960:75.

Carapace transverse, usually broad, depressed or slightly convex, surface often areolated. Front cut into 3–6 teeth exclusive of inner orbital angles. Anterolateral borders arched, longer than posterolateral, cut into 9 teeth including outer orbital, ninth may be enlarged. Chelipeds usually much longer and heavier than other legs; merus spined; inner and outer angles of carpus spiniform; palm prismatic, costate, usually spined; fingers strongly toothed and about as long as palm. Second to fifth legs compressed; last pair with merus and carpus short and broad, propodus and dactyl foliaceous and paddlelike. Abdomen of male triangular, 5-segmented, 3–5 fused.

Key to Species

(Adult or Subadult)

1. Carapace wide, anterolateral margins forming arc of a circle with center near posterior margin 2
   Carapace narrow, anterolateral margins forming arc of a circle with center near middle of cardiac region 4
2. Interocular teeth 6 (including entire inner orbital angle) 3
   Interocular teeth 8 (including bilobed inner orbital angle) . . . . ***P. gibbesii***
3. Carapace convex, mostly smooth and glossy; palms of chelae swollen, only 1 spine on upper margin . . . . . ***P. sayi***
   Carapace uneven, not smooth and glossy; 2 spines on upper margin of palm of chela (submesial teeth of front less advanced than laterals). ***P. anceps***
4. Posterodistal margin of merus of fifth legs rounded and unarmed (tuft of setae sometimes covering minute serrations); 2 spines on upper margin of palm near articulation of dactyl 5
   Posterodistal margin of merus of fifth legs armed with 1 or 2 spines, spinules, or both; 1 spine on upper margin of palm near articulation of dactyl. .6
5. Lateral spine of carapace similar to and very little larger than preceding spine or tooth; upper margin of dactyl on chela conspicuously fringed with long hairs . . . . . ***P. depressifrons***
   Lateral spine of carapace much larger than preceding spine or tooth and directed more outward; upper margin of dactyl on chela with hair inconspicuous. . . . . ***P. floridanus***
6. Chelipeds with mesiodorsal spine of carpus less than half length of palm. 7
   Chelipeds with mesiodorsal spine of carpus greater than half length of palm . . . . . ***P. spinicarpus***
7. Interocular teeth 6; superoexternal surface of chela flat and iridescent (iridescence may be lost with preservation). . . . . ***P. ordwayi***
   Interocular teeth 8 (including bilobed inner orbital angles); superoexternal surface of chela ridged, not iridescent. . . . . ***P. spinimanus***

Portunus anceps (Saussure)

Fig. 302

Lupea anceps Saussure 1858:434, pl. 2, figs. 11-11b.
Portunus (Achelous) anceps.—Hay and Shore 1918:431, pl. 33, fig. 8.
Portunus (Portunus) anceps.—Rathbun 1930a:42, pl. 15.
Portunus anceps.—Williams 1965:163, fig. 145.—Coelho and Ramos 1972:186.—Powers 1977:82.

Recognition characters.—Carapace twice as wide as long, pubescent, and with several indistinct, arching, granulate, transverse ridges. Six frontal teeth including inner orbitals; inner orbitals blunt and considerably shorter than lateral pair of true frontal teeth; submesial teeth short, smaller than inner orbitals. Anterolateral teeth small, acute, directed forward, last one sharp, slender, and about as long as space occupied by 4 preceding teeth.

Chelipeds long; merus with 4 spines in front, a distal one behind; carpus ridged, with strong internal and a smaller external spine; most ridges of palm continuing on fingers, superointernal ridge more elevated than others, ending distally in 2 spines, one behind other.

Measurements in mm.—Carapace: male, length 13, width 26; female, length 15, width 29.

Color.—Mottled gray and yellowish white so as to imitate sand; first pair of legs red or yellow; chelipeds and other legs same color in part (Verrill 1908a).

Habitat.—This species lives on or near sandy shores in tropical waters, but is sometimes carried northward in the Gulf Stream to the North Carolina capes; it is occasionally found on mud or calcareous algae (Coelho and Ramos 1972); surface to 103 m but usually 0–20 m (Park 1978).

Type-locality.—Cuba.

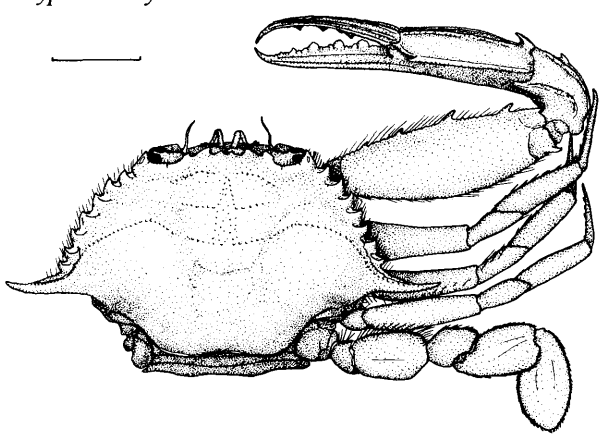

Fig. 302. *Portunus anceps* (Saussure). Male in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

Known range.—Cape Hatteras, N. C. (Park 1978), to Bahia, Brazil; Bermuda.

Remarks.—Ovigerous females are known from April in Florida (Camp, et al. 1977) to June in Cuba and October in North Carolina (Rathbun 1930a); Park (1978) reported them chiefly in July, but June-August, October and early December in the western Atlantic. He also reported a high population density whenever the species was taken.

Randall (1967) reported *P. anceps* from stomach contents of the spotted scorpionfish, *Scorpaena plumieri.*

Portunus depressifrons (Stimpson)

Fig. 303

Amphitrite depressifrons Stimpson 1859:58.
Portunus (Achelous) depressifrons.—Hay and Shore 1918:430, pl. 33, fig. 7.—Rathbun 1930a:84, pl. 41.
Portunus depressifrons.—Williams 1965:166, fig. 149.—Powers 1977:83.

Recognition characters.—Carapace approximately 1.6 times as wide as long, uneven, pubescent, and with indistinct transverse ridges. Six frontal teeth including inner orbitals much broader than others, tips of all teeth about on a line. External orbital tooth strong, tip rounded; anterolateral teeth acute, turned forward, lateral tooth scarcely longer than one next anterior, teeth and intervals between them fringed with hairs.

Chelipeds trigonal, serratogranulate and pubes-

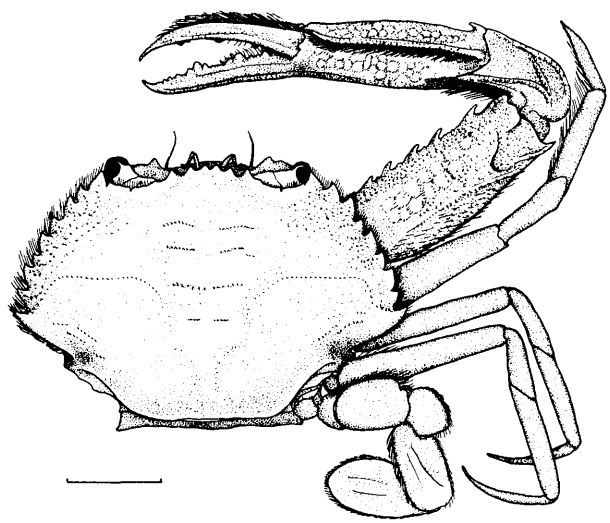

Fig. 303. *Portunus depressifrons* Stimpson. Male in dorsal view, legs of left side not shown, 10 mm indicated (from Williams 1965).

cent; merus with 5 spines in front and distal one behind; carpus with 2 spines, outer much smaller than inner; hand compressed, much longer in immature males than females, upper margin raised into crest terminating distally in stout spine, smaller spine at carpal articulation; fingers flattened, dactyl with border of hairs on superior margin. Walking legs unusually long and slender, articles of first pair fringed with hairs. Swimming legs shorter than in most species of genus, posterodistal margin of merus rounded and unarmed.

Measurements in mm.—Carapace: male, length 30, width 47; female, length 29, width 47.

Color.—Carapace irregularly mottled with light and dark gray, closely imitating colors of sand; chelipeds and posterior legs similar though paler; first pair of walking legs bright purple or deep blue in larger individuals, with some of same color usually apparent on next 2 pairs, but color of first pair in striking contrast with rest of crab. Very young specimens observed do not show this distinction in color of legs (Verrill 1908a).

Habitat.—Abundant in shallow water on sandy bottoms of coves and inlets at Bermuda (Verrill 1908a). Park (1969) found the species everywhere in Biscayne Bay, Fla., except on hard packed bottom. Surface to 29 m, rarely 93 m.

Type-localities.—South Carolina and Florida Keys.

Known range.—Fort Macon, N. C. (Coues 1871; Kingsley 1878-79), through northwest Florida to Bay of Campeche and Caribbean Sea; Bermuda.

Remarks.—This crab has not been collected in the Carolinas for a century so far as known, the record there being Coues's, repeated by Kingsley. Absence from concentrated collections in the Carolinas suggests that the old record is questionable or the result of accidental drift in the Florida current. Park (1969) found this species to be second most abundant among portunids in Biscayne Bay, Fla., but Rouse (1970) found it rare in southwest Florida. The 93-m depth record is from off Bay County, northwest Florida.

A number of specimens in the USNM collection were taken from the stomachs of the gray snapper *Lutjanus* (=*Noemaenus*) *griseus*, the yellow goatfish *Mulloidichthys* (=*Upeneus*) *martinicus*, and other predaceous fishes.

Rathbun (1930a) reported ovigerous females in June from Florida, and in August from Florida and the Caribbean. More recently, egg-bearing females have been taken on Campeche Banks in late August, and Park (1978) summarized their occurence in the western Atlantic as March, May-June, with a few in July-August; peak spawning was in May.

Park (1978) reviewed evidence for euryhalinity in this species.

Portunus floridanus Rathbun

Fig. 304

Portunus (Achelous) floridanus Rathbun 1930a:82, pl. 40.

Portunus floridanus.—Powers 1977:83.

Recognition characters.—Carapace narrow, without strong ridges but with extensive pattern formed by tracts of fine granules; branchial ridge short, starting well forward at gastric region, trending obliquely backward and forming an obtuse angle opposite seventh anterolateral tooth; pubescence short, inconspicuous; anterolateral teeth 2–7 small, spiniform and similar, sinuses U-shaped; lateral spine short, strong, larger than adjacent teeth, tip trending forward. Frontal teeth triangular, submesial pair much smaller and less advanced than broad, blunt lateral pair, not exceeding epistomial spine on almost same level. Eyes large; inner orbital obtuse, single conspicuous central fissure on upper orbital margin and almost obscured one lateral to it, outer orbital tooth narrow in dorsal view and advanced.

Chelipeds long, ridges appressed, granulate; merus with 3–5 spines on anterior border and small curved spine at distal end of posterior border; carpus ridged and finely granulate, small outer spine and broad inner spine larger than propodal spine at articulation; hand trigonal with distal and subdistal spine on upper crest. Merus of swimming leg longer than wide, armed distally along posterior margin with row of spinules.

Measurements in mm.—Carapace: male, length 23,

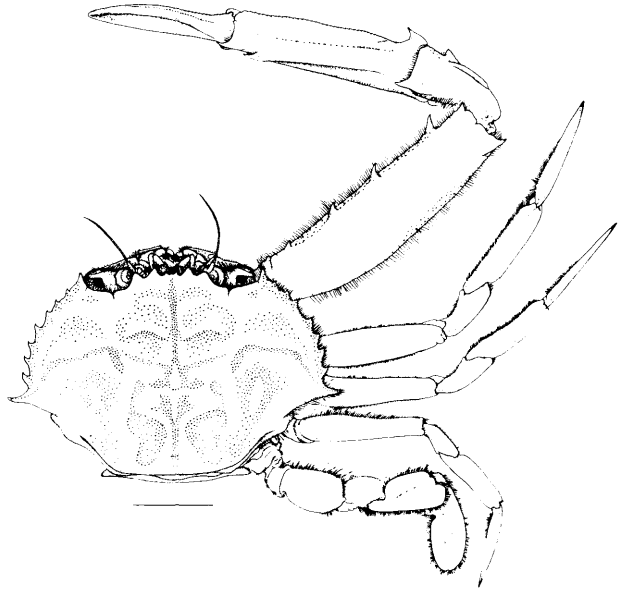

Fig. 304. *Portunus floridanus* Rathbun. Male in dorsal view, legs of left side not shown, 3 mm indicated (USNM 168179).

width 47; mature female, length 19.5, width 25 (occasionally 30).

Variation.—Rathbun (1930a) described the merus of the swimming leg as unarmed on the posterodistal extremity; however, the holotype shows clearly a row of spinules on the distal posterior edge. Specimens from over the range of distribution show this character in varying degree, the spinules being worn or obsolescent in some. In a lot of 5 males from east of Trinidad, this article varies from spinulate to nearly smooth.

Habitat.—Coral bottom reported from type-locality; hard bottom, but muddy sand or mud in some localities; 9 to 640 m, but most common 60–80 m (Park 1978).

Type-locality.—Off Key West, Fla., 24°25′45″N, 81°48′W.

Known range.—E Cape Lookout, N. C., to Honduras and Nicaragua, through West Indies and northern South America to Surinam.

Remarks.—Cain (1972) reported a range extension of *P. floridanus* to the *Lithothamnion* reef zone southeast of Cape Lookout, N. C., and other records are in the collection of the USNM.

The subspecies *P. (Achelous) floridanus isolamargaritensis* Türkay, 1968, from the island of Margarita off Venezuela was considered to be very near typical *P. floridanus*, distinguished by its having a row of spinules on the posterodistal margin of the merus of the swimming leg and a tooth and blunt lobe on the inner distal border of the merus of the cheliped. In *P. floridanus* the inner distal point of the merus of the cheliped is quite acute and might be interpreted as spinous. Adjacent to this is the raised lobelike condyle for articulation with the carpus. Türkay's type-specimen has not been seen by me, but it appears to differ little from typical *P. floridanus*, and it occurs within the distributional range of that species.

Ovigerous females are known off Surinam in March, North Carolina in April, and elsewhere in the western Atlantic in February (Park 1978).

Portunus gibbesii (Stimpson)

Fig. 305

Lupa gibbesii Stimpson 1859:57.

Portunus gibbesii.—Hay and Shore 1918:428, pl. 33, fig. 1.—Williams 1965:164, fig. 146.—Taissoun 1973:48, figs. 6, 8E, 9C.—Felder 1973:60, pl. 8, fig. 16.—Powers 1977:83.

Portunus (Portunus) gibbesi.—Rathbun 1930a:49, pls. 16–17.

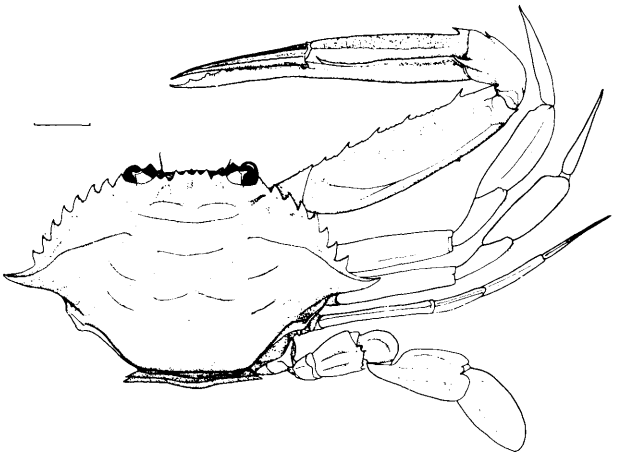

Fig. 305. *Portunus gibbesii* (Stimpson). Male in dorsal view, legs of left side not shown, 10 mm indicated (from Williams 1965).

Recognition characters.—Carapace approximately twice as wide as long, not tumid, thickly ornamented with tracts of small spherical granules, pubescent, and with naked, transverse ridges, 2 of which arise from lateral spines and arch toward gastric region. Eight frontal teeth including 2 slightly more advanced than lateral pair. External orbital tooth not much larger than teeth of anterolateral border; latter stout, acute, directed forward; last tooth or lateral spine, slender, sharp, curved slightly forward and about as long as space occupied by 3 preceding teeth. One or more small, naked, iridescent areas near anterolateral margin at base of teeth.

Chelipeds long, slender (especially in males); merus with 4-7 spines in front and 1 behind at distal end; carpus with 1 large internal and smaller external spine; hand slender, ribbed on all surfaces; ribs continued on fingers and roughened by sharp-pointed, appressed tubercles; hand with 2 spines, 1 at articulation with carpus, another near distal end of superior rib; fingers nearly straight with incurved tips. Merus of swimming leg with row of spinules on posterodistal edge.

Measurements in mm.—Carapace: male, length 37, width 76; ovigerous female, length 35, width 66.

Variation.—Some individuals have elongate lateral spines and suggestion of a spine on the posterodistal margin of the merus of the swimming legs.

Color.—Brownish red, transverse ridges on carapace, spines and margins of chelipeds carmine red; front side of legs brilliantly iridescent by lantern light, iridescence evident to some extent in preserved specimens.

It has also been described as a beautiful iridescent purple and red swimming crab (Anonymous 1975).

Habitat.—Faunal surveys in shallow shelf waters of the Carolinian Province and Caribbean Sea show this to be a common and abundant crab. Hay and Shore (1918) noted its abundance in deeper channels of Beaufort Harbor, N. C., as have others since, and Park (1969) reported it most common on coarse bottoms of cuts and channels in Biscayne Bay, Fla. Further southwest, Tabb and Manning (1961) found it in Coot Bay when salinity was 28–32‰, feeding on massive concentrations of cyprinodont fishes driven from mangrove swamps by oxygen depletion, and they noted it elsewhere in salinities as high as 38‰. In the same region, Rouse (1970) said it was the most often collected portunid, migrating in large numbers during summer. Dragovich and Kelly (1964) found it in their Tampa Bay sampling area, and Wass (1955) recorded it as exceeding other portunids in Alligator Harbor. Franks, et al. (1972) found it nearly year round off Mississippi and noted its presence in lower Aransas Bay, Tex., while Hildebrand (1955) reported it as common on the Campeche Bank shrimping grounds but rare on the Texas coast. Holthuis (1959) and Taissoun (1973) made similar finds off Surinam and Venezuela. To the north off Virginia, Musick and McEachren (1972) found it in temperatures as low as 6°C, possibly left in cold water by the meandering Gulf Stream which was 18°C on bottom nearby. Park (1978) reported it from mainly mud, but also sand and shell substrates. Recorded depths are surface to 393 m.

Type-localities.—South Carolina and St. Augustine, Fla.

Known range.—Southern Massachusetts through Gulf of Mexico along coast to French Guiana, but reported absent from the Antilles (Park 1978).

Remarks.—*Portunus gibbesii* has been reported as fossil from the Pleistocene of Barbados (Collins and Morris 1976).

Ovigerous females are known to occur from February to November between North Carolina and Surinam. Off Beaufort Inlet, N. C., Dudley and Judy (1961) found larvae from May to September 1.6 km offshore at a depth of 1 m, from May to October at depths of 1–8 m, predominantly 1 m, 6.5 km offshore, and from May to October variably at 1–8 m depths 10–13 km offshore. Ovigerous females occurred there from May 1 to August, mainly in June.

Gray (1957) computed gill area per unit weight for *P. gibbesii* as intermediate among a number of swimming crabs studied. Camp, et al. (1977) reported young *P. gibbesii* (≤ 10 mm wide) settling in shallow water near Cape Canaveral, Fla., then migrating offshore as they grew to become most abundant in depths of 40–45 m. Park (1978), from distribution records and sex ratios in samples (26% ♂; 16% of ♀ ovig.), concluded that the species is slightly euryhaline.

Portunus ordwayi (Stimpson)

Fig. 306

Achelous ordwayi Stimpson 1860a:224.

Portunus (Achelous) ordwayi.—Hay and Shore 1918:431, pl. 33, fig. 6.—Rathbun 1930a:71, pl. 33.

Portunus ordwayi.—Williams 1965:166, fig. 148.—Coelho and Ramos 1972: 186.—Powers 1977:84.

Recognition characters.—Carapace approximately 1.5 times as wide as long, uneven, elevations granulate and depressions pubescent, with a number of conspicuous, curving transverse ridges. Six frontal teeth including acuminate inner orbitals; true frontal teeth about equal in size, triangular, acute, middle pair advanced beyond others. Outer orbital tooth similar to remainder of anterolateral teeth which diminish slightly in size laterad to lateral spine, latter about as long as space occupied by 2 preceding teeth, tips of all acute and turned forward.

Chelipeds of moderate length; merus with 4–6 strong spines in front, single distal one behind; carpus ribbed, with strong internal and much smaller external spine; hand ribbed on all surfaces except for obliquely flat, iridescent, superior surface; superointernal ridge raised into crest terminating in strong, sharp, subdistal spine. Margins of carapace and chelipeds more or less fringed with silky hairs. Merus of swimming leg without posterodistal lobe but spinulose.

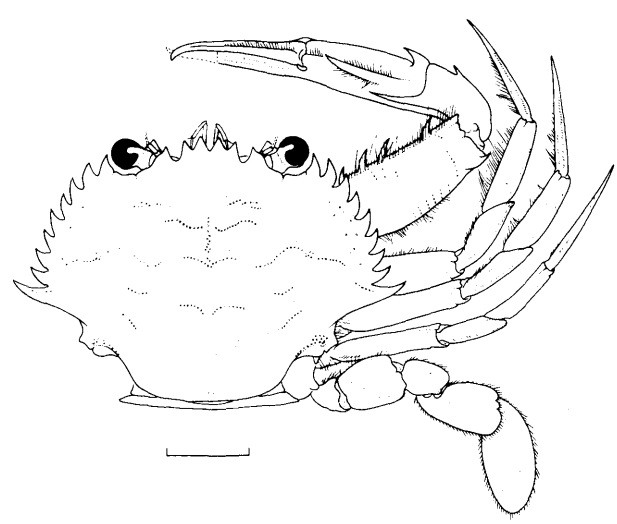

Fig. 306. *Portunus ordwayi* (Stimpson). Male in dorsal view, legs of left side not shown, 1 cm indicated (USNM 31048).

Measurements in mm.—Carapace: male, length 33, width 49; ovigerous female, length 32, width 50.

Color.—Carapace and legs reddish brown because of fine mottling with red, yellowish brown and gray; pale orange beneath, deeper orange on chelipeds and legs; chelae deep red brown above, finger with 2 cross bands of light orange red. Blue coloration also apparent near red and dark pigments; hairs on appendages deep red (Abramowitz 1935).

Habitat.—This is another of the tropical swimming crabs which move northward with warm water currents. It is reportedly associated with calcareous algae, occasionally fine material of organic origin (Coelho and Ramos 1972) and a variety of other soft substrates (Park 1978); surface to 106 m, occasionally 366 m.

Type-localities.—Key Biscayne and Tortugas, Fla.; St. Thomas [V. I.].

Known range.—Vineyard Sound, Mass.; North Carolina through Gulf of Mexico, West Indies and Caribbean Sea to near Rio de Janeiro, Brazil (Park 1978); Bermuda; Fernando de Noronha.

Remarks.—Ovigerous females are known from Florida in March and August, Ceará, Brazil, in March, Guyana in August, Honduras and Surinam in September, and Georgia-Florida in December. No ovigerous females have been found in the Antilles, indicating some degree of euryhalinity (Park 1978).

Park (1978) found this to be a fairly common species in samples of western Atlantic portunids, never abundant but associated with each of the three most abundant species, *P. spinicarpus, P. gibbesii* and *P. spinimanus.*

Specimens collected from a deep-water reef near Cape Lookout, N. C., in autumn died after 17-h exposure to temperature of 4°C (F. J. and W. B. Vernberg 1970).

Randall (1967) reported *P. ordwayi* from stomach contents of the spotted scorpionfish, *Scorpaena plumieri*, and porcupinefish, *Diodon hystrix.*

Portunus sayi (Gibbes)

(Gulf weed crab)

Fig. 307

Lupa sayi Gibbes 1850:178.

Portunus sayi.—Hay and Shore 1918:428, pl. 33, fig. 2.—Williams 1965:163, fig. 144.—Zariquiey Alvarez 1968:384.—Felder 1973:59, pl. 8, fig. 12.—Powers 1977:84.

*Portunus (Portunus) sayi.*Rathbun 1930a:37, figs. 6–7, pl. 14.

Neptunus sayi.—Monod 1956:197.

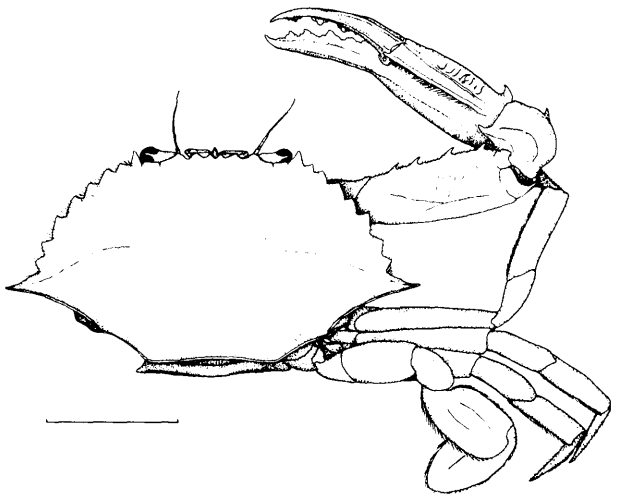

Fig. 307. *Portunus sayi* (Gibbes). Animal in dorsal view, legs of left side not shown, 2 cm indicated (from Williams 1965).

Recognition characters.—Carapace nearly twice as wide as long, somewhat tumid, smooth and polished to naked eye, finely granulate under magnification. Six frontal teeth including inner orbitals, 2 submesial teeth smaller but on line with lateral pair. External orbital tooth larger than those of anterolateral border except stout, acute lateral spine; remaining anterolateral teeth blunt, increasing slightly in size in middle of row.

Chelipeds of moderate length, somewhat larger in males than in females; merus with 3–4 stout, curved spines in front, none behind; carpus with 2 spines and noticeable ridge above lateral margin; hand with acute spine at articulation and smaller one near base of dactyl; external surface with 2 longitudinal ribs with lowermost extending on finger; superior surface with 3 ribs continuing on finger, innermost one with fringe of hair beneath.

Measurements in mm.—Carapace: male, length 31, width 61; ovigerous female, length 31, width 64 (length 40, width less lateral spines 63 [Milne Edwards and Bouvier 1900]).

Color.—Chocolate brown or purplish with cloudings of olive green or light brown and irregular white or flesh-colored spots; orange margins on spines of chelipeds.

Habitat.—Normally this is a pelagic form living among floating *Sargassum*, but it is occasionally carried into coastal areas by currents.

Type-locality.—South Carolina.

Known range.—North Atlantic Ocean from Nova Scotia through Gulf of Mexico to the Guianas; Bermuda; mid-Atlantic Ocean; Canary Islands and Morocco. The only record from Brazil is that of Gerstaecker for his *Lupea pudica* (=*sayi*), and modern collections have not confirmed this. Records

from Kerguelen Island and the south Indian Ocean need confirmation as do those from the western Mediterranean which Milne Edwards and Bouvier (1900) first reported, Bouvier later ambiguously accepted (1922), and finally disregarded (1940). These records were accepted by Zariquey Alvarez (1968) who also recorded the species from Cap Spartel, Morocco.

Remarks.—The numerous published records and notes on this species cannot be reviewed here. The species has a fossil record dating from the lower Miocene of North America (Rathbun 1935).

Ovigerous females are known from April to August in the southeastern United States and parts of the West Indies. They are also reported from Culebra in February, near Nantucket in September (Rathbun 1930a, in part) and off Morocco in June (Milne Edwards and Bouvier 1900). Park (1978) suggested that spawning sites are restricted to areas of attached *Sargassum.* Some of the larval stages were described by Lebour (1944) at Bermuda. Dudley and Judy (1971) found larvae attributed to this species from May to November off Beaufort Inlet, N. C.

Portunus spinicarpus (Stimpson)

Fig. 308

Achelous spinicarpus Stimpson 1871a:148.

Portunus (Achelous) spinicarpus.—Hay and Shore 1918:429, pl. 33, fig. 3.—Rathbun 1930a:92 (part), pl. 45.

Portunus spinicarpus.—Williams 1965:167 (part), fig. 150.—Holthuis 1969a:415, fig. 1 (top).—Coelho and Ramos 1972:187.—Taissoun 1973:50, figs. 7, 8C, 9B.—Felder 1973:60, pl. 8, fig. 13.—Powers 1977:85.

Recognition characters.—Carapace about twice as wide as long; sculptured, with number of naked, rather coarsely granulate, arching, transverse ridges separated by finely granulate and pubescent surfaces. Six frontal teeth, including inner orbitals with sinuate but unnotched outer margins; true frontal teeth narrow, acute, separated by broad usually U-shaped notches, median pair considerably advanced beyond others. External orbital tooth acute, larger than neighboring teeth of anterolateral margin; latter varying somewhat in size, concave sided, acute; lateral spines slender, curving, more than half as long as anterolateral border; posterolateral angle sharp, margin slightly recurved.

Chelipeds long, slender; merus with 4 or 5 stout, curved spines in front, and single, similar distal spine behind. Carpus with 2 spines, outer small and weak, inner long, extending along side of hand to near base of dactyl. Hand with serratotuberculate ridges prolonged on fingers, and 2 spines, one at carpal articulation, another on superior surface near base of dactyl.

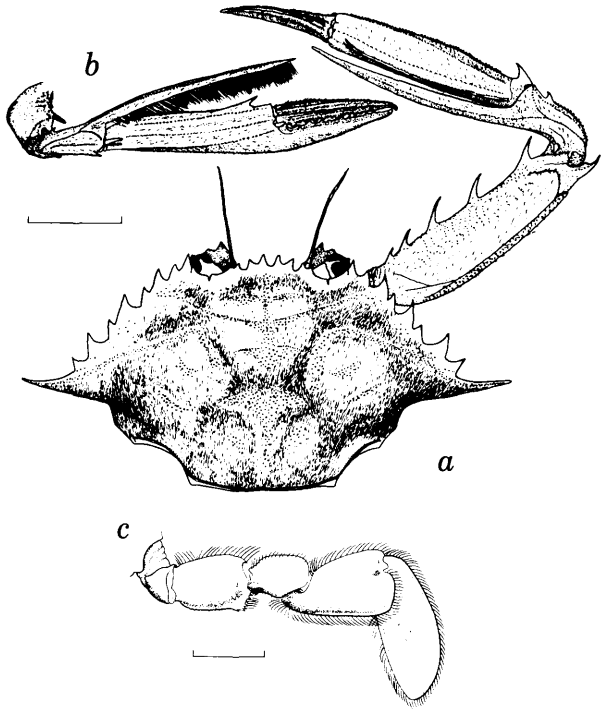

Fig. 308. *Portunus spinicarpus* (Stimpson). *a*, Male in dorsal view, legs not shown except for right cheliped; *b*, right chela in frontal view (from Williams 1965); *c*, right fifth leg; *a-c*, 5 mm indicated.

Measurements in mm.—Carapace: male, length 34, width 64; female, length 32, width 58; ovigerous females, width 18–58 (Holthuis 1969a); occasionally larger.

Variation.—The internal carpal spine of the chelipeds may extend beyond midlength of the fingers in males but in females it does not reach beyond the superior spine of the palm. The lateral spine is relatively longer in young than in old individuals and changes in angle of projection with age, extending straight laterally or slightly backward in the young but curving slightly forward in adults (Rathbun 1930a).

Color.—Carapace grayish green marbled with short, curved reddish brown line and streaks; a dark median longitudinal line over cardiac and intestinal regions; epibranchial line dark red distally. Eyestalks with conspicuous red spot on anterior surface. Third maxillipeds with last 3 articles iridescent. Cheliped with merus very lightly spotted, a prominent dark or contrasting submarginal streak paralleling its outer margin and similar color on inside of anterior spines at their bases; carpus with long spines uninterruptedly red proximally fading to white intervals distally and fringed with long red

hairs, an inconspicuous streak on basal part of outer margin; outer surface of palm uncolored except for red spot at base of proximal spine, inner surface in females uncolored except for red proximal spot and a very distinct proximal red band on fingers, that of males with some long reddish hairs. Walking legs grayish green with pink dactyls. Swimming legs similar but with a distinct red spot distally on dactyl. Reddish color, especially on merus, tending to persist in alcohol (Holthuis 1969a).

Habitat.—On shrimping grounds in the western Gulf of Mexico, Hildebrand (1954) reported this form as found only along the seaward side in depths of 27 to 68 m. Coelho and Ramos (1972) reported it on mud and sand bottom; 9 to 550 m (Holthuis 1969).

Type-locality.—Straits of Florida S of Dry Tortugas, 24°23'N, 82°57'W to 24°24'N, 82°56'W (Holthuis 1969a, restricted).

Distribution.—ESE Oregon Inlet, N. C., 35°42'N, 74°54'30"W (Musick and McEachren 1972) to Santa Catarina, Brazil.

Remarks.—This species is very close to *P. binoculus* which Holthuis (1969a) distinguished from it in the West Indies and Caribbean Sea. The two occasionally occur together, and are more easily differentiated by color than by other characters whose variabilities overlap, such as acuteness of frontal spines and shape of the notches between them, or length of anterolateral processes on the third maxillipeds. Since *P. binoculus* usually has persistent red color spots on the two branchial lobes, and it has not been seen in a rather extensive set of samples from the Carolinian Province, no confusion in identity is likely to occur there. Treatment of these species in the older literature should be viewed with caution. Park (1978) found *P. spinicarpus* most often and in greatest density among samples of portunids from the western Atlantic.

Ovigerous females are known from January to October in the area stretching from North Carolina to Surinam, and in November in Florida and Texas, but Park (1978) found none in the Antilles. Bookhout and Costlow (1974) described seven zoeal stages and a megalopa from laboratory hatching and rearing, giving particular attention to types of setae on all appendages. They also gave great detail on kinds of spination in crab larvae and differentiated the larval stages of *P. spinicarpus* from those of *Callinectes sapidus*. Freshly hatched larvae were reared to megalopa in temperatures of 20° and 25°C in salinities of 30, 35, 40, and 45‰, but did not reach megalopa in 20 and 25‰. None survived to megalopa in this full range of salinity at either 15° or 30°C. Two percent of the larvae survived to first crab stage at 20° and 25°C in 35‰ salinity water, but there was no survival in other combinations. Molting rates at 20°C and 35‰ were not only slower, but survival was consistently lower in each stage leading to megalopa in contrast to the 25°C–35‰ combination. At 20°C, 24% of larvae reached megalopa in a a mean of 46.8 days, whereas at 25°C, 40% reached that stage in an average 38.3 days.

W. B. and F. J. Vernberg (1970) considered *P. spinicarpus* to be a species with metabolically tropical affinities. Assessing lethal limits, F. J. and W. B. Vernberg (1970a) found that animals from Cape Hatteras region in December died after 3-h exposure to 30°C; those collected from a deep water reef near Cape Lookout, N. C., in October died after 7-h exposure to 4°C.

Pearse (1932b) found the barnacle *Dichelaspis sinuata* on a number of individuals. Several small specimens, all apparent females, have been noted bearing one or two sacculinid parasites (Holthuis 1969a).

Portunus spinimanus Latreille

Fig. 309

Portunus spinimanus Latreille 1819:47.—Hay and Shore 1918:429, pl. 33, fig. 4.—Rathbun 1972:186.—Taissoun 1973:43, Foto 8, figs. 8B, 9E.—Felder 1973:59, pl. 8, fig. 15.—Powers 1977:85.

Portunus (Achelous) spinimanus.—Hay and Shore 1918:429, pl. 33, fig. 4.—Rathbun 1930a:62, text-fig. 10, pls. 26–28.

Recognition characters.—Carapace considerably less than twice as wide as long, finely granulate and pu-

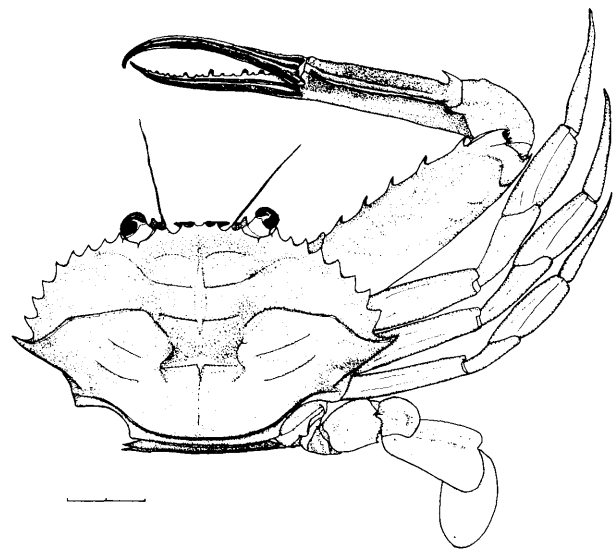

Fig. 309. *Portunus spinimanus* Latreille. Male in dorsal view, legs of left side not shown, 2 cm indicated (from Williams 1965).

bescent, with number of prominent, curved, coarsely granulate, transverse ridges. Eight frontal teeth, including inner orbitals, each notched at summit and presenting 2 points; submesial pair of teeth slightly narrower and more advanced than next lateral pair, all considerably more advanced than inner orbitals. Outer orbital tooth not much larger than those of anterolateral border; latter strong, acute or acuminate, about equal in size except lateral spine about twice as large as others and usually curved forward.

Chelipeds long, pubescent, serratogranulate all over; merus with 4, occasionally 5 strong, curved spines in front and 1 at distal end; carpus with 2 spines; inner one much stronger, and with 4 conspicuous ridges on upper surface; hand slender, all surfaces with ridges which extend on fingers; strong spine at carpal articulation and another near base of dactyl; fingers nearly straight, tips incurved.

Measurements in mm.—Carapace: male, length 65, width 110; ovigerous female, length 57, width 94.

Variation.—Large males have relatively much longer, thinner chelipeds and walking legs than large females.

Color.—Pubescence yellowish or reddish brown, ridges of carapace, spines of chelipeds, fingers and tips of legs reddish brown; anterolateral teeth reddish at base, white at tips; merus, carpus and hand of chelipeds with white blotches.

Habitat.—Common in water of inner continental shelf, occasionally in deeper channels or harbors such as Beaufort, N. C., *P. gibbesii* is often found in company with *P. spinimanus*, both in the Atlantic off the Carolinas and on the Campeche Banks (Hildebrand 1955). Park (1969) found *P. spinimanus* on open sand with light cover of *Diplanthera* or algae in Biscayne Bay, and Olsen, et al. (1978) also reported concentrations on sand, but it is commonly on coral reefs in Florida and the Bahamas (Park 1978); on beach under *Sargassum*; surface to 91, occasionally 393 m.

Type-locality.—American waters, common in Brazil.

Known range.—New Jersey through Gulf of Mexico and West Indies to Santa Catarina, Brazil; Bermuda.

Remarks.—This species, which somewhat resembles *P. gibbesii*, can be readily distinguished from the latter by its narrowed, rounder form, and by the lack of iridescent patches on the carapace.

Ovigerous females are known virtually the year round in Florida (Camp, et al. 1977; Wass 1955; Williams 1965), May to October in North Carolina (Dudley and Judy 1971), February to May in the Virgin Islands (Olsen, et al. 1978), and otherwise from March to November in the region outside the United States from Bermuda to Rio de Janeiro (Holthuis 1959; Lebour 1950; Rathbun 1930a; Taissoun 1973; USNM). At Bermuda, Lebour found an ovigerous female among *Sargassum* and from the eggs reared larvae which she illustrated.

Gray (1957) computed gill area per unit weight for *P. spinimanus* as intermediate among a number of swimming crabs studied. Johnson (1964) studied histology of the reproductive system, comparing it with other decapods. Sikora, et al. (1972) listed *P. spinimanus* as a prey species of the hakes, *Urophycis regius* and *U. floridanus*. Camp, et al. (1977) found this to be one of the commonest decapod crustaceans in samples from nearshore east Florida waters in a salinity range of 32 to 39.3‰ at 19.2°–32°C, and Olsen, et al. (1978) judged it to be a potential fisheries resource in the Virgin Islands.

Superfamily Xanthoidea

Key to Families

(Amplified)

1. Carapace always nearly oval or hexagonal in dorsal view; frontoorbital width never more than 4/5 greatest width of carapace; males without or with variable small part of sternite 8 visible between second abdominal segment and coxa of fifth leg (visible, e.g., in *Panopeus, Rhithropanopeus, Eurytium*); male opening coxal, genital duct not lying in sternal groove . . . . . **Xanthidae**

   Carapace either subquadrate in dorsal view, or xanthoid as above in *Glyptoplax, Panoplax, Nanoplax* or *Speocarcinus*; frontoorbital width from about 1/2 to 9/10 greatest width of carapace; male with part of sternite 8 visible between second abdominal segment and coxa of fifth leg; male opening either coxal with genital duct extended and lying in sternal groove, or sternal with involuted edges of groove covering genital duct . . . . . **Goneplacidae**

Family Xanthidae

Crabs with body transversely oval or transversely hexagonal. Front broad, never produced in form of rostrum. Last pair of legs normal. Antennules folding obliquely or transversely. Male openings coxal. (Rathbun 1930a; Balss 1957.)

Containing more genera than any other brachyuran family, the family Xanthidae has been treated either as too complex to organize easily along natural lines (Rathbun 1930a; Monod 1956; Williams 1965; Glaessner 1969), separable into families and subfamilies (Ortmann 1893), or as separable into subfamilies (Balss 1957). Guinot (1971, summary of her previous papers) did not make more than preliminary subfamily groupings even though she discussed affinities of some provisional subfamilies, and in 1978 did subdivide the Xanthoidea into both families and subfamilies. The problem is compounded by relationship of these crabs to the family Goneplacidae, for the two families share certain characters which form a continuum that allows no clear distinction if reliance for separation is placed on these alone (Guinot 1971). For example, in one character that illustrates this relationship: males of the xanthid genus *Neopanope* show no part of sternite 8 visible between the second abdominal segment and the coxa of the fifth leg, whereas in *Panopeus* a small part is left uncovered, and in *Rhithropanopeus* a sizeable lateral piece is uncovered; in males of the goneplacid genus *Cyrtoplax* (Caribbean-Pacific) a still broader part of sternite 8 is exposed, and in *Prionoplax* (oriental) the part exposed is equal in size to the readily visible part of sternite 7. In development of this character the families merge, yet presence or absence of a visible piece of sternite 8 lateral to the male second abdominal segment is the usual key difference used to separate the families. Guinot (1971) considered at least certain of the Goneplacidae to be an evolutionary grade not completely distinct from the Xanthidae. Still, the families, at least their representatives in the area considered here, are distinct enough to be separable with reasonable accuracy.

Because revisionary studies of the Xanthidae are still in progress, formal subdivision into subfamilies is not attempted here; the statements I made in 1965 still apply, but the arrangement of genera is somewhat different than used then. Because many of the genera occurring in the region contain a single species, the generic key is in large part also a key to species. Parts of the key have been adapted from Rathbun (1930a) and Ryan (1956).

Arrangement of the genera is not alphabetical but based on similarities and differences in the first pair of male pleopods. Though no attempt is made to divide the family into subfamilies, at least three well-marked groups appear, and perhaps one of these groups (Fig. 333) could be split into additional groups.

Key to Genera and Some Species of Xanthidae

1. Low anteroposterior ridges on endostome (palate or roof of mouth) absent or not reaching to anterior margin of buccal frame 2
   Low anteroposterior ridges on endostome (palate or roof of mouth) present and reaching to anterior margin of buccal frame 13
2. Frontoorbital width less than ½ greatest width of carapace; body lobulate, granulate or eroded 3
   Frontoorbital width more than ½ greatest width of carapace; body rough or smooth 4
3. Carapace and legs covered with nodules, granulate, often hairy . . . . . ***Paractaea rufopunctata nodosa***
   Carapace and legs with surface deeply and intricately eroded . . . . . ***Glyptoxanthus erosus***
4. Chelipeds with large notch clearly forming an open hole between carpus and palm when viewed frontally with cheliped fully pressed against body . . . . . ***Carpoporus papulosus***
   Chelipeds lacking notch forming an open hole between carpus and palm when viewed frontally with chelipeds fully pressed against body 5
5. Transverse groove between extreme edge of frontal margin and row of granules or nodules paralleling it above (under magnification) 6
   Front lacking such transverse groove, each half presenting but a single edge (under magnification) 8
6. Body covered with smooth, coarse lobules and tubercles, with tracts between obscured by feltlike covering of hairs . . . . . ***Allactaea lithostrota***

Body smooth or rough but never pronouncedly as above 7

7. Carapace and chelipeds more or less roughened, granulate or spiny along anterolateral margin; marine species . . . . . ***Pseudomedaeus***

Carapace not granulate but with low, transverse ridges on dorsum; chelipeds not roughened; estuarine species . . . . . ***Rhithropanopeus harrisii***

8. Anterolateral border with 4 or 5 easily discernible stout teeth or lobes, including outer orbital; first and second teeth more or less united; edges of teeth smooth or at most granular, tips may be acute but not spinelike; carapace may be granular but not nodose 9

Anterolateral border with 3–4, rarely 5 (*M. urinator*) spine-tipped or denticulate teeth, including outer orbital; second tooth obsolescent, fifth somewhat so (except in *M. urinator*); carapace more or less nodose . . . . . ***Micropanope***

9. Five anterolateral teeth including outer orbital. 10

Only 4 broad, low, lobular anterolateral teeth including outer orbital; carapace very convex longitudinally; front truncate; chelae elongate . . . . . ***Tetraxanthus rathbunae***

10. Dactyl of major chela lacking enlarged, terminally rounded tooth proximally on prehensile edge, but low, pointed tooth not much larger than other teeth may be present. 11

Dactyl of major chela with enlarged, terminally rounded tooth proximally on prehensile edge 12

11. External maxillipeds with red spot on internal face of ischium. . . . . ***Eurypanopeus***

External maxillipeds without red spot on internal face of ischium . . . . . ***Neopanope sayi***

12. Third and fourth teeth of anterolateral border definitely swept forward, their lateral margins curved outward; external maxillipeds of males and some females with conspicuous red or orange spot on inner surface of ischium . . . . . ***Panopeus***

Third and fourth teeth of anterolateral border triangular and pointed outward or slightly forward, their lateral margins not conspicuously curved outward; external maxillipeds of both sexes lacking red or orange spot on inner surface of ischium . . . . . ***Hexapanopeus***

13. Antennae separated from orbits 14

Antennae not separated from orbits 15

14. Merus of external maxillipeds as long as broad, or nearly so; anterolateral spines strong and outstanding; large species. . . . . ***Eriphia gonagra***

Merus of external maxillipeds twice as broad as long; carapace and chelipeds armed with slender, acute, often black spines; small species . . . . . ***Domecia acanthophora acanthophora***

15. Chelipeds smooth or nearly so 16

Chelipeds spiny 17

16. Fingers white; anterolateral teeth pointed or rounded, never large-sized. . . . . ***Eurytium limosum***

Fingers black; anterolateral teeth broad, not pointed, with occasional exception of fifth tooth; attains large size. . . . . ***Menippe mercenaria***

17. Carapace smooth, front definitely more than ⅓ carapace width including lateral spines; eyes noticeably large . . . . . ***Melybia thalamita***

Carapace spiny or nodose, front less than ⅓ carapace width including lateral spines; eyes not noticeably large 18

18. Carapace and chelipeds variably spiny, not nodose; with long plumose (clubbed) hairs, short hairs, or both . . . . . ***Pilumnus***

Carapace with patches of nodules along anterolateral border and extending backward from front; with close pile of short hair only; body massive . . . . . ***Lobopilumnus agassizii***

Genus *Paractaea* Guinot 1969

Guinot 1969:241.

Carapace oval, more or less swollen, covered dorsally with numerous lobules (prominent, widely separated, or flattened). Front convex or quite advanced. Anterolateral border cut into 4 lobes, probably from fusion of outer orbital and adjacent anterolateral lobe (*retusa* group), or 5 lobes (*rufopunctata* group). Legs often nodose or flanged, ornaments occasionally obsolescent. Orbits with well-developed infraorbital fissures. Basal antennal article applied against subfrontal prolongation, not united to latter at internal angle, barely penetrating orbital hiatus. Third maxillipeds almost parallel-sided, not separated in front, ischium a little widened and merus little wider than long; lacinia of first maxilliped leaving large part of endostome uncovered. First male pleopod thick, tip forming more or less flattened lobe; subapical hairs implanted linearly, mainly along one side. (Translation paraphrased from Guinot 1969.)

Paractaea rufopunctata nodosa (Stimpson)

Fig. 310

Actaea nodosa Stimpson 1860a:203 [75].
Actaea rufopunctata var. *nodosa* Miers 1886:122.
Actaea rufopunctata nodosa.—Rathbun 1930a:257, pl. 105, figs. 1–2.
Paractaea rufopunctata forma *nodosa*.—Guinot 1969:252, fig. 25.—Coelho and Ramos 1972:189.

Recognition characters.—Ovoid carapace with length not quite ¾ but more than ⅔ width, surface broken by deep, broad grooves into numerous very complex lobules (about 27 excluding those along orbits and front) covered with closely packed vesicular granules; grooves filled with dense, short, and a few longer hairs. Front strongly deflexed, rather sharply bilobed. Swollen supraorbital margin cut by two fissures and separated from lower margin by fissure. Anterolateral border with 4 rounded lobules in addition to reduced outer orbital.

Chelipeds and walking legs with lobulation similar to carapace, edges fringed with coarse hair; lower outer surface of palm with granules arranged in rows; dactyls of walking legs furred, corneous tips grooved below.

Measurements in mm.—Carapace: male, length 14.3, width 20.8; female, length 16.4, width 25; ovigerous female, length 4.1, width 6.0.

Habitat.—Variety of bottoms from sand to broken shell and coral, sometimes associated with sponges; to 172 m.

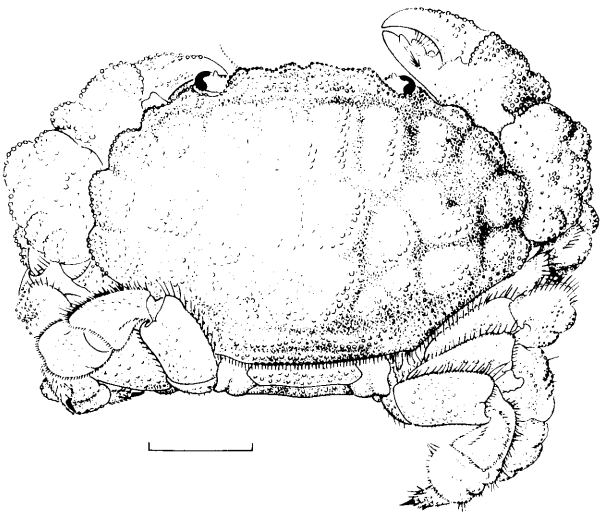

Fig. 310. *Paractaea rufopunctata* forma *nodosa* (Stimpson). Female in dorsal view, 5 mm indicated (USNM 15010).

Type-locality.—Tortugas, Florida.

Known range.—SE Cape Lookout, N. C. (34°12.2′N, 76°08′W, 90 m, to 34°12.27′N, 76°08′W, 50 m; 33°55.5′N, 76°28.4′W); off Mississippi River Delta through West Indies to Rio de Janeiro, Brazil; Ascension Island (USNM, UNC-IMS).

Remarks.—This crab has been treated as a form of *P. rufopunctata* by Guinot (1969) because its relation to other members of the *rufopunctata* complex in the eastern Atlantic and western Indian Ocean remains unclear. The fringe occurrences off North Carolina include an ovigerous female, indicating that breeding populations of a tropical species can occur where warm environment sustains them.

Genus *Allactaea* Williams 1974

Williams 1974a:19.

Allactaea lithostrota

Figs. 311, 331*a*

Allactaea lithostrota Williams 1974a:19, figs. 1–3.—Soto 1980:125, fig. 1A-B.

Recognition characters.—Conspicuously tuberculate. Carapace wider than long, arched anteroposteriorly, regions prominently indicated by smooth raised lobules arranged in characteristic radiating pattern emanating from urogastric region; tracts between lobules almost completely obscured by thick covering of club shaped hairs. Front divided by narrow U-shaped median notch, dorsally submarginal row of about 8 coalesced lobules extending

from this to each antennal notch resulting in transversely doubled appearance. Orbital margin thickened raised and smooth dorsally, fissures closed; eyestalks with 2 spiniform tubercles in corneal emargination and smaller tubercles at base of cornea. Anterior lateral border with 4 teeth exclusive of outer orbital reduced to anteriorly directed mammillary lobules; row of smaller intercalary teeth slightly below these on margin; hepatic and subbranchial region slightly tuberculate; row of tubercles on posterolateral border.

Chelipeds dissimilar, right larger than left; outer surfaces with spaces between lobules and tubercles covered with club-shaped hairs, inner surfaces smooth; merus with dorsal crest of sharp forward-curved spines; palm and carpus wih distally directed lobules varying from sharpest along dorsal crest to flared at tip with narrower bases on external surface of carpus and outer dorsal part of palm, becoming smaller, sharper and tending to alignment in longitudinal rows on outer surface of palm; carpus with spiniform lobule at inner angle and another below it, anterior border with few small teeth hidden in hairs; fingers dark colored, moderately toothed, crest of tubercles at base of dactyl.

Measurements in mm.—Carapace: male, length 11.6, width 16.2; female, length 18.1, width 28.1.

Variation.—Lobules tend to be rather sharply pointed in juveniles, but grow progressively blunter as they increase in size, many of them finally becoming flattened knoblike expansions on somewhat restricted bases. Also, small lobules proliferate with increasing size. Clusters on front and mesial areas tend to be tripartite with an opening in the clusters directed forward and outward.

Habitat.—Offshore *Lithothamnion* reef off North Carolina; 50 to 640 m.

Type-locality.—Approximately SE Cape Lookout, N. C., 33°43′N, 76°40′W, 90 m, to 33°42.7′N, 76°40.2′W, 110 m, *Eastward* Stn. 1087.

Known range.—Near edge of continental shelf SE of Cape Lookout, N. C.; Florida Straits; off Cape Catoche, Yucatan; off Venezuela and Surinam (USNM); Bermuda (Markham and McDermott 1981).

Remarks.—Ovigerous females are known in July from North Carolina and Venezuela and October off Venezuela. Changes in carapace dimensions with growth were calculated by Soto (1980).

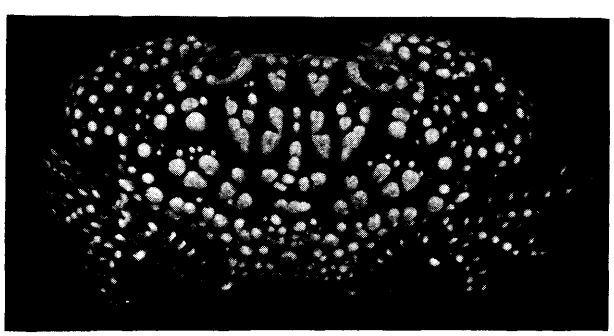

Fig. 311. *Allactaea lithostrota* Williams. Female in dorsal view, 10 mm indicated (from Williams 1974a).

Genus *Glyptoxanthus* Milne Edwards 1879

Rathbun 1930a:263.—Guinot 1967b:554.

Glyptoxanthus erosus (Stimpson)

Figs. 312, 331*b*

Actaea erosa Stimpson 1859:51.

Glyptoxanthus erosus.—Rathbun 1930a:263, pl. 107.—Williams 1965:185, figs. 167, 183A.—Guinot 1967b:556, fig. 30a, b.—1969:237–241.—Felder 1973:60, pl. 9, fig. 9.

Recognition characters.—Surface of body and legs covered with rough vermiculations, furrows or cavities between them narrow, making regular pattern and giving body an eroded appearance; elevations between furrows or cavities formed by masses of small granules crowded together producing rough surface in young and half-grown individuals, but variably worn smooth in old ones; margins of cavities with short pubescence. Carapace areolated, but divisions obscured to large extent by character of surface; lateral boundaries of gastric region and median suture from front to middle of gastric region deep. Front steeply inclined, median lobes evenly rounded, margins granulate. Ischium of third maxilliped with deep, longitudinal, central groove.

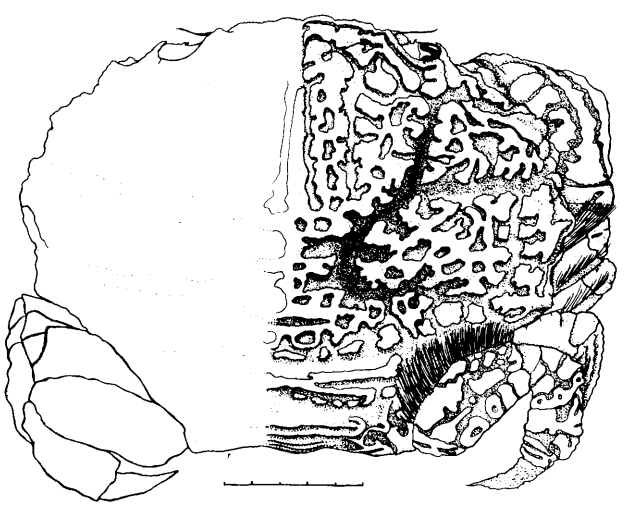

Fig. 312. *Glyptoxanthus erosus* (Stimpson). Animal in dorsal view, detail shown on right side, 5 mm indicated (from Williams 1965).

Chelae short and broad, upper surface divided by furrows into transverse tuberculate ridges, outer surface divided into longitudinal tuberculate ridges; fingers short, deeply grooved, even-toothed; dactyls tuberculate at base on upper side. Walking legs with hairy edges, dactyls pubescent.

Measurements in mm.—Carapace: male, length 39, width 54; female, length 47, width 67.

Color.—Rathbun (1930a) described a specimen in formalin as cream white with blotches and small spots of bright red, color especially persistent on walking legs, with dactyls red at base and yellowish distally.

Habitat.—The species has been taken from rocks and the alga *Halimeda* in shallow water, from coarse sand, and sponges and coral reefs in deeper water. Low-tide mark to 70–90 m (Cain 1972).

Type-locality.—Florida.

Known range.—Cape Lookout, N. C., southward; off Grand Isle, La., southeastward; Yucatan; through West Indies to Guadeloupe.

Remarks.—Ovigerous females have been taken off northeast Florida in January and North Carolina in September.

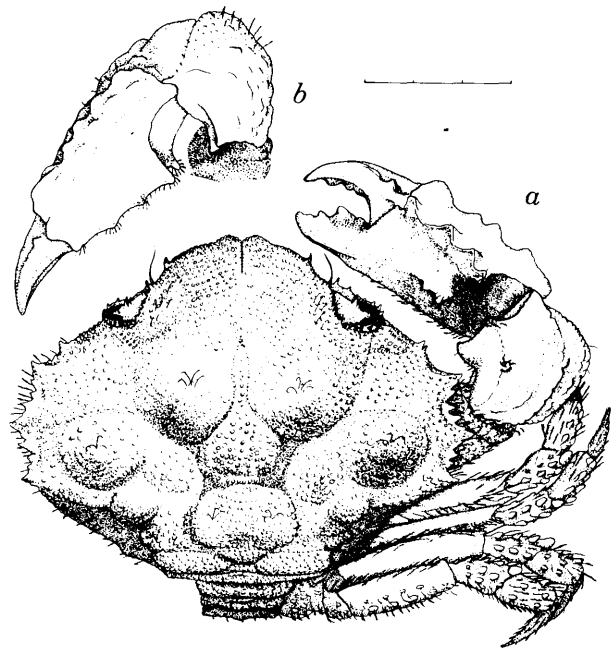

Fig. 313. *Carpoporus papulosus* Stimpson. *a*, Animal in dorsal view, legs of left side not shown; *b*, cheliped partially extended in frontal view; 3 mm indicated (from Williams 1965).

Genus *Carpoporus* Stimpson 1871

Rathbun 1930a:269.—Hemming 1958b:14.

Carpoporus papulosus Stimpson

Figs. 313, 331*c*

Carpoporus papulosus Stimpson 1871a:139.—Rathbun 1930a:269, pl. 110, figs. 3–6, pl. 111.—Williams 1965:186, figs. 168, 183B.

Recognition characters.—Carapace subhexagonal, nearly as long as broad, naked above; regions protuberant, somewhat wartlike and granulated, gastric and epibranchial regions prominent. Two or 3 small, spiniform lateral teeth, interspaces armed with denticles. Front strongly projecting at middle, bilobed, margin concave, inner end rectangular, outer end spiniform. Peduncle of eye granulated; orbit with margin granulate above. Exposed surface of third maxilliped with beadlike granules.

Chelipeds when retracted each having large hole between carpus and hand for passage of water to afferent branchial apertures; inner surface of hand with 2 unequal peglike spines near middle forming a kind of filter in front of branchial opening; carpus and hand sculptured externally with granulated protuberances, arranged in 4 or 5 serial rows on hand; hand serrate above with 4 teeth partly joined; fingers stout, short. Walking legs hairy below.

Measurements in mm.—Carapace: male, length 14.6, width 18.3; female, length 12.4, width 15.3.

Habitat.—Variety of bottoms from sand to rock and coral; 32–113 m.

Type-localities.—Southwest of Tortugas and off Carysfort Reef, [Fla.].

Known range.—Between Capes Hattteras and Lookout, N. C.; Gulf of Mexico off Mobile Bay southeastward; Cape Catoche, Yucatan.

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).

Genus *Pseudomedaeus* Guinot 1968

Guinot 1968:726.—Williams 1978:547.

Key to Species

1. Median frontal notch V-shaped, usually narrow; margins of anterolateral teeth either spinous or with beadlike granules; carpus of chelipeds with strong internal spine, sometimes double . . . . . ***P. agassizii***

Median frontal notch U-shaped; margins of anterolateral teeth almost always smooth (rarely granulated); carpus of chelipeds with stout internal double spine . . . . . ***P. distinctus***

Pseudomedaeus agassizii (A. Milne Edwards)

Figs. 314, 331*d*

Leptodius agassizii A. Milne Edwards 1880:270, pl. 49, fig. 3.—Hay and Shore 1918:441, pl. 34, fig. 6.—Rathbun 1930a:307, pl. 141, figs. 4–5.—Williams 1965:192, figs. 174, 183H.

Medaeus latifrons Chace 1942a:83, pl. 25.

Medaeus agassizi var.—Monod 1956:309–310, figs. 381–382.

Pseudomedaeus agassizi.—Guinot 1968:726, figs. 25, 58.—Felder 1973:67, pl. 9, fig. 11.

Pseudomedaeus agassizii.—Williams 1978:551, fig. 3.

Recognition characters.—Carapace broad, suboval, flattened,finely granulate posteriorly but anteriorly ornamented with bead granules in transverse lines or clusters, scattered hairs along anterior margin of lines. Front little advanced, divided at middle by V-shaped notch; margin transversely grooved, appearing doubled, upper edge less pronounced than lower but hiding lower edge if viewed dorsally; both edges of front and orbital margin granulate. Of 5 anterolateral teeth only last 2 or 3 well developed, sharp, turned forward, anterior margins granulate; second tooth, and sometimes third, triangular, obtuse or rounded, first (outer orbital angle) represented by elevated mass of granules.

Chelipeds unequal; carpus strong with sharp internal spine, sometimes doubled, and with many irregular, granulate rugae above; each hand with upper surface granulate and tuberculate, tending to arrangement in row on crest of palm; larger hand with strong blunt-tipped fingers; smaller with more slender, acute, and more conspicuously grooved fingers showing tendency to be spoon shaped at tips; fingers dark, color continued to oblique line on palm. Walking legs each ragged, stout; hairs along upper and lower crests of articles and spiny, especially on upper margin; dense pile on propodi and dactyls, prominent smooth outer condyles at articulation between them.

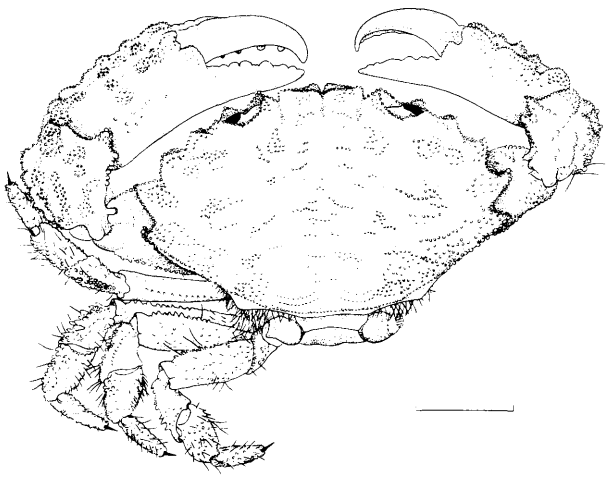

Fig. 314. *Pseudomedaeus agassizii* (A. Milne Edwards). Male in dorsal view, walking legs of right side not shown, 5 mm indicated (USNM 18008).

Measurements in mm.—Carapace: male, length 11.8, width 19.2; ovigerous female, length 19.5, width 31.

Variation.—Small specimens from near Beaufort, N. C., have the last anterolateral teeth well developed, but a series of specimens from Pensacola, Fla., in the USNM show that these spines may be reduced to two in larger individuals. There is considerable variation in depth of sculpturing dorsally on the anterior carapace and chelipeds.

Habitat.—Primarily from rock and other hard substrates with fouling growth of sponges, bryozoans, etc., but also on sand; 7.3 to 82 m (rarely to 221 m, Wenner and Read 1982).

Type-locality.—Florida reefs, 21.9 to 32.9 m.

Known range.—Cape Hatteras, N. C., to southern Texas. The species is not known to occur in the Virgin Islands as previously reported (Williams 1965). That record was based on specimens of *Cataleptodius* (=*Leptodius*) *floridanus* (Gibbes) in the USNM collection mistakenly identified as *P. agassizii* (see Williams 1978).

Remarks.—Ovigerous females are known from February to November in various parts of the range. From an ovigerous female collected near Cape Lookout, N. C., Costlow and Bookhout (1968) reared larval stages in the laboratory at 25°C in 35‰ salinity on a 14-h day. They described four zoeal stages and a megalopa typical of xanthid crabs.

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).

Pseudomedaeus distinctus (Rathbun)

Figs. 315, 331*e*

Micropanope sculptipes.—A. Milne Edwards 1880:325, pl. 54, fig. 2–2c.—1880a:14.

Lophopanopeus distinctus Rathbun 1898b:272.—1930a:331, pl. 155, figs. 1–2.—Cerame Vivas and Gray 1966:263 (in faunal list).

Micropanope distinctus.—Menzies 1948:24 (new combination).

Pseudomedaeus distinctus.—Williams 1978:547, figs. 1, 2, 4*b*,

Recognition characters.—Carapace broad, regions well marked, lobulate and granulate on highest parts, with tendency to form transverse series; sparsely hairy. Front little advanced, deflexed, double edged, upper edge more coarsely granulate than lower, true margin; median notch broad, each lateral lobe with concave margin and obtuse angle at outer end. Orbital margin granulate; inner angle and outer suborbital angles prominent. Five anterolateral teeth, outer orbital angle (first) inconspicuous; second tooth low and broad, granulate subhepatic eminence below it; following 3 teeth subequal, last 2 with pointed tips and equally produced laterally in adults but fifth tooth less produced in young.

Chelipeds subequal, narrow, pubescent and covered with sharp granules; merus spinulous along upper margin; carpus with stout inner doubled spine, outer surface irregularly furrowed; palm with longitudinal furrow subdorsally on outer and inner surfaces, and another shallower furrow along dorsal surface (absent in larger adults); fingers elongate, little or no gape, shallow teeth on opposed edges. Walking legs spined along crests of articles; pubescence dense and ragged, especially on distal articles.

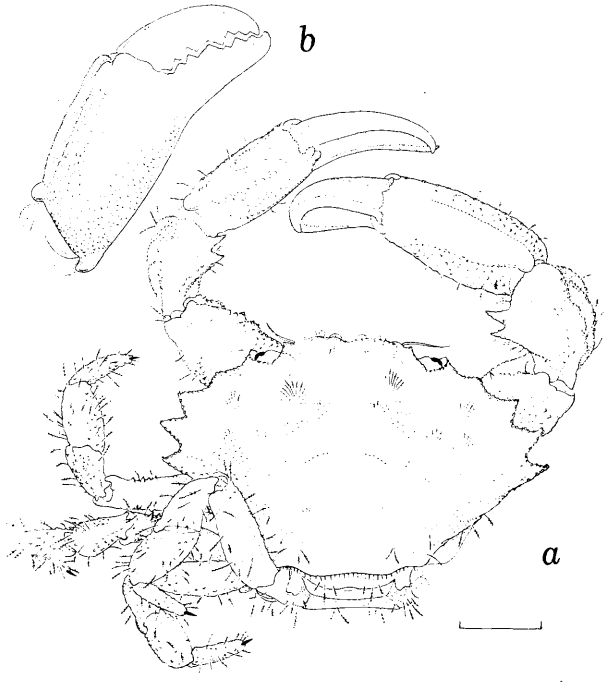

Fig. 315. *Pseudomedaeus distinctus* (Rathbun). *a*, Male in dorsal view, walking legs of right side not shown; *b*, major chela, external view; 5 mm indicated (from Williams 1978).

Measurements in mm.—Carapace: male, length 19.4, width 30; female, length 10.8, width 16.8.

Color.—"Large adult; body mottled gray and reddish gray or light brown, longitudinally elongate spot in anterior extension of mesogastric area darkest; fingers light brown. Small specimen; body more darkly blotched, legs banded with brownish speckled bands of same color as blotches on body" (Williams 1978).

Habitat.—Has been found on hard substrate; 47.5 to 185 m.

Type-locality.—Gulf of Mexico, NW Dry Tortugas, 25°33′N, 84°21′W, 184.7 m.

Known range.—Off Cape Hatteras, N. C., 34°57′N, 75°19′W, through Straits of Florida to NW of Dry Tortugas; Puerto Rico; Barbados.

Remarks.—*Pseudomedaeus distinctus* is a problem species, as indicated by its synonymy. Williams (1978) placed it in *Pseudomedaeus* with two similar species but remarked that the three may eventually be placed in separate genera.

Genus *Rhithropanopeus* Rathbun 1898

Rathbun 1930a:455.—Hemming 1958b:37.

Rhithropanopeus harrisii (Gould)

Figs. 316–317, 331*f*

Pilumnus harrisii Gould 1841:326.

Rhithropanopeus harrisii.—Hay and Shore 1918:441, pl. 35, fig. 5.—Rathbun 1930a:456, pl. 183, figs. 7–8.—Williams 1965:187, figs. 169, 183C.—Christiansen 1969:81, fig. 23.—Felder 1973:67, pl. 9, fig. 14.

Recognition characters.—Carapace subquadrate, approximately as long as wide, much less convex from side to side than from front to back, sparsely pubescent toward anterolateral angles; protogastric regions with 2 transverse lines of granules; similar line from posterior lateral tooth to opposite one across mesogastric region. Front almost straight, slightly notched, with its margin transversely grooved, appearing double when viewed from front. Postorbital angle and first anterolateral tooth completely coalesced; first and second developed anterolateral teeth of about same size and perhaps larger than last tooth.

Chelipeds unequal and dissimilar; carpus scarcely grooved above and with moderately developed in-

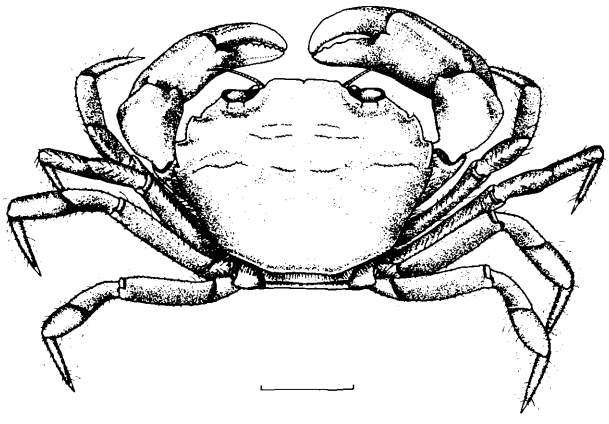

Fig. 316. *Rhithropanopeus harrisii* (Gould). Male in dorsal view, from Copenhagen, Denmark, 5 mm indicated (from Christiansen 1969).

ternal tooth; chelae indistinctly costate above. Major chela with short fixed finger and strongly curved dactyl. Minor chela with proportionately longer fixed finger and long straight dactyl. Walking legs long, slender, compressed, and somewhat hairy.

Measurements in mm.—Carapace: male, length 15.6, width 21.3; female, length 12.4, width 16.

Variation.—The chelipeds are nearly smooth in old individuals, but in juveniles the carpus is rough with lines and bunches of granules, its distal groove deep, the upper margin of palm with 2 granulate ridges, and the upper edge of the fingers granulate.

Color.—Brownish above, paler below; fingers light.

Habitat.—Ryan (1956) found this species distributed primarily in upper Chesapeake Bay and tributaries of the lower Bay in depths of about 0 to 9 m in a salinity range of fresh to 18.6‰, always associated with some kind of shelter—oyster bars, living and decaying vegetation, old cans, and other debris. Similar habitat is known for upper Delaware Bay (McDermott and Flower 1952) and the tributaries of the Neuse River estuary in North Carolina, as well as estuarine streams in southern Florida (Odum and Heald 1972). Surface to 36.6 m.

Type-locality.—Cambridge Marshes and Charles River, Mass.

Known range.—The original range of this species is presumed to be in fresh to estuarine waters from the southwestern Gulf of St. Lawrence, Canada, to Veracruz, Mexico. The species has been introduced on the west coast of the United States and in parts of Europe

Remarks.—Rhithropanopeus harrisii thrives in a wide range of salinities, an attribute which helps to explain transport from its original range to two widely separated areas of the earth. One of these is the west coast of the United States where it was reported in the San Francisco Bay area by Jones (1940) and Filice (1958), and at Coos Bay, Ore., by Ricketts and Calvin (1952). An older and wider introduction in Europe was reviewed by Buitendijk and Holthuis (1949) who considered the European form a separate subspecies (*R. h. tridentatus* (Maitland)). Originally confined to the old Dutch Zuider Zee, the species gradually diminished in abundance there with the closing of that inland sea in 1936 and in that year was first reported outside the Netherlands. In 1939 it was first reported in large numbers from southern Russia in the Dnestr River and Bug River estuaries, and according to fishermen there was first observed in 1936 but certainly not present before 1932. Gadzhiev (1936) and Turoboyski (1973) reviewed its occurrence in the Black Sea and Caspian Sea areas of eastern Europe, and Christiansen (1969) its presence in northwestern Europe (SW France, Normandy, Netherlands, Denmark, Germany, Poland) as well as in Bulgaria, Roumania and the U.S.S.R. Williams (1965) listed specimens from northeastern Brazil, but reexamination shows that occurrence to be an error. The remarks that follow apply only to the Western Hemisphere.

Osmotic capabilities of the adults consist of hyper-regulation of chloride and osmotic pressure in salinities up to 60%–70% that of sea water and a slight tendency to hypo-regulate in higher salinities (Smith 1967). There is a high rate of water turnover, but inward permeability decreases in the lower salinities.

Connolly (1925) stated that four zoeal stages and a megalopa comprise the larval and postlarval development of this species. These conclusions were based on study of plankton taken from the Miramichi River estuary, New Brunswick, Canada, in August. Chamberlain (1962) confirmed and supplemented Connolly's account with eggs taken from Chesapeake Bay and cultured in the laboratory. Duration of larval stages was twice as long when zoeae were fed copepod nauplii and algae as when fed nauplii alone. In an array of salinities and temperatures, development was found to proceed best at 6 to 10‰ salinity. Developmental time increased wih decreasing temperature. Developmental times of larvae in nature were found to agree with results of laboratory culturing at similar salinities and temperatures. Mortality rates for zoeae in nature were found to be lower than expected. A relatively high rate was postulated for the megalopa or early crab stages. Presence of adult crabs in fresh water was deemed a result of migration after larval stages are complete. Hood (1962) also described a series of larval and postlarval stages from eggs hatched

and reared under laboratory conditions in Mississippi.

Christiansen and Costlow (1975) reared the species from hatching through the first or second crab stages under experimental conditions in 11 combinations of salinity and cyclic temperatures (5, 20, 35‰ S at 20°–25°, 25°–30°, 30°–35°C; 25‰ S at 20°–25°, 30°–35°C). Larvae survived to megalopa plus first crab in all combinations except 5‰ S at 30°–35°C. Best survival to megalopa (94%) and first crab (90%) occurred in 20‰ S at 20°–25°C. In all other combinations there was a reduction in survival to the first crab stage. Duration of larval stages was affected significantly by temperature whereas the effect of salinity on mean days from hatching to the first crab was not consistent in different temperatures cycles. Development to first crab was shortest in 20‰ salinity, 20°–25°C (22.6 and 21.6 days ($\bar{x}$) respectively). Megalopae reared in 35‰ salinity at all cycles of temperature, as well as larvae in 20 and 25‰ S, 30°–35°C, showed abnormality, with highest percentages occurring in 35‰ S, 30°–35°C. The authors concluded that larval development of *R. harrisii* is strongly influenced by environmental factors and not solely related to genetic differences.

Earlier Costlow, et al. (1966) had found that time of development in non-cycled temperatures was not significantly affected by salinities of 5–35‰. Survival to first crab occurred in 2.5 to 40‰ salinity; 60–90% of zoeae survived to megalopae in 15–25‰ salinity, but in lower and higher salinities there was reduction in percent survival to first crab. Duration of stages as well as mortality was affected by temperature. The authors suggested that the capacity to develop normally within this broad range of environments may have contributed to the wide distribution of this species.

Field studies fill out and corroborate this experimental evidence. Herman, et al. (1968) found zoeae present from May to October in the Patuxent River, Md., with peak occurrence in June-July. Sandifer (1973d) found larvae common to abundant mostly at 0–10‰ salinity in the upper York and Pamunkey rivers tributary to lower Chesapeake Bay, and to lesser extant in the Bay proper. Zoeae first appeared in May, were most numerous in July-September, and nearly disappeared by October. Most occurred in a temperature range of 25°–29°C. All four zoeal stages were found in both surface and bottom samples, stage I comprising 55% of the total and being more numerous in bottom than surface samples. Numbers of larvae in surface samples decreased steadily with successive stages. Bousfield (1955) found the larvae in salinities <20‰ at the level of no net motion in the Miramichi estuary. Pinschmidt (1963) noted occurrence of larvae in the Newport River, N. C., roughly paralleling that in the York River, but most abundant at 31°C in a salinity range of 13–19‰. Herman (1968), Tagatz (1968), and Williams (1971) added supporting evidence for period of occurrence of larvae (as late as November in Florida), level of salinity, etc. Sandifer (1975) contended that stratification of larvae on bottom indicates retention of larvae in estuaries as the major means of recruitment for the species, and Wheeler and Epifanio (1978) showed that larval response to differences in hydrostatic pressure may be related to this type distribution. Cronin (1979) found that larvae of all stages maintain an average depth near the zone where net tidal flow is zero.

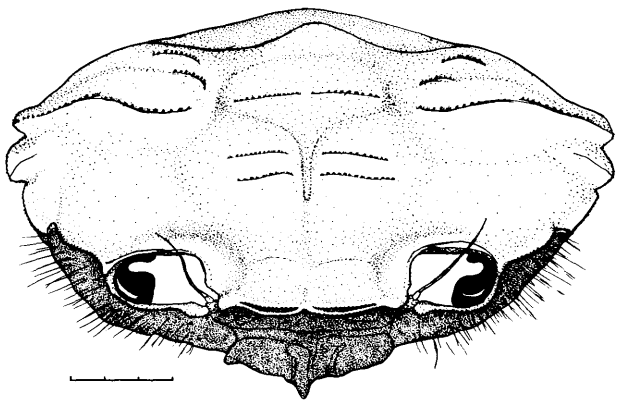

Fig. 317. *Rhithropanopeus harrisii* (Gould). Frontal aspect of body viewed from above, 3 mm indicated (from Williams 1965).

Ryan (1956) summarized life history data for *R. harrisii* in the Chesapeake Bay area. He collected ovigerous females from June to September. Though juveniles were found in all months of the year, they occurred most frequently in samples taken from July to October. Immature forms of undetermined sex ranged from 2.2 to 2.6 mm in width, immature males from 3.2 to 5.0 mm, and similar females from 3.3 to 5.7 mm in width. Ryan considered maturity to be reached the following summer at a carapace width of 4.5 mm for males and 4.4 to 5.5 mm in females.

Adults continue to grow and molt after maturity is reached. No concrete data on number of instars throughout life are available but it is estimated that there may be four instars between attainment of the 5 and 10 mm carapace widths.

Success of *R. harrisii* in the estuarine environment is emphasized by its role in the food web. Odum and Heald (1972) found more than 40 animals per m in an estuarine stream draining a *Juncus* marsh in south Florida. An omnivorous diet was dominated by mangrove leaf detritus. Crustaceans such as small amphipods and harpacticoid cope-

pods were eaten more often by small crabs. Sikora, et al. (1972) found *R. harrisii* preyed on by two species of hake, *Urophycis regius* and *U. floridana*, in a Georgia estuary, and Heard (1975) reported it as forming a significant part of the diet of *Ictalurus catus*, the white catfish.

Boschma (1972) reviewed occurrence of specimens from the Gulf of Mexico bearing the parasite *Loxothylacus panopei*.

Rhithropanopeus harrisii has proved to be a hardy experimental animal from an environment of great interest to developmental and physiological ecologists. This circumstance is reflected by a flow of papers dealing with subjects beyond the scope of this sketch. A few of these are: Capen (1972), osmoregulation; Christiansen, et al. (1977a, b), effects of hormone mimics on development; Costlow (1966), effect of eyestalk removal on development; Costlow and Sastry (1966), free amino acids in developmental stages; Forward (1976), shadow-sinking response of larvae; Gooch (1977), and Morgan, et al. (1978), allozyme genetics; Jones (1941) osmoregulation; Kalber and Costlow (1966; 1968), ontogeny of osmoregulation and its neurosecretory control; Rosenberg and Costlow (1976), effects of cadmium on development.

Genus *Micropanope* Stimpson 1871 (restr.)

Guinot 1967a:349.

Key to Species

1. Carapace with last anterolateral tooth obsolescent; legs spinulous. . . . . ***M. sculptipes***
   Carapace with last anterolateral tooth small but easily discernible. 2
2. Anterolateral teeth with granular margin; second tooth absent or fused with first (orbital) tooth; outer surface of hands rough with beadlike granules . . . . . ***M. nuttingi***
   Anterolateral teeth with denticulate bases; second tooth present; outer surface of hands spiny. . . . . ***M. urinator***

Micropanope nuttingi (Rathbun)

Figs. 318, 331*g*

Xanthias nuttingi Rathbun 1898a:271, pl. 4, fig. 1.
Micropanope nuttingi.—Rathbun 1930a:450, fig. 74.—Williams 1965:194, figs. 177, 183J.—Coelho and Ramos 1972:192.—Felder 1973:66, pl. 9, fig. 22.

Recognition characters.—Carapace suboval, convex anteroposteriorly, nearly flat transversely; regions distinct, anterior half rough with squamous tubercles, especially in tract adjacent to margins. Front convex, bilobulate, with granulate margins separated by V-shaped sinus, outer angle of each lobe subrectangular. Anterolateral teeth with sharply granulate margins; second normal tooth united with small first tooth; 3 remaining teeth sharp pointed, posterior tooth smallest.

Chelipeds heavy, quite unequal; merus spinulose on upper edge; carpus covered with beadlike tubercles, deep distal groove, inner angular eminence tipped with spinule, second spinule below. Females with whole outer surface of both chelae tuberculate. Major chela of males with upper and approximately ⅔ of outer surface beaded, tuberculate; lower ⅓ and distal extremity smooth and shining; fingers broad, not gaping, brown with light tips, color of fixed finger not continued on palm and ending in line with articulation of dactyl; dactyl with large basal tooth. Minor chela almost entirely tuberculate, growing less so toward distal and lower margins; upper margin with longitudinal

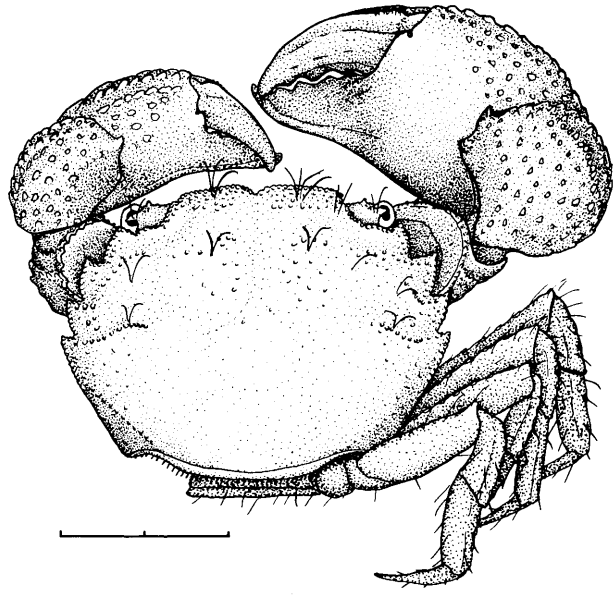

Fig. 318. *Micropanope nuttingi* (Rathbun). Animal in dorsal view, walking legs of left side not shown, 2 mm indicated (from Williams 1965).

groove, fingers deeply grooved. Upper margin of walking legs tuberculate or granulate.

Measurements in mm.—Carapace: male, length 4, width 6; female, length 3.8, width 6.3.

Color.—General overall color orange; carapace brown-orange with distinct red-orange granules anteriorly, anterolateral teeth white tipped, branchial region and posterolateral margins white, irregularly shaped white splotches behind each supraorbital margin parallel with third anterolateral tooth, 2 more at posterolateral margin of cardiac regon, and 1 posteriorly on intestinal region; chelipeds bright orange becoming white ventrally, numerous bead granules bright red-orange, fingers salmon, distinct white spot at articulation of dactyl; walking legs irregularly orange-brown with distinct white patches posteriorly at articulation of merus and carpus, spinules on meri and spinules and granules on remaining articles red-orange (R. H. Gore, personal communication).

Habitat.—Has been taken from boulder-covered beach, from *Porites* clumps and *Halimeda* (USNM records); shallow water to 183 m.

Type-locality.—Bahama Banks.

Known range.—Cape Hatteras, N. C., through Gulf of Mexico and West Indies to Bahia, Brazil.

Remarks.—As Felder (1973) remarked, this species probably does not belong in the genus *Micropanope*, judging from the structure of the male first pleopods. Also, the third maxillipeds have the merus produced anterolaterally, the hands of some specimens (USNM 75811, male) have fingers bent downward at an angle with the palm, and the second abdominal segment of males has each posterolateral corner obliquely truncated to reveal a small portion of sternum. All of these features suggest goneplacid rather than xanthid affinities.

Ovigerous females are known from Puerto Rico in January and Florida in July.

Micropanope sculptipes Stimpson

Fig. 319

Micropanope sculptipes Stimpson 1871a:140.—Rathbun 1930a:428, pl. 178, figs. 1–3.—Lunz 1937a:13.—Williams 1965:193, fig. 175.—Guinot 1967a:349, figs. 1, 4.—1971:1075 (listing).—Felder 1973:66, pl. 9, fig. 15.

Recognition characters.—Carapace naked, distinctly areolated; anterior and anterolateral regions somewhat roughened in front with small, sharp, toothlike tubercles partially disposed in lines. Anterolateral teeth sharp, denticulate, fifth (last) obsolescent, first and second almost entirely fused. Frontal lobes abruptly deflexed, with convex outline; margin thin, minutely crenulate, with slight furrow above it. Small tubercle on subhepatic region below second anterolateral tooth.

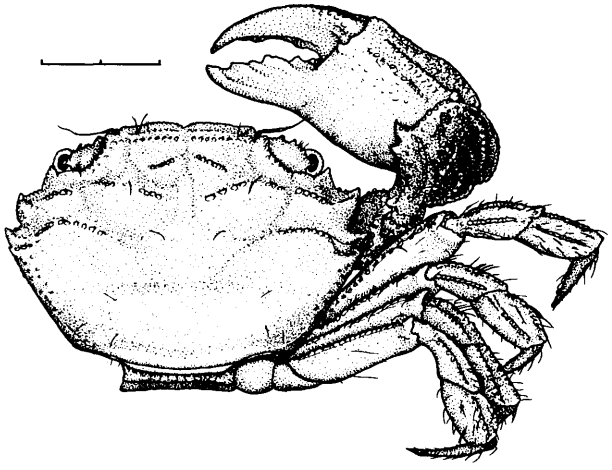

Fig. 319. *Micropanope sculptipes* Stimpson. Animal in dorsal view, legs of left side not shown, 2 mm indicated (from Williams 1965).

Chelipeds granulate above; carpus with granules arranged more or less in raised reticulated rugae, inner margin denticulate and with sharp double spine; hands with double denticulate crest above and minute granules on outer surface showing tendency to arrangement in rows (becoming obsolete in distal lower half of major chela), upper part of inner surface granulate; fingers grooved, thin superior crest on dactyls. Walking legs with minute spines above forming rows on carpus, single row in young.

Measurements in mm.—Carapace: male, length 4.3, width 6.5; female ovigerous, length 4.1, width 6.0.

Habitat.—11 m (Wenner and Read 1982).

Type-localities.—Seven hauls in Florida Keys, 27.4 to 124 m.

Known range.—SE Cape Lookout, N. C., to Port Aransas, Tex; West Indies to Barbados.

Remarks.—Guinot (1967a; 1971) in preliminary studies restricted the genus *Micropanope* to *M. sculptipes* and *M. lobifrons* in the Western Atlantic.

Micropanope sculptipes has been taken in numerous samples from offshore reefs of North Carolina (Cerame-Vivas and Gray 1966). 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).

Micropanope urinator (A. Milne Edwards)

Fig. 320

Pilumnus urinator A. Milne Edwards 1881:289, pl. 53, figs. 2–2b.

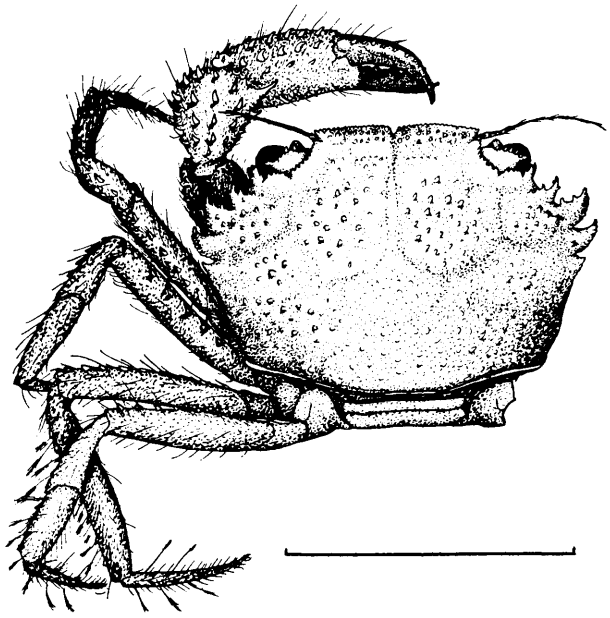

Fig. 320. *Micropanope urinator* (A. Milne Edwards). Male in dorsal view, legs of right side not shown, 5 mm indicated (from Williams, et al. 1968).

Micropanope urinator.—Rathbun 1930a:451, pl. 182, figs. 3, 4; pl. 183, figs. 1–3.—Williams, McCloskey, and Gray 1968:51, fig. 7.

Recognition characters.—Carapace broad, rough, regions plainly marked, granulate except in depressions, furred with thin, short pubescence. Frontal lobes slightly arcuate, edge finely denticulate, small median notch, outer angle subrectangular and edged with white granules. Orbital margin spinulous, diminishing to granules on mesiodorsal margin, interrupted laterally by broad sinus, somewhat larger on lower margin and continuing inward to large, triangular, granulated tooth. Five anterolateral spines including small outer orbital; second to fifth set in stouter denticulate bases; third and fourth largest, subequal, curved; first, second and fifth subequal, second curved, first and fifth straight.

Chelipeds spiny; merus with 2 curved spines dorsally; carpus heavily spined, longest spine at inner angle, second of equal size below it on minor cheliped; minor palm spinous over outer surface, major with spine changing to coarse granules distoventrally; fingers deeply grooved, especially on minor hand where accented by sharply granulate ridges. Walking legs rough on most surfaces; with long hairs below and on upper surface of distal 3 articles; dactyl long, slender, slightly curved, with acute brown horny tip.

Measurements in mm.—Carapace: male, length 7, width 10.

Color.—Preserved specimens have white-tipped spines, spinules and granules; body darker.

Habitat.—Hard substrates; 146 to 457 m.

Type-locality.—Near Santa Cruz [St. Croix], West Indies, 448 m.

Known range.—Off Capes Hatteras and Lookout, N. C.; Florida Keys to St. Croix, West Indies.

Genus *Tetraxanthus* Rathbun 1898

Rathbun 1930a:458.

Tetraxanthus rathbunae Chace

Fig. 321

Tetraxanthus bidentatus.—Rathbun 1898a:275.—1930a:458, pl. 184.

Tetraxanthus rathbunae Chace 1939a:52.—1940:37.—Coelho and Ramos 1972:192.

Tetraxanthus rathbuni W. E. Pequegnat 1970:173, 195.

Recognition characters.—Carapace subquadrate, smooth to naked eye but microscopically granulate; very convex anteroposteriorly, less so transversely; gastric and hepatic regions feebly indicated. Front advanced, nearly straight, median emargination very small. Orbit half as wide as front, dorsal fissures obsolescent; outer orbital angle small, triangular. Anterolateral border with 3 other lobes or teeth behind orbital; second very shallow and broad; third obtuse angled with short, nearly transverse anterior and rather convex, nearly lon-

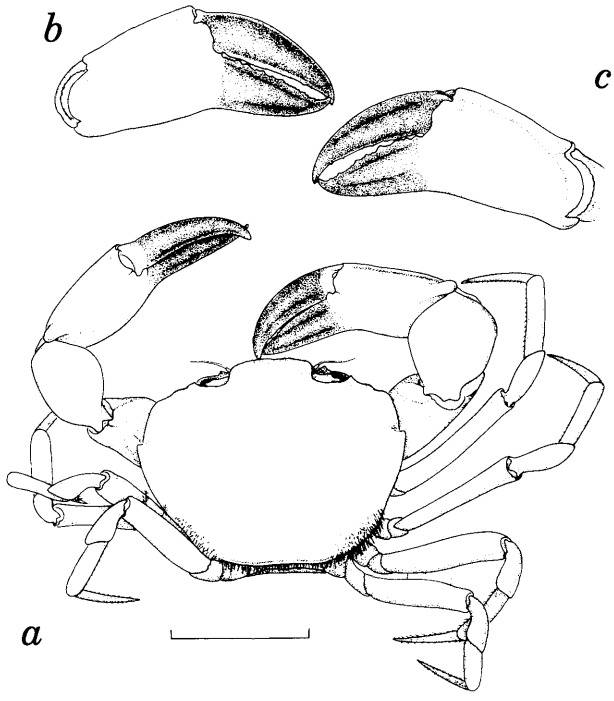

Fig. 321. *Tetraxanthus rathbunae* Chace. *a*, Male in dorsal view; *b*, right, *c*, left chela in external view; 1 cm indicated (USNM 92160).

gitudinal posterior margins; last lobe dentiform, short, elevated.

Chelipeds long, strong, smooth, unequal; especially in male; broad central lobe on upper margin of merus and mesial lobe at inner angle of carpus. Chelae elongate, increasing in width distally, margins convex; fingers long, deflexed, little or no gape; prehensile teeth uneven, largest one at base of major dactyl; dark color not covering finger tips or base of fixed finger. Walking legs slender, unarmed, pubescent distally.

Male abdomen with sixth segment free, broader than long, sides sinuous; telson broader than long, rounded and pubescent distally.

Measurements in mm.—Carapace: male, length 20, width 25; female, length 15.5, width 19.6.

Color.—Fingers red except for white tips (Henderson *in* Rathbun 1930).

Habitat.—Variety of bottoms; 27 to 430–476 m.

Type-locality.—Old Bahama Channel due N Punta Caldera, Camaguey Province, Cuba, 22°44'N, 78°41'W, 274–329 m.

Known range.—Off Cape Lookout, N. C., to Rio de Janeiro, Brazil (Coelho and Ramos 1972), including Gulf of Mexico (W. E. Pequegnat 1970; USNM).

Remarks.—This crab seems to be primarily distributed on the upper continental slope, but it has been recorded a number of times from shallower depths. Ovigerous females are known from off Florida and Yucatan in January, Louisiana in June, and Veracruz in July.

Until now the species has been considered a xanthid, but has a number of features linking it to the Goneplacidae, suggesting that it is one of the transitional or evolutionary grades between these groups (Guinot 1969a, b; 1971) (smooth, granular ornamentation; long, slender walking legs; deflexed fingers; shape of male first pleopods; shape of male abdomen leaving a tiny section of sternite 8 visible between it and the fifth coxa).

Genus *Eurypanopeus* A. Milne Edwards 1881

Rathbun 1930a:403.

Key to Species

1. Fingers of both chelae with acute tips, not spooned . . . . . ***E. abbreviatus***
   Fingers of minor chela spoon-shaped at tip . . . . . ***E. depressus***

Eurypanopeus abbreviatus (Stimpson)

Figs. 322, 331*i*

Panopeus abbreviatus Stimpson 1860a:211.

Eurypanopeus abbreviatus.—Rathbun 1930a:404, text-fig. 63, pl. 172, figs. 1–2.—Williams 1965:94, fig. 178, 183K.—Coelho and Ramos 1973:191.—Felder 1973:68.

Recognition characters.—Carapace approximately ⅔ broader than long, moderately convex in 2 directions, naked above, granulate and uneven on front and along anterolateral border, smooth and polished elsewhere; areolations slightly but distinctly indicated, a number of well-marked rugae among granules. Front deflexed, 4–lobed, median lobes prominent, separated by V-shaped notch. Anterolateral margin thin, divided into 4 lobes, first and second teeth coalesced, separated by slight concavity; third tooth obtuse; fourth with outer margin longitudinal or nearly so; fifth subtriangular, directed outward. Low granulate swelling below interval between first 2 teeth.

Chelipeds quite unequal in males; carpus with blunt internal tooth; fingers slender, pointed, widely gaping in major chela; fitting closely in minor, tips crossing in both; major dactyl with large basal tooth, color of fingers not extending on palm.

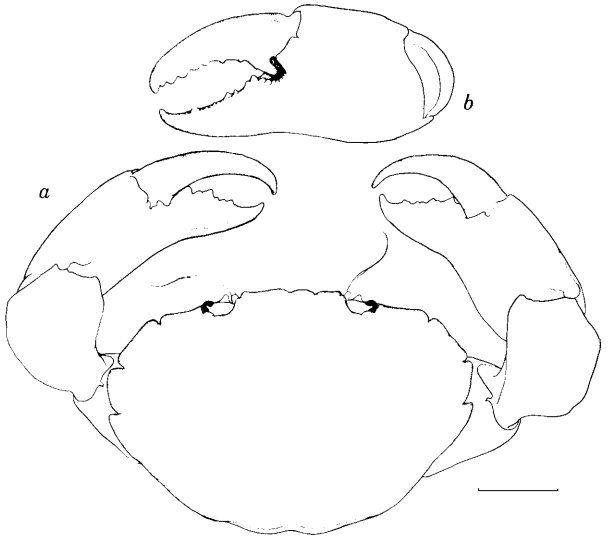

Fig. 322. *Eurypanopeus abbreviatus* (Stimpson). *a*, Male in dorsal view, walking legs not shown, front with anomalous notch to right of midline; *b*, right chela in external view; 5 mm indicated (from Williams 1965).

Measurements in mm.—Carapace: male, length 15.8, width 25; female, length 12.8, width 20.

Color.—Yellowish or brownish above, front margin of carapace and chelipeds roseate or tinged with bluish purple; fingers black with paler tips. Brazil-

ian specimens with a number of large dark spots on upper half chelipeds.

Habitat.—Specimens have been found near shore on oyster beds, under rocks, and among sponges and bryozoan growth; shore and shallow water to unknown depth.

Type-locality.—Barbados, British West Indies.

Known range.—South Carolina, through West Indies and Gulf of Mexico to Santa Catarina, Brazil.

Remarks.—Ovigerous females are known from April to November in the West Indies, and August to November in southern Brazil (Rathbun 1930a, in part). Ogawa and Rocha (1976) calculated that females of carapace length 6.0–10.5 mm bear 2,560 eggs ($\bar{x}$).

Eurypanopeus depressus (Smith)

(Flat mud crab)

Figs. 323, 331*j*

Panopeus depressus Smith 1869a:283.

Eurypanopeus depressus.—Hay and Shore 1918:437, pl. 34, fig. 4.—Rathbun 1930a:410, text-fig. 65, pl. 173, figs. 3–4.—Williams 1965:195, figs. 179, 183L.—Felder 1973:67, pl. 9, fig. 17.

Fig. 323. *Eurypanopeus depressus* (Smith). *a*, Animal in dorsal view, walking legs not shown; *b*, major chela in external view; 5 mm indicated (from Williams 1965).

Recognition characters.—Carapace transversely oval, approximately ¾ as long as wide, flattened posteriorly, slightly convex in anterior half; areolations well defined, finely granulate, with several pairs of transverse rows of granulations. Anterolateral teeth 4, outer margins curved granulate; first 2 teeth coalesced to form broad lobe with slightly sinuate margin; third tooth blunt or spine tipped; fourth and fifth spine tipped, pointing obliquely upward and forward. Front nearly straight, median notch small or absent.

Chelipeds dissimilar and quite unequal. Smaller one more rugose than larger and with margin of fingers nearly straight and completely closing for considerable distance distally, opposed margins of tips thin edged and hollowed out—"spoon shaped." Larger cheliped with nearly smooth articles, hand heavy and inflated; dactyl strongly curved, obscurely toothed at base and meeting fixed finger only at tip; internal tooth of carpus tipped with small spinule; in unworn condition both fingers show indication of spoonlike flattening.

Measurements in mm.—Carapace: male, length 17.5, width 25; female, length 12.5, width 18.7.

Variation.—Ryan (1956) described a persistent, central, oval, blood-red spot or structure on the inner surface of the ischium of the third maxillipeds of both sexes. The spot is often ⅔ the length of the article, with its surface raised slightly above the surface of the ischium. When pressure is applied, the hard spot cracks and is easily dissected out. A similar spot has been noted on *P. herbstii.*

The normal male abdomen is narrow, with the third, fourth, and fifth segments fused. A few (parasitized?) variant males have wide abdomens with seven segments, resembling females.

Color.—Mottled grayish olive or dark olive brown, especially on upper surfaces of chelipeds and anterior parts of carapace; fingers dark brown with dark color of fixed finger extended on palm; body and legs light colored underneath.

Habitat.—In Chesapeake Bay, Ryan (1956) found this species in greater abundance on oyster bars than any other species of mud crab, and evidence was presented showing a positive relationship between presence of oyster shells and this species. Others have noted a similar habitat preference (Lunz 1937a; Rouse 1970; Tabb and Manning 1961; Grizzle 1974). In the Bay, the depth range was 1.8 to 27 m (Cowles 1930, in part), and the salinity range 4.5 to 20.4‰. Elsewhere the species occurs from shore to 48 m.

Type-locality.—New Haven, Conn.

Known range.—Massachusetts Bay through Florida to southern Texas; Dutch West Indies; Uruguay; Bermuda (USNM).

Remarks.—Ryan (1956) gave much detail on the life history of this species in Chesapeake Bay. Ovigerous females were collected there from June to September, but otherwise are known from April to November in Virginia, and year round in Florida, with isolated records elsewhere (Rathbun 1930a; Lunz 1937a; Ryan 1956; USNM). Zoeal stages were studied by Hyman (1925) from plankton tows made in the Beaufort, N. C., area, but Costlow and Bookhout (1961b) worked out the entire larval and postlarval history in the laboratory, illustrating four zoeal stages and a megalopa. Sandifer (1973d) found these larvae only three times during an extensive plankton survey in southern Chesapeake Bay (June and July), but reviewed larval findings of others: May to October in Newport River, N. C., mainly in salinities >26‰ (Pinschmitt 1963); in low concentrations outside Beaufort Inlet from May to October (Dudley and Judy 1971); May to October with peak in June-July in the Patuxent River, Md. (Herman, et al. 1968); and April to October with maximum in August in St. Johns River, Fla. (Tagatz 1968).

Ryan (1956) found that immature males from Chesapeake Bay range in carapace width from 3.2 to 6 mm, and females from 3.6 to 6.4 mm. He considered maturity to be attained at widths of 5.1 to 6 mm in males and 5.5 to 6.4 mm in females. Ovigerous females observed ranged from 6 to 21 mm in width. The range of sizes suggested that growth and molting continue after maturity is reached. Maturity may be reached in the first summer after eggs have hatched.

Walton and Williams (1971) studied populations of *E. depressus* on artificial reefs in three small experimental estuarine ponds in North Carolina, finding the crab to be the most abundant xanthid following heavy seeding with estuarine plankton a year before. The crabs matured in the ponds, males reaching a mean carapace width of 20 mm, females 16 mm. When sampling began in late June, up to 50% of females were gravid in one pond. This percentage varied in samples from each pond during summer, once being as high as 100% in an estimated population of 276. There was general reduction of gravid females after the end of August.

Grant and McDonald (1979) showed that *E. depressus* loses tactile responses when it is experimentally desiccated to 30% loss of body water. Desiccation tolerance increased exponentially with size. Still, crabs are more abundant on exposed oyster reefs in high summer temperatures than in the cold of winter, and it is thought that moisture-seeking behavior in interstices of the reefs as well as predator avoidance combine to protect intertidally exposed crabs from drying.

McDermott (1960) found that *E. depressus* is a predator on oyster spat in southern New Jersey but not so serious a pest as *P. herbstii.*

A population of *E. depressus* in the York River, Va., parasitized by a sacculinid, *Loxothylacus panopaei,* was first reported in 1966 by Van Engel, et al. The parasite, known from the Caribbean, Gulf of Mexico, southern California and British Colombia, and not found at that time in other areas of Chesapeake Bay or in other xanthids, was considered to be a recent introduction brought with live oysters from the Gulf of Mexico.

Genus *Neopanope* H. Milne Edwards 1800

Rathbun 1930a:366.

Neopanope sayi (Smith)

Figs. 324, 331*k*

Panopeus sayi Smith 1869a:284.

Neopanope texana sayi.—Hay and Shore 1918:438, pl. 34, fig. 8.—Rathbun 1930a:369, text-fig. 58, pl. 168, figs. 3–4.—Williams 1965:190, figs. 172, 183F.

Neopanope texana nigrodigita Rathbun 1934:3–4, illus.

Neopanope sayi.—Abele 1972:268, figs. 2B, C, D; 3D.

Recognition characters.—Carapace subhexagonal, length contained in width about 1.3 times, greatest width at fifth pair of anterolateral teeth, quite convex; carapace minutely granulate, and lightly pubescent especially near anterior and lateral regions. Five anterolateral teeth somewhat upturned, first 2 coalesced and separated by shallow sinus, third and fourth larger and directed forward, fifth smaller and directed somewhat outward; each of last 2 teeth with oblique ridge extending inward and backward. Front with small median notch, each half only slightly sinuate, with whole forming a much flattened curve extending from eye to eye.

Chelipeds unequal; merus armed with stout rectangular tooth on upper crest, carpus usually smooth, shallow groove parallel to distal margin and usually a strong spine on inner distal margin; dactyl of major chela about as long as palm, fingers armed with low, blunt teeth decreasing distally. Walking legs long and slender, dactyl of fifth leg as long as or shorter than propodus, its dorsal and ventral borders covered with thick pubescence.

Resembles *Eurypanopeus depressus.*

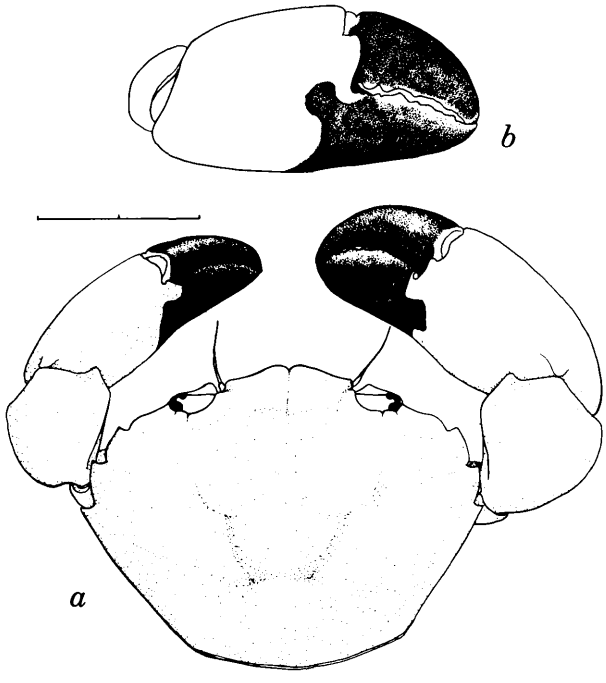

Fig. 324. *Neopanope sayi* (Smith). *a*, Male in dorsal view, walking legs not shown; *b*, major chela in external view; 1 cm indicated (from Williams 1965).

Measurements in mm.—Carapace: male, length 21.1, width 29.7; female, length 14.4, width 19.8.

Color.—Carapace a dark, slaty bluish green, brown or buff, with dark reddish-brown speckles on yellowish background, or bluish purple on gray background, especially on anterior portion of carapace and upper portion of chelae; outer face of chelae yellowish gray; fingers dark or black, color extending extensively on palm, tips light.

Habitat.—Most studies indicate greatest abundace on mud or oyster shell bottoms, though the species occurs in other situations such as sea grass beds as well (Marsh 1973), and, in the Chesapeake area, in a salinity range of 12.6 to 31.62‰. Low-tide mark to 46 m.

Type-localities.—New Haven, Conn., and Cape Cod Mass.

Known range.—Miscou Harbor, mouth of Chaleur Bay, New Brunswick, Prince Edward Island, and Cape Breton Island, Nova Scotia, Canada (Bousfield 1956, Bousfield and Laubitz 1972), to Florida Keys (Abele 1972). Introduced, Swansea, Wales (Naylor 1960).

Remarks.—Abele (1972) accorded *N. sayi* full specific rank, defining its range along the east coast of the United States and restricting that of *N. texana* (Stimpson) to the northern rim of the Gulf of Mexico.

Swartz (1978) described the reproductive systems of male and female *N. sayi*, and the spermathecae and sperm plugs in some detail. From observations at Gloucester Point, Va., he found that pairs copulate in the hard condition, that there is evidence that copulation may occur more than once, and that males probably copulate as often as possible during the mating season. Females usually mate once and sometimes more often between successive spawnings, but they do not copulate after spawning the last egg mass in a given molt cycle nor during molt cycles in which they fail to spawn. There is no trans-molt retention of sperm, but there is sometimes trans-spawning retention which is not always sufficient to fertilize the next egg mass. Mating behavior is apparently integrated with molting and spawning cycles, and different from species that mate in the soft condition.

Swartz found that most reproduction occurs in the 24°–30°C range (April in South Carolina [Lunz 1937a] to October in Chesapeake Bay for ovigerous females). Mature females spawned fertile eggs 10–16 days after molting. Embryonic development lasts 9–10 days in the normal spawning season; mean interval between hatching one batch of eggs and spawning of the next batch is 2.9 days; mean duration from hatching of the last egg mass deposited in a molting cycle to time of molt is 5.3 days. Thus, mean duration of a molt interval, including one spawning, is 27.8 days; an additional spawning lengthens a molt cycle by 12.9 days. If a mature female did not spawn between successive molts, the intermolt interval was 14.9 days. If a female spawns more than once between molts, her seasonal fecundity is reduced even though she spends a greater part of the spawning season bearing eggs. Females have constant relative size increments at post-pubertal molts. The reduction in fecundity necessitated by molting is more than compensated for by a logarithmic increase in fecundity accompanying growth. This may explain why the observed mean number of intermolt spawnings is close to unity. An 8 mm female will molt four to five times during the first spawning season, increasing to a carapace width of 17.2 mm by September. She will have 1400 eggs in the first mature instar (8 mm), 2400 in the second (9.7 mm), 4000 in the third (11.7 mm), 6900 in the fourth (14.2 mm), and, if there is a fifth at the end of the season, 11,600 eggs (17.2 mm). The total for that season is 15–30,000 eggs (four or five instars). Assuming a maximum life span to end in the middle of the third summer, and production of two to three egg masses in the second spawning season, lifetime fecundity of a female would be ~100,000 eggs. Most females do not grow larger than 15 mm in width and produce fewer than 30,000 eggs before death.

Chamberlain (1957, 1961) discussed develop-

ment time for larval stages, finding four zoeal stages (sometimes preceded by a brief prezoeal stage) and a megalopa. Development time varied with temperature (14 days at 30°C, 37 at 21°C) and with food. Larvae matured most rapidly when fed *Artemia salina* nauplii, did moderately well on *Artemia* and algae, but did not transform at all when fed pure algae. Sulkin and Norman (1976) found rotifers to be an unbalanced diet for developing larvae. Ryan (1956) summarized the work of Hyman (1925) on zoeal and megalopal stages.

From plankton tows along a transect of York River, Va., and lower Chesapeake Bay to its mouth, Sandifer (1973d) found zoeae at all stations in the euhaline to mesohaline range (10.87–32.34‰ salinity), but mostly in the lower Bay near the mouth of the river with maximum concentrations in June and mainly in 20–25‰ salinities. Larvae were taken from June to October, mainly in a temperature range of 19.3° to 29.6°C in bottom samples. Elsewhere, occurrence in plankton conforms to length of warm season, June to September in Narragansett Bay (Hillman 1964), June to October in Delaware Bay (Deevey 1960), and March to November in St. Johns River, Fla. (Tagatz 1968). In the ocean, Dudley and Judy (1971) found zoeae from May to early October at 1–8 m depths as far as 10–13 km off Beaufort Inlet, N. C. Megalopae were found in June, August, and September. Sage and Herman (1972) found zoeae of *N. texana* (=*N. sayi*) in zooplankton of the Sandy Hook Bay area in midsummer with peak numbers in early July. Sandifer (1975) felt that *N. sayi* adults may occur outside estuaries, for 69% of the larvae of this species were in bottom samples and the last two larval stages were much more abundant in bottom than in surface samples; transport of zoeae and migration of megalopae in bottom water strata could tend to replenish the estuarine populations.

Ryan (1956) concluded that mature females range in carapace width from 6.1 to 18.7 mm. Swartz (1972) concluded that the largest young of the year reached a carapace width of 8–10 mm, occasionally 12 mm, by early November. By the following midsummer almost all of that year class were mature, but at the same time a scarcity of crabs 15–25 mm wide suggested that the previous year class (now two years old) had nearly disappeared. Most mature females observed reached 18–18.9 mm carapace width, males 20–20.9 mm. Swartz (1976b) showed that females molt less often than males during vitellogenesis, and perhaps in the initial stage of egg brooding, hence never reach the size of mature males even though a few crabs may live into their third summer.

McDermott and Flower (1953) considered *N. sayi* to be the most abundant xanthid in Delaware Bay, but within the area studied it was more common on oyster beds than in littoral or low-salinity areas. They found (also McDermott 1960) that *N. sayi* readily preys on *Balanus improvisus*. Farther north, Landers (1954) reported the crab abundant in Narragansett Bay where it is a serious predator on young *Mercenaria mercenaria*. Ryan (1956) found the species widely distributed in Chesapeake Bay, but apparently not so abundant as in the more northern bays. Here it ranged in depth from 3.7 to 46 m (Rathbun 1930a, in part), depths similar to those reported by Sumner, et al. (1913a, b) for the Woods Hole region.

Parasites and microbial diseases of *N. texana* (broad sense) were reviewed by Sinderman and Rosenfield (1967). Two species of hake were observed to prey on this crab in Georgia (Sikora, et al. 1972).

Swartz (1972, 1976a, b) studied social behavior of *N. sayi*, showing it to be "more complicated than that usually reported for totally aquatic brachyurans. Ritualized visual displays, especially the Lateral Merus, are important in agonistic encounters. Fights are rare. During sexual interactions stereotyped periodic movements immediately after the male grabs the female may be responsible for the species, sexual, and mate discrimination. Behavior prior to the Grab resembles advanced agonistic encounters, which may explain why males almost always copulate with females smaller than themselves." Many details of reproductive biology too complex for summary here are given in these references.

Genus *Panopeus* H. Milne Edwards 1834

Rathbun 1930a:333.

Key to Species

1. Dark color of fixed finger continued more or less on outer surface of palm, especially in males; no distal groove on carpus of chelipeds . . .*P. herbstii*

Dark color of fixed finger not continued on outer surface of palm; carpus of chelipeds with shallow groove parallel to distal margin . . . .
of chelipeds with shallow groove parallel to distal margin . . . .
. . . . *P. occidentalis*

Panopeus herbstii H. Milne Edwards

(Common mud crab)

Figs. 325, 331*l*

Panopeus herbstii H. Milne Edwards 1834:403.—Hay and Shore 1918:437, pl. 34, fig. 9.—Rathbun 1930a:335, text-figs. 52–53, pl. 156, figs. 1–3; pl. 157, figs. 1–3.—Williams 1965:196, figs. 180, 183M.—Chace and Hobbs 1969:154, figs. 46c, 47.—Coelho and Ramos 1973:190.—Felder 1973:69, pl. 9, fig. 21.—Holthuis 1979:159.

Recognition characters.—Carapace approximately ⅔ as long as wide, regions well marked, surface sparingly granulate. Anterolateral margins with 5 teeth; first 2 coalescent; third and fourth larger, prominent, and with arcuate outer margins and acute tips; fifth smaller, acute at tip and with outer margin nearly straight. Transverse ridge extending inward from fifth tooth, and shallow groove from fourth tooth. Front wide, not produced, with narrow median fissure; anterior margin of each half sinuous. Male abdomen with side of penultimate segment nearly parallel; terminal segment broader than long, rounded at tip.

Chelipeds heavy, finely granulate; carpus without groove on superior surface and with blunt internal spine; hands unequal and dissimilar, large one with dactyl curved and strongly toothed at base, dactyl of smaller more nearly straight; fingers dark, with color extending somewhat on palm.

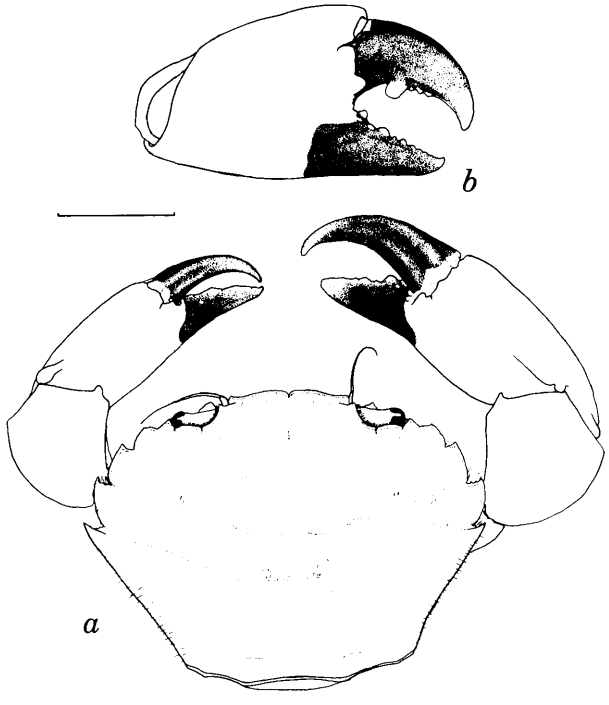

Fig. 325. *Panopeus herbstii* H. Milne Edwards. *a*, Animal in dorsal view, walking legs not shown; *b*, right chela in frontal view; 5 mm indicated (from Williams 1965).

Measurements in mm.—Carapace: male, length 43, width 62; female, length 36, width 53.

Variation.—Rathbun (1930a) separated this species into a number of forms on the basis of structural characteristics but considered these the result of response to environment rather than genetic differences. The forms are not always easily separated and are now being restudied by a number of workers.

Ryan (1956) described a persistent, central, oval, red spot or structure on the inner surface of the ischium of the third maxillipeds of both sexes. Mrs. Peggy Keney (personal communication) in a sample of 596 specimens from the Beaufort, N. C., area found this spot on 100% of males and 55% of females.

Habitat.—Depth distribution for the species ranges from the intertidal zone to 22 m. Ryan (1956) found the species to be rare in Chesapeake Bay in a salinity range of 13.95 to 19.04%. . . . Depth distribution was 3.7 to 11 m and at each collection spot the bottom was composed of soft mud with few oyster shells. In North and South Carolina, this is one of the most common estuarine crabs, found wherever the bottom is muddy or covered with shells or stones. In some localities along edges of the higher marshes, it is found in burrows, frequently associated with *Sesarma reticulatum* and *Uca minax*.

In the West Indies, collections have been made from mangrove roots, sponges, and coral reefs.

Type-locality.—Oyster beds of eastern United States.

Known range.—Boston, Mass., to State of Santa Catarina, Brazil; Bermuda.

Edmondson (1962) gave the first Hawaiian record for *P. herbstii* as December 1947 when a specimen was taken from fouling on a boat in Pearl Harbor. In 1953 numerous specimens were taken in Maunalua Bay, Oahu, where the species appears to be well established. He thought its introduction doubtless came about through transport on the bottom of a ship in very recent times, and further stated that the species has long been seen on "west American shores."

Remarks.—The genus *Panopeus* has a fossil record dating from the Paleocene (Glaessner 1969), and *P. herbstii* was considered by Rathbun (1935) to date from the Miocene in North America.

Ovigerous females are known virtually the year round in Florida, through late spring and summer in the Carolinas, from February to September in various parts of the West Indies, and August to October in southern Brazil. Ryan (1956) gave cara-

pace widths of mature males as 8.3 to 37.3 mm and mature females as 21.6 to 27.8 mm in Chesapeake Bay.

Costlow and Bookhout (1961a) reviewed early descriptions of larvae and described and illustrated four zoeal and one megalopa stage reared in the laboratory. Costlow, et al. (1962) reared the larval stages under 12 different conditions of salinity and temperature. Eggs were maintained in salinities of 12.5, 20.1, 26.5, and 31.1‰, and all larvae hatched as first stage zoeae. Succeeding stages showed higher percentages of survival under different conditions, with shortest development time in the highest salinity. The lowest salinity tested did not permit development to be completed. In addition, low temperature affected duration of all larval stages and mortality of some stages. Larval development was completed to first crab in 48–52 days at 20°C., and 18–28 days at 30°C. From data, the effects of salinity and temperature on mortality of larval stages were projected by statistical methods over a wide range of combinations. They hypothesized that effect of temperature on successive larval stages limits the productive spawning period. Low temperatures favor the spring brood of larvae [in these latitudes], prolonging larval development until warmer water produces favorable conditions for the megalopal stage. Larvae hatched in fall are not so favored, therefore mortality in late zoeal and megalopal stages would be high.

Sandifer (1973d) found larvae of *P. herbstii* rather commonly in plankton samples from the Pamunkey River to off the mouth of Chesapeake Bay over a salinity range of 1.76 to 32.4‰, but less abundantly there than the larvae of any xanthid except *Eurypanopeus depressus*. Greatest numbers were taken in the lower York River where salinity was 15–25‰. Occurring from June to September, larvae were most abundant in July-August when temperature was 25°–28°C. All four zoeal stages were taken in surface and bottom samples but stages III and IV were rare. Stage I comprised 70% of the total and there was little difference between surface and bottom concentration of stages I and II.

Further south the spawning season is longer. Pinschmidt (1963) found larvae from May to September in the Newport River, N. C., with peak numbers from May to August at temperatures of 28°–31°C in salinities of 12–36‰. Dudley and Judy (1971) found *P. herbstii* larvae: 1.6 km off Beaufort, N. C., from May to November at 1–8 m depths and *Panopeus* sp. megalopae at 1–8 m in September and 8 m in October; 6.5 km offshore at depths of 1–8 m from May to August and at 8 m; July in 1–8 m, November at 1 m, and *Panopeus* sp. megalopae in October at 8 m. Sandifer (1973d) found zoeae near Cape Lookout, N. C., in November. Tagatz (1968) observed *Panopeus* sp. larvae in St. Johns River, Fla., from April to November with greatest concentration in August.

In a study of the relationship of habitat to oxygen consumption by estuarine crabs, Ayers (1938) found *P. herbstii* to be intermediate in a scale of partial adaptation of the respiratory mechanisms to life in air. Teal (1959) found this species active on Georgia marshes when the tide was high or the sky cloudy. When the marsh was exposed, it was found in burrows, usually near the top, in air or water. Among various marsh crabs studied (see remarks, *Uca minax*) only *P. herbstii* was active at temperatures below 12°C. Respiration in this crab was most affected by reduced oxygen pressure among species tested, showing a rate reduction of 90% at 4 mm Hg.

Menzel and Nichy (1958) found that *P. herbstii* and *Menippe mercenaria* are the only xanthids large enough to kill significant numbers of adult oysters. McDermott (1960), studying predatory activities of xanthid crabs on oyster beds in New Jersey, found that *P. herbstii* destroyed 1- and 2-year-old oysters at a rate of 0.15 oysters per crab per day. The crab also preyed actively on oyster spat as well as barnacles (*Balanus improvisus*). He concluded that *P. herbstii* is potentially the most destructive of the five species of mud crabs occurring on New Jersey oyster beds. The species is also common on oyster beds in Delaware Bay, where it commonly cracks and eats small oysters and the barnacle *Balanus eburneus* (see McDermott and Fowler 1953). The toadfish was considered a common predator. Other predators are the hakes *Urophycis regius* and *U. floridanus* in Georgia estuaries (Sikora, et al. 1972).

Panopeus occidentalis **Saussure**

Figs. 326, 331*m*

Panopeus occidentalis Saussure 1857:502.—Rathbun 1930a:348, text-fig. 55; pl. 161. figs. 1–3.—Williams 1965:198, figs. 181, 183N.—Coelho and Ramos 1972:190.

Recognition characters.—Similar to *Panopeus herbstii*, but differing in having more convex carapace, especially in gastric region; front narrow, advanced; second anterolateral tooth usually narrower and separated by deeper sinus from first tooth, third to fifth teeth thicker, more prominent and widely separated, third blunt, forming almost right angle at tip; abdomen of male wider, sides of penultimate segment not parallel; narrowed toward proximal end.

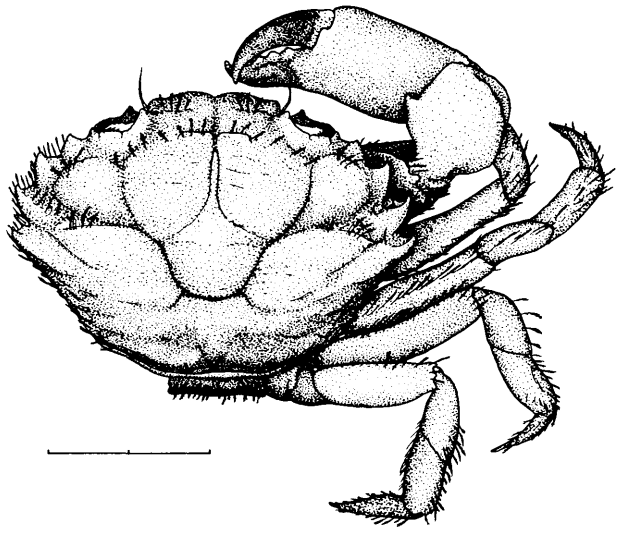

Fig. 326. *Panopeus occidentalis* Saussure. Animal in dorsal view, legs of left side not shown, 1 cm indicated (from Williams 1965).

Carpus of chelipeds with groove parallel to distal margin, sometimes rugose; dark color of fixed finger not continued on palm. Walking legs somewhat longer and more slender.

Measurements in mm.—Carapace: male, typical form, mean length 27.7, width 40.5; serrate form, mean length 19.9, width 27.5; ovigerous females, width 13.3 to 25.3 (de Oliveira 1940).

Variation.—There is considerable variation even in a single lot of specimens. The carapace may be smooth and shining, or with light, granulate, transverse lines; the second anterolateral tooth may be small, subacute, and similar to the first rather than broadly rounded and large; the female abdomen may have sides of the sixth segment parallel instead of converging slightly toward the proximal end. Variations in teeth of the anterolateral border were noted in 12% of females studied by de Oliveira (1940). In these the first, second, and third teeth of one side were depressed, giving the impression of but one sinuous tooth while those of the other side were normal.

This species, like *P. herbstii*, has been divided into two environmental forms (typical and serrate), and both occur in the Carolinian province (Rathbun 1930a).

Color.—Carapace dull yellow spotted with brown and red; legs yellow with brown maculations and speckles on chelipeds; walking legs with brown or rose streaks. Color of Brazilian specimens (de Oliveira 1940): carapace dark yellow with red blotches or chocolate varying in tone; legs same color but spotted with reticulated points, points of fingers chocolate to almost black; body yellow ventrally, legs yellow to grayish; some rare specimens completely yellow.

Habitat.—This species has been found among rocks, mangrove roots, sponges, ascidians, and seaweed, and on pilings of piers along shore; shore to 18.2 m.

Type-locality.—Guadeloupe.

Known range.—North Carolina to State of Santa Catarina, Brazil; Bermuda.

Remarks.—In the vicinity of the Ilha Pinheiro, near Rio de Janeiro, Brazil, the species is primarily crepuscular or nocturnal, living chiefly in ditches, between and beneath stones, and among mangrove roots, often burrowing to a depth of 30 cm (de Oliveira 1940). That author found both sexes together except when the eggs were deposited; then females were not so often seen.

Molting individuals and copulating pairs were rarely found, the latter in November to December, on one occasion in water of 22‰ salinity at 22°C. Periods of egg deposition extended from January to May, and again from July to August (also September, Rathbun 1930a). Such females bore 3,000 to 70,000 eggs, depending on size. Females were observed to aerate and clean the eggs in water at low tide in the evening. Eggs in the laboratory hatched in about 15 days. Molting of females followed hatching of eggs. (Otherwise ovigerous females are known from January to July in the Caribbean area (USNM) and in winter in southwest Florida [Rouse 1970].)

In Brazil, young of the species were found throughout the year, as others have noted.

The species was believed to have few predators. Material from the gut consisted of varied plant and animal matter. In addition to the ecological discussion, de Oliveira gave observations on autotomy and its effect on movement and behavior.

Genus *Hexapanopeus* Rathbun 1898

Rathbun 1930a:383.

Key to Species

(After Felder 1973)

1. Carpus of cheliped roughened and irregular in contour but lacking distinct knoblike tubercles; less than 8 granulated lines on gastric, cardiac, and branchial regions of carapace . . . . . ***H. angustifrons***

Carpus of cheliped with about 10–15 irregular, coarsely granulate, knoblike tubercles; at least 8 distinct granulated lines on gastric, cardiac, and branchial regions of carapace . . . . . ***H. paulensis***

Hexapanopeus angustifrons (Benedict and Rathbun)

(Narrow mud crab)

Figs. 327, 331*n*

Panopeus angustifrons Benedict and Rathbun 1891:373, pl. 22, fig. 3; pl. 24, fig. 18.

Hexapanopeus angustifrons.—Hay and Shore 1918:436, pl. 34, fig. 7.—Rathbun 1930a:384, pl. 169, figs. 1–2.—Williams 1965:188, figs. 170, 183D.—Felder 1973:70, pl. 9, fig. 24.

Recognition characters.—Carapace hexagonal, about ⅔ to ¾ as long as wide, convex from front to back, regions fairly well marked, surface finely granulate. Anterolateral edge thin, upturned, and divided into 5 teeth, first 2 separated by well-defined sinus, third and fourth successively broader, fifth shorter, narrower, more distinctly directed outward; each of last 2 teeth with ridge extending obliquely inward and backward for distance twice length of teeth. Front narrow, produced, divided in half by prominent V-shaped notch; each half bilobate, with markedly sinuate anterior border forming broad inner and small, inconspicuous outer lobe.

Chelipeds strong, granulate, and finely rugose; merus with well-developed tooth on upper margin; carpus with moderately deep groove parallel to distal margin, an obtuse tooth at inner angle, and with superior surface rough and more or less tuberculate. Hands unequal and dissimilar; palm usually with fairly strong ridge above and indication of one on outer surface, both ridges continued on fingers; fingers strong, slightly hooked at tips; dactyl of larger hand with strong tooth at base.

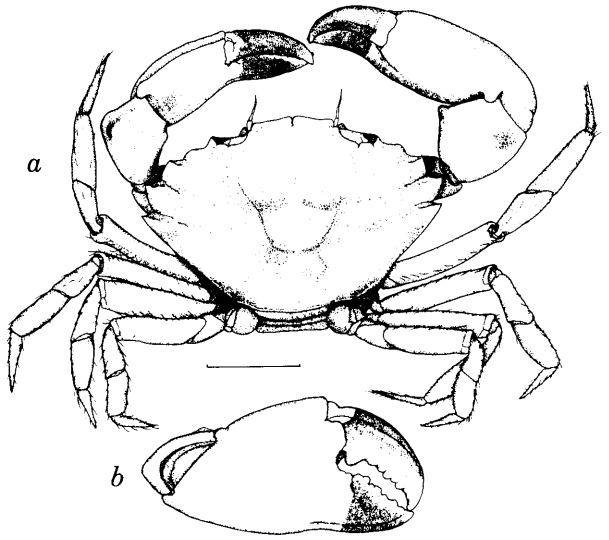

Fig. 327. *Hexapanopeus angustifrons* (Benedict and Rathbun). *a*, Animal in dorsal view; *b*, major chela in external view; 5 mm indicated (from Williams 1965).

Measurements in mm.—Carapace: male, length 20, width 28; female, length 16.1, width 23. Ryan (1956) gave the range in carapace width of mature males as 9.7 to 28.9 mm and of mature females as 8.4 to 20.2 mm in Chesapeake Bay. Rathbun (1930a) considered specimens from Chesapeake Bay southward to average smaller than those from farther north.

Color.—Usually dark reddish brown or dark gray, sometimes uniform brownish yellow or light buff; females usually darker than males often more or less spotted; fingers black or dark brown at base, lighter at tips, color not continued on palm. Often a light yellow band along anterior border of carapace (Wass 1955, in part).

Habitat.—Results of faunal surveys show that this species occurs in salinities ranging from 9 to 53‰, usually 20's to low 30's, from nearshore regions of estuaries to the sublittoral region of the ocean (Cowles 1930; Rathbun 1930a; Lunz 1937a; Behre 1950; McDermott and Flower 1953; Wass 1955; Ryan 1956; Dragovich and Kelly 1964). It often occurs in shelly situations, but may be found on soft or sandy bottoms; near shore to 139 m.

Type-locality.—Long Island Sound.

Known range.—Vineyard Sound, Mass., to Port Aransas, Tex.; Bahamas; Jamaica.

Remarks.—Rouse (1970) found ovigerous females throughout the year in SW Florida, but scattered records indicate that the spawning season is limited to warmer months farther north. Chamberlain (1961) reported four zoeal stages and the megalopal stage in larval development of the species but did not describe them in detail. He found that larval development time varied with temperature (17 days at 30°C, 28 at 21°C) and with food. Larvae matured most rapidly when fed *Artemia salina* nauplii, matured well on *Artemia* and algae, but did not transform at all when fed algae alone. Costlow and Bookhout (1966c) described and figured four zoeal stages and the megalopa from laboratory hatching and rearing in 30‰ salinity at 25°C on a diet of *Artemia salina* nauplii.

Zoeae of this species were the most common

xanthid larvae found in a plankton survey of lower Chesapeake Bay (Sandifer 1973d), mainly in salinities above 20‰ from June to October with peak abundance in August. Williams (1971) found the same pattern in a plankton survey of North Carolina inlets. Sandifer (1975) also found 58% of zoeae in bottom samples, later stages being much more abundant there than in surface samples, and felt that distribution of the species may thus be maintained by retention of larvae in estuarine circulation currents and megalopal migration.

Hexapanopeus angustifrons is preyed upon by two species of hake (*Urophycis regius* and *U. floridanus*) in Georgia estuaries (Sikora, et al. 1972).

Hexapanopeus paulensis Rathbun

Figs. 328, 331*o*

Hexapanopeus paulensis Rathbun 1930a:395, pl. 170, figs. 5–6.—Williams 1965:189, figs. 171, 183E.—Coelho and Ramos 1972:191.—Felder 1973:70, pl. 9, fig. 23.

Recognition characters.—Carapace hexagonal, approximately ⅔ to ¾ as long as wide, convex, regions fairly well marked, surface with approximately 12 transverse granulated lines on gastric, cardiac, and branchial regions. First tooth of anterolateral border small; second larger, broad and shallow, with arcuate outer margin; third with nearly straight margin directed forward and inward; fourth and fifth acute and prominent; sometimes with small denticle between first, second, or third pairs of teeth. Front with edge thin, arcuate; small median, V-shaped notch; each half with small lobule at outer end. Inner suborbital angle large; raised line of granules on subhepatic region.

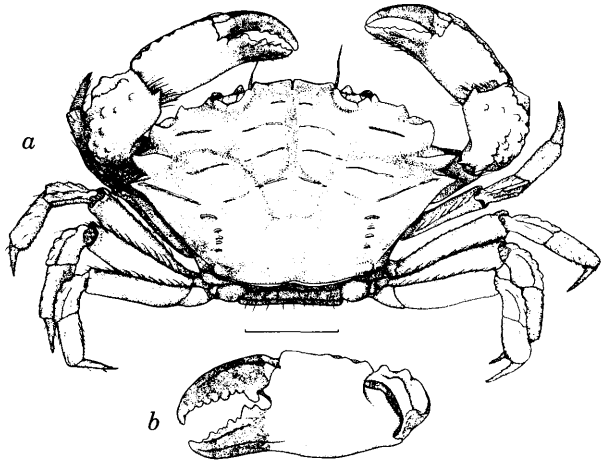

Fig. 328. *Hexapanopeus paulensis* Rathbun. *a*, Animal in dorsal view; *b*, major chela in external view; 5 mm indicated (from Williams 1965).

Chelipeds with carpus and upper part of palm roughened; carpus with approximately 15 tubercles above, an internal tooth, and below it a small tooth or denticle, distal groove deep. Hand with superior groove and another on outer surface below upper edge, ridges bordering groove with low tubercles; fingers deeply grooved, dark or horn colored, color continued somewhat on palm ending in oblique, scalloped line; tips light.

Measurements in mm.—Carapace: male, length 13, width 19.2; female, length 12, width 18.2.

Habitat.—Offshore marine waters on hard substrates among sponges, ascidians and bryozoans; also on sand and shell fragments; to 14+ m (Felder 1973).

Type-locality.—Santos, São Paulo, Brazil.

Known range.—South Carolina, through Gulf of Mexico to Uruguay (Milstein, et al. 1976).

Remarks.—This species has been reported from only a few widely separated areas. Rathbun (1930a) reported ovigerous females in September from Brazil.

Genus *Eurytium* Stimpson 1859

Rathbun 1930a:422.—Hemming 1958b:32.

According to Glaessner (1969) the genus has a fossil record dating from the Pleistocene of Panama.

Eurytium limosum (Say)

Figs. 329, 331*p*

Cancer limosa Say 1818:446.

Eurytium limosum.—Hay and Shore 1918:438, pl. 35, fig. 7.—Rathbun 1930a:423, pl. 176, figs. 1–2.—Williams 1965:199, figs. 182, 183.—Chace and Hobbs 1969:153, figs. 45, 46*b*.—Coelho and Ramos 1972:193.

Recognition characters.—Carapace broad, approximately 1.5 times as wide as long, quite convex from front to back, nearly plane from side to side; surface smooth to eye but finely granulate under magnification, granulations coarser near frontal and anterolateral margins. Front approximately ¼ width of carapace, divided into 2 lobes by median notch giving rise to shallow groove disappearing over gastric region. Orbital margins somewhat elevated; external orbital tooth coalesced with first tooth of anterolateral border, division between these teeth indicated by shallow indentation. Anterolateral teeth with raised margins, second and third teeth rounded at tip, fourth more prominent and subacute.

Chelipeds massive, unequal, and dissimilar, more

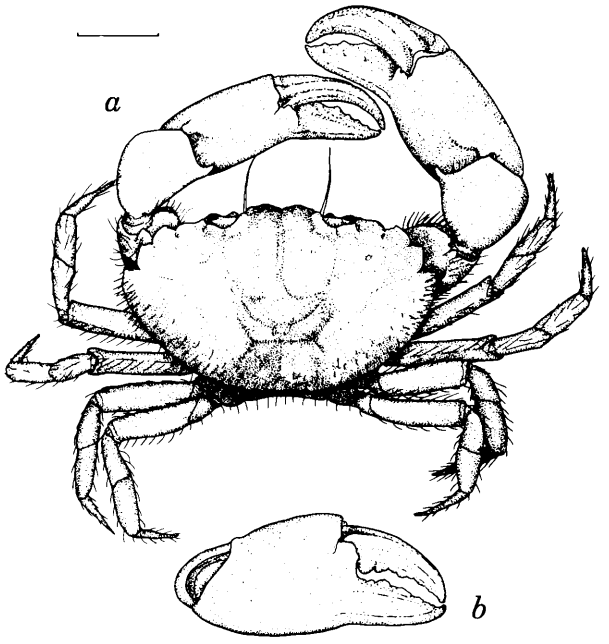

Fig. 329. *Eurytium limosum* (Say). *a*, Animal in dorsal view; *b*, major chela in external view; 1 cm indicated (from Williams 1965).

so in male than in female; merus with coarsely tuberculate superior border and distal spiniform tooth; carpus with narrow internal spine, not grooved; fingers pointed, deflexed, large basal tooth on major dactyl.

Measurements in mm.—Carapace: male, length 27, width 43; female, length 22, width 33.

Color.—Carapace brilliant purplish blue, dark gray, or black; carpus and hand bluish; proximal upper half of dactyl pink or purple; remainder of fingers porcelain white; lower part of chelipeds and carpal teeth yellow or orange; color of fingers not continued on palm.

Habitat.—This primarily tropical species lives mainly in muddy or marshy banks a bit below the high-tide mark in burrows partly filled with water, among stones at the high-tide mark, in burrows in sand, intertidally under stones, and on coral reefs (Rathbun 1930a; Rouse 1970; Tabb and Manning 1961). High-tide mark to 71 m.

Type-locality.—"Inhabits shores of the Northern States."

Known range.—South Carolina and Louisiana through West Indies and Caribbean Sea to São Paulo, Brazil; Bermuda. Behre (1950) and Hoese (1972) gave Louisiana records. According to Rathbun (1930a, citing DeKay), the species has been reported from New York, and specimens at the Philadelphia Academy are labelled as from New Jersey. Modern records do not extend this far north.

Remarks.—According to Rathbun (1935) this species has a fossil record in North America dating from the Miocene of North Carolina and Florida.

Teal (1959) found this species active on Georgia marshes when the tide was high or the sky cloudy. When the marsh was exposed, it was found in burrows, usually near the top, either in air or water. Respiration rates in water were higher than in air. The species showed internal regulation of metabolism in that it was independent of oxygen tension but not of temperature.

Ovigerous females are known from Panama in July (USNM) and Florida in August (Wass 1955).

Genus *Domecia* Eydoux and Souleyet 1842

Rathbun 1930a:553.—Hemming 1958b:144.—Guinot 1964:267.

Domecia acanthophora acanthophora (Desbonne and Schramm)

Figs. 330, 331*q*

Neleus acanthophorus Desbonne and Schramm 1867:35.

Domecia hispida.—Rathbun 1930a:554, pl. 227 (part, Atlantic localities only).—Pequegnat and Ray 1974:237, figs. 16, 17.

Domecia acanthophora forma *acanthophora.*—Guinot 1964:271, figs. 4, 5, 7, 8, 15.

Domecia acanthophora acanthophora.—Williams, McCloskey, and Gray 1968:52.—Manning and Holthuis 1981:122 (discussion).

Recognition characters.—Carapace somewhat transversely oval but much contracted posteriorly, anterior parts armed with spines; clothed with short,

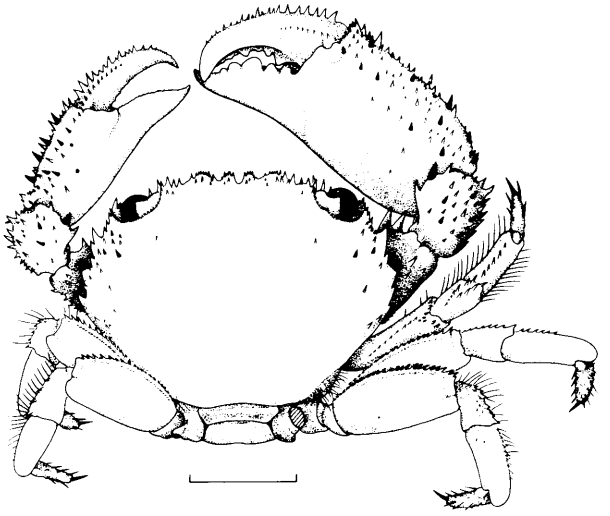

Fig. 330. *Domecia acanthophora acanthophora* (Desbonne and Schramm). Male in dorsal view, right fifth and left first and second walking legs missing, 3 mm indicated (USNM 24315).

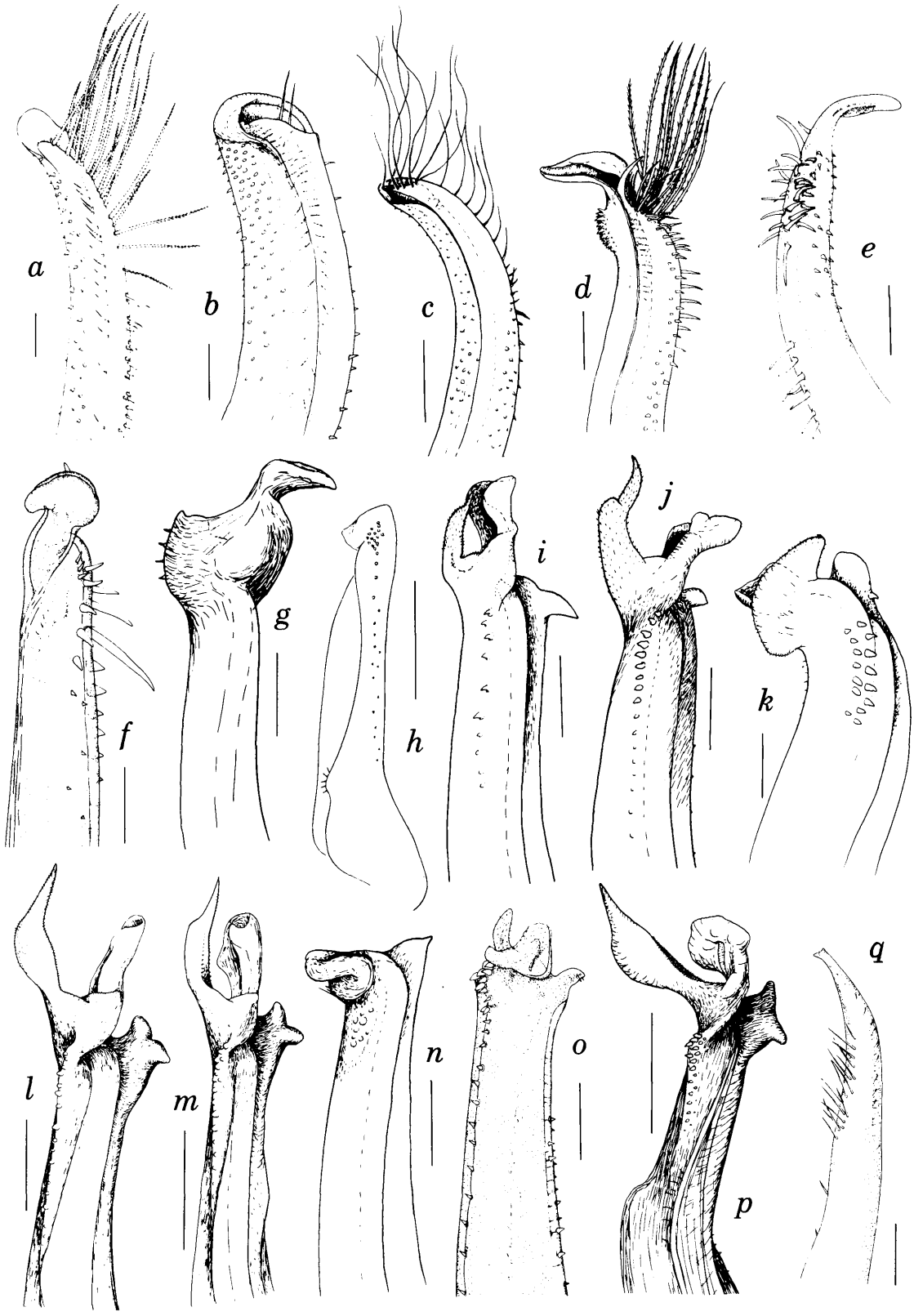

Fig. 331. Tips of right first pleopods of male Xanthidae, mesial view: *a, Allactaea lithostrota* Williams; *b, Glyptoxanthus erosus* (Stimpson); *c, Carpoporus papulosus* Stimpson; *d, Pseudomedaeus agassizii* (A. Milne Edwards); *e, P. distinctus* (Rathbun); *f, Rhithropanopeus harrisii* (Gould); *g, Micropanope nuttingi* (Rathbun); *h, M. sculptipes* Stimpson; *i, Eurypanopeus abbreviatus* (Stimpson); *j, E. depressus* (Smith); *k, Neopanope sayi* (Smith); *l, Panopeus herbstii* H. Milne Edwards; *m, P. occidentalis* Saussure; *n, Hexapanopeus angustifrons* (Benedict and Rathbun); *o, H. paulensis* Rathbun; *p, Eurytium limosum* (Say); *q, Domecia acanthophora acanthophora* (Desbonne and Schramm); *a*, 0.1 mm; *b-f, i-k, n- o*, 0.25 mm; *g-h, l-m, p-q*, 0.5 mm indicated (*m* from Guinot 1967a; others from Williams 1965 except *a*, 1974a; *e*, 1978).

short, sparse, light-colored hairs and scattered longer ones. Frontoorbital border not much less than greatest breadth of carapace; front divided on each side into narrow submesial and broader lateral lobes with sharply spined margin, row of smaller, scattered spines behind lobes. Eyes large. Orbits at anterolateral angles; margins not fissured but denticulate above, spinous below; upper and lower inner angles broadly in contact or nearly so to exclude antennae from orbit. Anterolateral borders with 4 to 6 (including orbital angle) principal acute, dark-tipped spines, often smaller intercalated spines; scattered smaller dorsal spines just inside border and also behind frontoorbital border. Third maxilliped with merus remarkably broad and short, ornamented with median transverse patch of spines and few granules as well as on ischium distally. Anterior border of buccal cavity spined. Thoracic sternum terminating in moderately acute anterior point.

Chelipeds unequal; merus, carpus and palm studded with acute spines above and few proximally on inner surface on palm, crests of dactyl finely and closely spined. Walking legs moderately spined and hairy, meri rather broad, superior crest of merus on last leg spined throughout length.

Measurements in mm.—Carapace: male, length 7.5, width 10.8; ovigerous female, length 9.9, width 14.4; female, length 15 (Pequegnat and Ray 1974).

Variation.—There is slight variation in development of spines but the pattern of spination is constant.

Color.—Light yellowish red, front darker; spines blackish (Verrill *in* Rathbun 1930a).

Habitat.—Associated usually with coral, reef formations, and incrustations on pilings; to 55 m; occasionally in surface waters far from shore (32°N, 74°W).

Type-locality.—Guadeloupe.

Known range.—Bermuda; Cape Lookout Shoals, N. C., NW Gulf of Mexico through West Indies and Caribbean Sea to Alagoas, Brazil.

Remarks.—In her review of the genus, Guinot (1964) distinguished three species, the Pacific *D. hispida* and *glabra*, and Atlantic *acanthophora* which in turn was separated into western and eastern "forms. Guinot (1964) added *D. acanthophora* sensu lato to a number of species having amphi-Atlantic distribution (Monod 1956). Manning and Holthuis (1981) recognized the eastern and western populations of *D. acanthophora* as subspecies.

Ovigerous females are represented in the USNM collection in every month from December to August in various parts of the range.

Patton (1967; 1967a) discussed adaptations of *D. acanthophora* to reef habitats, especially its association with *Acropora* which harbors numerous commensal decapods in the Indo-Pacific but apparently only this one in the Caribbean. The mouthparts of the species differ from those found in typical xanthids; the mandible is weakly calcified and the second maxilliped possesses rows of peculiar paddle-tipped spines on the distal margin of the dactyl. Most likely food for the crab seems to be organic detritus which it separates from the surrounding water.

Randall (1967) listed *D. a. acanthophora* (= *D. hispida*) from stomach contents of the longspine squirrel fish, *Holocentrus rufus*, dusky squirrelfish, *H. vexillarius*, and rock hind, *Epinephelus adscensionis*.

Genus *Eriphia* Latreille 1817

Rathbun 1930a:545.—China 1966:255.

Eriphia gonagra (Fabricius)

(Calico crab)

Figs. 332, 333*a-c*

Cancer gonagra Fabricius 1781:505.
Eriphia gonagra.—Hay and Shore 1918:439, pl. 35, fig. 6.—Rathbun 1930a:545, text-fig. 83, pl. 222.—Williams 1965:182, figs. 164A, B, C; 165.—Coelho and Ramos 1972:192.

Recognition characters.—Carapace approximately quadrate, about ¼ wider than long, flattened, with regions clearly marked off on anterior ⅔; surface nearly smooth posteriorly but granulate anteriorly, and with 2 transverse lines of subspinous granules, 1 in front of epigastric lobes and another across protogastric and hepatic lobes. Front wide, almost straight, strongly deflexed, and divided into 4 lobes, both submesial lobes broader and more advanced than lateral ones, and with finely granulate border; lateral lobes (inner orbital lobes) forming mesiodorsal margin of orbits and in contact beneath with prolongation of infraorbital plate, thus completely excluding antenna from orbit. Anterolateral margins evenly arched, each with row of 5 spines including outer orbital, behind and inside these a few squamiform tubercles.

Chelipeds unequal, strong, swollen; hands covered with large, round, flattened, squamiform tubercles, more elevated on small than on large hand; carpus with less prominent tubercles; dactyls with squamiform tubercles above at base; major dactyl with large rounded tooth at base. Walking legs

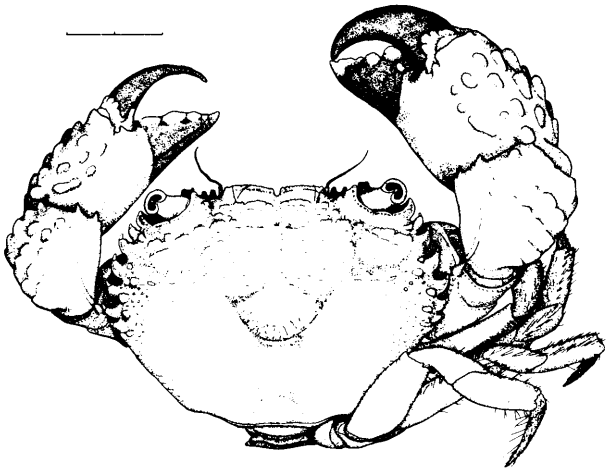

Fig. 332. *Eriphia gonagra* (Fabricius); Male in dorsal view, walking legs of left side not shown, 1 cm indicated (from Williams 1965).

rather slender, their distal 3 articles with fine stiff hairs.

Measurements in mm.—Carapace: male, length 34, width 48; female, length 30, width 34.

Color.—Gaily colored. Anterior half of carapace and a broad median stripe extending to posterior margin dark purplish brown, legs a lighter tint of same color; front margined with brownish orange. Sides of carapace, upper surface of chelipeds, dactyls, bases of legs, and a narrow band on distal margin of other articles, light yellow. Tubercles on upper half of chelipeds dark blue, on lower half yellow. Underparts of body and chelipeds white, fingers brown. Rathbun (1930a) gave another detailed color description.

Habitat.—The species has been found in a variety of situations: under flat rocks above the watermark, in seaweed, sponges, brackish ponds, tide pools, and on coral reefs. Shoreline to shallow water of uncertain limits.

Type-locality.—Jamaica.

Known range.—North Carolina to Patagonia; Bermuda.

Remarks.—Ovigerous females are known from March to September in various parts of the West Indies and southern Florida, in October from Santa Catarina, and February from Bahia, Brazil (Rathbun 1930a, in part). Lewis (1960) observed ovigerous females from March to June in Barbados. He regarded this as one of the commonest crabs of the intertidal region there.

Genus *Menippe* de Haan 1833

Rathbun 1930a:472.

Menippe mercenaria (Say)

(Stone crab)

Figs. 333*d-e*, 334

Cancer mercenaria Say 1818:448.

Menippe mercenaria.—Hay and Shore 1918:439, pl. 35, fig. 8.—Rathbun 1930a:472, text-fig. 78, pls. 191–193.—Williams 1965:183, figs. 164D, E, 166.—Felder 1973:64, pl. 9, figs. 2–3.

Recognition characters.—Carapace transversely oval, approximately ⅔ as long as wide, convex, nearly smooth to unaided eye, minutely granulate and punctate. Anterolateral border divided into 4 lobes: first 2 wide, third wide but dentiform, fourth much narrower and dentiform. Front with median notch and broad trilobulate lobe on each side. Orbital border thick, fissures indistinct.

Chelipeds large and heavy, unequal, nearly smooth; inside surface of hands with patch of fine, oblique, parallel striae serving as a stridulating organ and adapted for playing against thick edge of second and third anterolateral teeth and outer suborbital tooth; dactyl of major chela with large basal tooth, and fixed finger with large subbasal tooth; fingers of minor chela with numerous small teeth. Walking legs stout, hairy distally.

Measurements in mm.—Carapace: male, length 91, width 129; female, length 79, width 116. This is the largest xanthid species in the area.

Color.—Juveniles dark purplish blue, very young always with a white spot on carpus. Older individuals become dark brownish red or less mottled and spotted with dusky gray; fingers dark; walking legs with reddish and yellow bands (Futch 1966).

Habitat.—Adult stone crabs burrow in mud flats just below low-tide mark, among rocks on jetties, on offshore reef areas, under rocks or coral heads, and among dead shells or grass clumps (Whitten, et al. 1950; Wass 1955; Powell and Gunter 1968; Costello, et al. 1979). Apparently colonial burrows beneath scattered clumps of oysters have been observed on mud flats in south Texas, but most were solitary (Powell and Gunter 1968). There was usually a conical depression at the entrance to each burrow where the crabs often rested, and a mound of mud and debris. No freshly broken oyster shell was noticed near burrows, but this has been seen by others there and in Louisiana (Menzel and Hopkins 1956). Size of burrow was not correlated with size of crab nor with amount of debris around the hole. Mouths of burrows were plugged in cold weather. Burrows of crabs between 44 and 73 mm wide dropped straight down for 25–60 cm; there they more or less leveled off or made several turns

before ending blindly with the crab resting sideways at the end with the minor chela toward the entrance. Larger crabs (90 mm or wider) occupied more or less horizontal burrows in the edge of shoals or banks that extended as much as 75 cm to end in a chamber where the occupant rested facing the entrance, much as described by earlier authors. McRae (1950) recorded a burrow extending 127 cm.

Crabs of less than 30 mm carapace width (juveniles) do not dig burrows (Powell and Gunter 1968), but live in deep channels, on grass flats, under shell fragments, in crevices among rocks, among oyster shells, around pilings, and even cling to buoys (Hay and Shore 1918; Lunz 1937a; McRae 1950; Wass 1955; Manning 1961; Costello, et al. 1979). Larger juveniles to subadults have often been observed on oyster reefs (Menzel and Nichy 1958).

In an unusual occurrence, Clark (1965) found a small *M. mercenaria* resting beneath the deformed and peaked posterior shield of a weakened hawksbill turtle taken near Sarasota, Fla. The crab rested on a place eaten away through the carapace to the flesh.

The species is well adapted to salinity ranges near the mouths of estuaries and can survive extremes considerably lower or higher than than 35‰ (Karandeyva and Silva Lee 1976).

Surface to 51 m.

Type-locality.—"The Southern States."

Known range.—Cape Lookout, N. C., to Yucatan, Mexico; Bahamas; Cuba; Jamaica.

Remarks.—Summary of literature for this species is selective. The genus *Menippe* has a fossil record dating from the Middle to Upper Eocene (Glaessner 1969), the thick, hard exoskeleton no doubt enhancing its chances of fossilization. The record for *M. mercenaria* dates from the Pleistocene (Rathbun 1935).

Reproduction in *M. mercenaria* has been a subject for active investigation during the past 20 years, although Binford (1912) first discussed spermatogenesis and fertilization in the species and gave notes on spawning habits in his often cited "unpublished" account. Savage (1971) observed and described mating of a male and female *M. mercenaria* held in an outdoor aquarium. A fresh molt of the female was found on the morning of May 31, 1970, and at 9:00 the following morning the pair was found mating, the male in superior position cradling the inverted female. By 1:30 p. m. the pair had separated and the female had righted herself. Among mating crabs observed in the field, males were always with freshly molted or presumed freshly molted females, coupled in the described posture.

Females in laboratory experiments have produced more than 10 broods of viable eggs within the same intermolt period without copulation taking place in intervals between production of the different broods (Cheung 1968). Eggs of all these broods were successfully attached to hairs of pleopods, and developed to hatch as normal zoeae. Moreover, females from the wild held in isolation through a molt were found to retain sperm through ecdysis, a special adaptation (late disposal of the old invaginating exoskeletal wall between sperm and new wall) enabling retention. Yang (1971) recorded 10 spawnings within one intermolt for a single female over a 120-day period, the interval between hatch of one brood and oviposition of the next being 2–3 days. Cheung (1969) also showed that ovarian development is closely correlated with water temperature, optimum being at 28°C. Seasonally, spawning built to a peak in August-Sep-

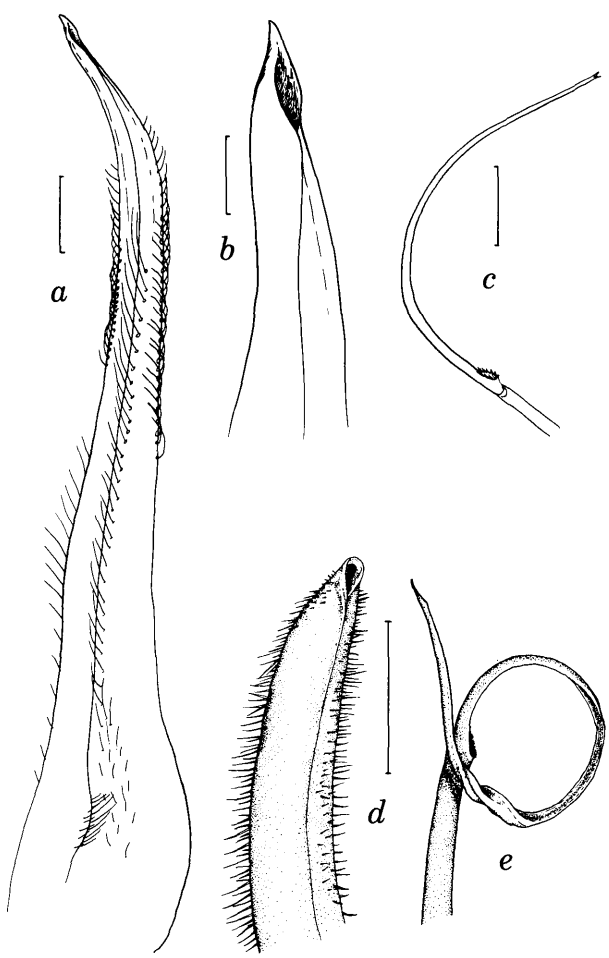

Fig. 333. Male first and second pleopods of *Eriphia gonagra* (Fabricius); *a*, entire first pleopod; *b*, tip of first pleopod; *c*, tip of second pleopod; and *Menippe mercenaria* (Say); *d*, tip of first pleopod; *e*, tip of second pleopod; *a*, *c*, 0.75 mm; *b*, 0.25 mm; *d-e*, 5 mm indicated (from Williams 1965).

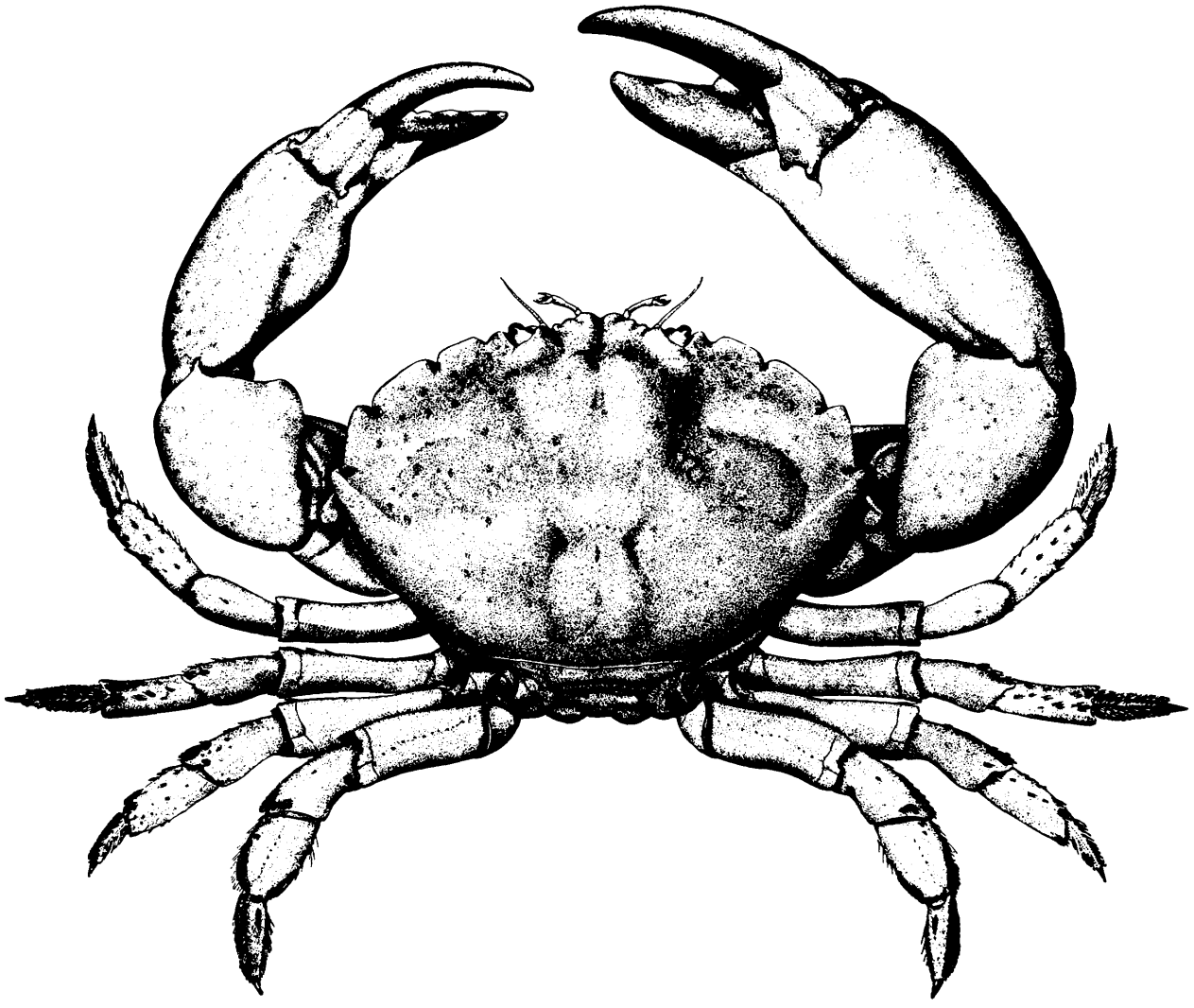

Fig. 334. *Menippe mercenaria* (Say). Male in dorsal view, approximately × 0.6 (from Rathbun 1884).

tember in southern Florida, but dropped to a low in winter. Elsewhere, ovigerous females are known from May to August in North Carolina and in August in Texas (Powell and Gunter 1968).

Porter (1960) described development of larvae, hatched from an ovigerous female taken near Beaufort, N. C., that were reared individually in compartmented plastic boxes by feeding on *Artemia* nauplii. He found a prezoeal and 6 zoeal stages, but considered the prezoea and last zoeal stages to be atypical. Length of larval life was approximately 27 days under the conditions imposed. Ong and Costlow (1970), with much more sophisticated equipment, reared larvae hatched also from North Carolina females in 18 environments (6 salinities, 3 temperatures). Both of these factors were found to affect rate of development and survival. Optimal condition for development was about 30°C in a salinity range of 30 to 35‰, at which the megalopa was reached in 14 days and the first crab in 21 days with survival of 60%–72%. Development was slower in 20‰ salinity than in 30–40‰, and markedly retarded in decreasing temperatures from 30° to 20°C. In all temperatures tested there was total mortality at 10‰ salinity. At 20°C, larvae developed only to the megalopa, but survival was less in 20–25‰ than in 30–40‰; survival was higher at 25° and 30°C. The authors felt that the stone crab might be a good subject for large-scale rearing experiments. Yang (1971) successfully reared mass cultures of larvae from ovigerous females captured in Biscayne Bay, Fla. Hatching took place in about 10 days at 29°–30°C. Duration of larval period was 14 days at 30.5°–32°C in 30‰ salinity in mass cultures, about 20–21 days in individual compartments, and included five zoeal stages and a megalopa. The results confirmed Porter's judgment regarding number of larval stages. Mass-cultured crabs fed beyond larval stages on mixtures of ground squid and fish, dried shrimp

shells, calcium phosphate, vitamin E, yeasts, marine protein concentrate and crushed oyster shells reached sexual maturity in a year (Yang 1972). In time, F2 progeny were produced from this culture. Yang and Krantz (1976) collated all of this information in a manual for "intensive" culture of the species. A related Caribbean species, *M. nodifrons*, has a similar larval development that is judged to represent the most primitive pattern in the Xanthidae (Scotto 1979).

Dudley and Judy (1971) found stone crab larvae in plankton 1.6 and 6.54 km off Beaufort Inlet, N. C., at 1–8 m depths from June to August; none were found 10–13 km offshore. Mootz and Epifanio (1974) determined an energy budget for larvae fed *Artemia salina* nauplii, finding that larval growth is exponential during zoeal stages but decreases during the megalopal stage even though consumption reaches a peak during this stage.

From study in the Aransas Pass, Tex., area (reviewed briefly here), Powell and Gunter (1968) found that the number of *M. mercenaria* increased from January to August, male to female ratios changing from 5:1 to 2.65:1 during that time. Only one ovigerous female was found, and they concluded that the breeding population lived outside the area of study.

Daily observations indicated that time of greatest activity was evening before dark, but the crabs were somewhat active both day and night. Behavior patterns in response to disturbance resembled those shown by other brachyurans. Stone crabs will usually push an intruder away with a quick lateral motion of the cheliped rather than attack with the chela. Ordinarily the crabs adopt passive means of defense, but the fingers of the chelae are powerful and if fastened upon a hard object can hardly be pried apart. Strength of this grip by one male on a hard object was so great that it crushed its own chela and bled to death. The crabs can hug objects tightly or clasp them with the legs; crabs that are held fast can autotomize appendages to gain freedom.

Sinclair (1977) observed agonistic behavior in experimental tanks and the field, during daylight or at night under red light in the laboratory or by flashlight in the field, and with the aid of SCUBA. Fights with extensive bilateral aggression were infrequent. There is a relatively high degree of ritualization. Dominance is correlated with size, males, and prior possession of a burrow, in which case a smaller individual can dominate one larger. Interactions between animals of different sizes or of different sexes are characterized by lower frequency of fights than encounters between animals of a similar size or of the same sex. During the period of observation, crabs were seen outside burrows only twice, once by day and once at night. They are solitary except while mating, may be territorial, may move hundreds of feet to dig new burrows, but can live as closely as 1/m (Menzel and Hopkins 1956). Although the large chelae are easily capable of crushing a conspecific, such pressure is not applied during a grasp and vulnerable mouth and eye areas are rarely contacted.

Cheung (1976) confirmed by statistical study the earlier contention of Przibram (1931) that the pincer claw is a more primitive condition than the crusher. He showed that right or left crushers are identical functionally and structurally in a rather rigidly unvarying size range for best survival, but that the smaller pincers, owing to loss and regeneration, are not always structurally or functionally identical. Savage, et al. (1974) showed how sutural structures on proximal segments of the cheliped allow extraction of the larger diameter propodus-carpus during molting, briefly describing behavior of the molting crab with the aid of photographs. In molting, the proximal suture lines of the cheliped merus are fractured and simultaneously there is a forced expulsion of hemocoelic fluid from the chela (Hiatt 1948) allowing the larger distal elements to be withdrawn. Turgidity is regained following ecdysis. These authors also (1975) classified claws of crabs trapped in Florida by means of the pattern of striae on the inner surface of the palm: oblique unbroken = normal; randomly granular = early regenerated; dashed or elongated granules = later stage in regeneration; beaded oblique lines = still later stages of regeneration. From several thousand claws taken in the commercial fishery over several months they found that 90.5% were normal and most were major claws. Dashed patterns were conspicuously more numerous than granular patterns, and both were most commonly on minor claws. Frequency of natural claw loss was postulated to be 5.6% and mean calculated regeneration following commercial harvesting was 8.2% in November and 2.8% in April. The composite ratios of major to minor claws taken in the fishery permitted the formulation of a hypothesis that the largest crabs are caught early in the season and this population is gradually depleted to a point at which the fishery depends on smaller crabs to provide harvestable claws. In the laboratory, crabs with both claws removed regenerated new claws 70% of original size at the first succeeding molt.

Juvenile *M. mercenaria* carapace length and width increase in a constant relationship (Savage and McMahan 1968). Crabs grow to maturity in about two years and may live beyond this age, although Cheung (1973) suggested that males reach a terminal molt after which further growth and regen-

eration ceases. In Florida, harvest of 2-year-old or older crabs which presumably have spawned at least once is allowed (Costello, et al. 1979). In an extensive review of the species biology and economic role in fisheries, these authors showed that the Florida fishery extends to 30 miles (48 km) offshore in depths of up to 18 m or more off most of the west coast counties from Monroe to Franklin, but with 75% caught in the extreme southwestern corner of the Everglades-Florida Bay area, mostly in traps made of wooden slats. The largest commercial catch was during the 1977–78 season when 2.1 million pounds were landed and potential for still greater harvest remained. There have been local hand fisheries for stone crabs since the early settlement days.

Powell and Gunter (1968) judged stone crabs to have a strong influence on the life of sand and mud flats that are exposed by wind or lunar low tides, because their water-filled burrows are refuges for small aquatic organisms that cannot withstand drying. Commensals found in burrows include sea anemones, tube worms, bivalve and gastropod mollusks, barnacles, amphipods, caridean and brachyuran decapod crustaceans and fishes, to name a few.

Food of the juvenile and adult crabs included the above organisms as well. Menzel and Hopkins (1956) found the stone crab in Louisiana to be an active predator on oysters. The powerful crabs killed small and large oysters alike, predation being lowest in winter and highest in fall. Powell and Gunter (1968) thought that earlier estimates of predation of the crabs on oysters may be high and that other foods such as acorn barnacles are preferred, but there is no question that *M. mercenaria* preys on a variety of macroorganisms in its habitat. The animals expend from 45% to 82% of assimilated food energy for growth and reproduction (Sushchenya and Claro 1973).

Manning (1961) gave data on relative growth, showing that juveniles have a relatively broader front than adults. Both he and Wass (1955) pointed out the superficial resemblance of young *M. mercenaria* to *Panopeus herbstii* and *Eurytium limosum*, and Manning gave distinguishing characters for each species at comparable sizes. Further, the stridulating mechanism was shown not to be visible in small specimens and, indeed, stridulation itself had not been observed (Guinot-Dumortier and Dumortier, 1960) until its production by both juveniles and adults was seen and heard by Powell and Gunter (1968). Bender (1971) observed stridulation over 70 times. Two patterns were observed: (1) downward rasping of the striated ridges of one palm against the interocular teeth followed by circular waving of the cheliped 3–5 times in a manner similar to motions made by fiddler crabs, followed by similar movements of the opposite cheliped; (2) scraping of one cheliped up and down against the carapace for 15-second periods. Stridulation was observed in crabs (many females) of 3 to 10 cm carapace width. Function of the behavior was not determined.

In studies on the relationship of number and volume of gills to oxygen consumption, Pearse (1929) and Ayers (1938) found this form, along with other mud crabs, intermediate between the sluggish common spider crab and the more active, partially terrestrial, fiddler and ghost crabs. Pearse also found that *M. mercenaria* could withstand considerable dilution of its environment with fresh water. Gray (1957) found gill area per gram of weight to be intermediate in an array of species ranging from land to shallow-water habitats.

Genus *Pilumnus* Leach 1815

Rathbun 1930a:481.—Hemming 1958b:35.

Key to Species

1. Hairy covering of carapace not forming so thick a coat as to conceal surface beneath 2
   Hairy covering over whole carapace forming thick coat concealing surface beneath (hair sometimes worn off) 3
2. Two or more superhepatic spines . . . . . ***P. sayi***
   No superhepatic spines . . . . . ***P. dasypodus***
3. Chelipeds spinose above; transverse row of long hairs across front . . . . . ***P. floridanus***
   Chelipeds not spinose above; carapace tuberculate, but tubercles often sparse and low 4
4. Tubercles of carapace neither numerous nor prominent, upper margin of orbit not spinose . . . . . ***P. lacteus***

Tubercles on anterior half of carapace and upper surface of chelipeds numerous, upper margin of orbit with truncate spines (but occasionally these poorly developed) . . . . . ***P. pannosus***

Pilumnus dasypodus Kingsley

Fig. 335, 340*a*

Pilumnus dasypodus Kingsley 1879:155.—Rathbun 1930a:493, pl. 200, figs. 5–6.—Williams 1965: 178, figs. 157C, 159.—Felder 1973:61, pl. 9, fig. 7.

Pilumnus desypodus.—Coelho and Ramos 1972:193.

Recognition characters.—Carapace thinly covered on anterior ⅔ with long, fine hair and occasional stouter setae; upper surface of chelipeds and walking legs similarly clothed; small sharp granules on anterolateral region. Anterolateral border with 4 spines including small outer orbital; spines with bases conical, extremities long, slender, incurved. Orbital border with 3 or 4 spines above and about 7 below. Frontal lobes separated by median V- or U-shaped notch; margins furnished with short spines or sharp granules, with an outer tooth separated from remainder of margin by U-shaped notch.

Chelipeds unequal, spinose, and granulate except for smooth and naked lower distal ⅔ of outer surface of major palm, spines and granules not arranged in rows on upper part of major palm; fingers of minor chela grooved on outside, dactyls with rows of sharp granules and hairs at base. Walking legs hairy and spinose above.

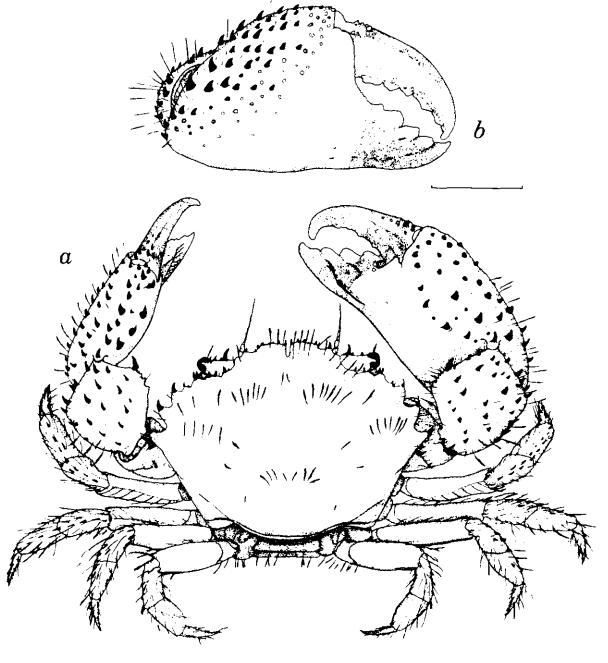

Fig. 335. *Pilumnus dasypodus* Kingsley. *a*, Male in dorsal view; *b*, major chela in external view; 5 mm indicated (from Williams 1965).

Measurements in mm.—Carapace: male, length 11, width 15; ovigerous female, length 6.5, width 10.3.

Color.—Body and claws brownish-red, legs much lighter; fingers and extremities of spines brown (Milne Edwards *in* Rathbun 1930a).

Habitat.—This species has been taken from pilings, jetties, buoys, and offshore reefs (Lunz 1937a; Pearse and Williams 1951; Rathbun 1930a) including loggerhead sponge *Speciospongia vespara* (see Pearse 1934); 1 to 52 m.

Type-locality.—Key West, Fla.

Known range.—Off Cape Hatteras, N. C., through Gulf of Mexico, Caribbean Sea and West Indies to Santa Catarina, Brazil.

Remarks.—This species is not so common in the Carolinian area as *P. sayi*, and small specimens of the latter are not always easily distinguished from it. Rathbun (1930a) stated that "*dasypodus* is less heavily clothed with hair than *sayi* and less ragged looking. The front is more deflexed and less advanced, therefore appears wider. The spines and tubercles of the major palm in *sayi* are arranged more or less in rows and these rows have a tendency to encroach on the lower distal half; in *dasypodus* there are seldom any definite rows and the lower distal two-thirds or one-half in both sexes is smooth and bare. The immovable finger of the major chela in *dasypodus* is a little longer than in *sayi*."

Ovigerous females are known year-round in the West Indies (USNM), December to May in south Florida (Rouse 1970) as well as in summer (Camp, et al. 1977, in part), and April through August in the Carolinas (Lunz 1937a).

From ovigerous females taken in August on a jetty near the mouth of Charleston Harbor, S. C., Sandifer (1974a) reared four zoeal stages and a megalopa on a diet of *Artemia* nauplii under constant light at 28°C in artificial seawater of 35‰ salinity. Development to megalopa required a minimum of 11–12 days under these conditions. Bookhout and Costlow (1979) reared four zoeal stages and a megalopa from ovigerous females taken on heads of a scleractinian coral, *Oculina arbuscula*, off Cape Lookout, N. C., in filtered seawater of 30‰ at constant 25°C on the same diet. Similar comments in both studies compared larval differences between *P. dasypodus* and *sayi*, and contrasted developmental stages of these species with those of

other xanthids. McCloskey (1970) discussed association of this crab with *Oculina arbuscula* in the Carolinas. Gore, et al. (1976; 1978) characterized a population of *P. dasypodus* on sabellariid reefs along east Florida as moderately abundant but fluctuating in density from year to year. Stomach analyses showed that the species is omnivorous, a facultative predator-scavenger that also consumes diatoms and algae.

Pilumnus floridanus Stimpson

Figs. 336, 340*b*

Pilumnus floridanus Stimpson 1871a:141.—Rathbun 1930a:507, pl. 205, figs. 3–4.—Williams 1965:179, figs. 157D, 160.—Coelho and Ramos 1972:193.—Felder 1973:61, pl. 9, fig. 8.—Pequegnat and Ray 1974:238, figs. 23, 24.

Recognition characters.—Carapace covered with dense, short pubescence thinning behind, and with few longer clavate hairs, conspicuous transverse series of these crossing frontal region. Anterolateral margin with 4 somewhat conical spines; small subhepatic spine between outer orbital and second spine; hepatic region slightly roughened but with no spines. Frontal lobes almost bare, edge slightly oblique, minutely crenate, with median triangular notch and rounded lateral notches; tooth at outer angle minute, deflexed. Orbital margin essentially unarmed above, with 8 to 10 spinules below.

Chelipeds spinose above; merus with 2 spines near distal end on upper surface; carpus armed over entire exposed surface; spines on hand becoming pointed tubercles on outer surface. Male with large hand smooth and bare on outer lower half or less of surface, smooth part more restricted in female. Walking legs spined above.

Measurements in mm.—A small species. Carapace: male, length 8.5, width 12.8; female, length 6.3, width 9.

Habitat.—In North Carolina this species has been taken from an offshore reef (Pearse and Williams 1951) and found in sponges. Rathbun (1930a) and Felder (1973) listed it from rocks, grass, and a variety of primarily hard bottoms. Low-tide mark to about 146 m.

Type-locality.—Tortugas, [Fla.].

Known range.—Off Cape Lookout, N. C., through Gulf of Mexico, and Yucatan Channel, to Honduras; through West Indies to Bahia, Brazil.

Remarks.—This species is not common north of Florida. Ovigerous females are known from March to August in Florida (Rathbun 1930a, in part) and they have been taken in February in North Carolina.

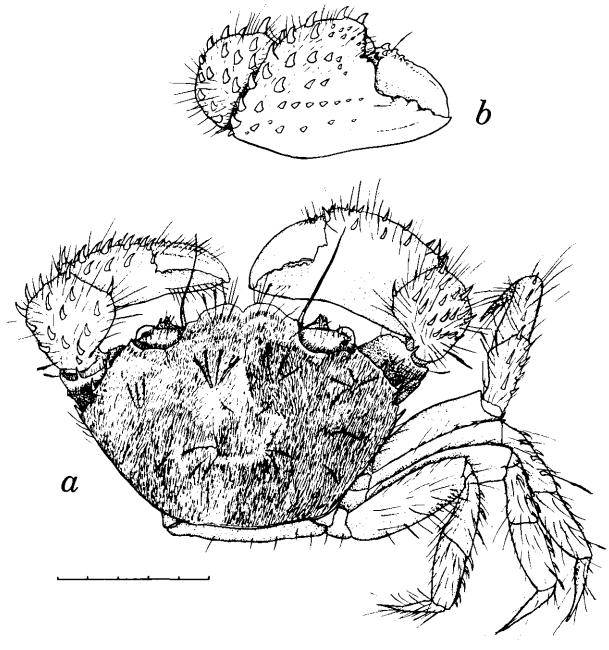

Fig. 336. *Pilumnus floridanus* Stimpson. *a*, Animal in dorsal view, walking legs of left side not shown; *b*, major chela in external view; 5 mm indicated (from Williams 1965).

Pilumnus lacteus Stimpson

(Small hairy crab)

Figs. 337, 340*c*

Pilumnus lacteus Stimpson 1871a:142.—Hay and Shore 1918:440, pl. 35, fig. 3.—Rathbun 1930a:511, pl. 205, figs. 1–2.—Williams 1965:180, figs. 157E, 161.

Recognition characters.—Carapace about ¾ as long as wide, covered with short velvetlike pubescence easily rubbed off (and often is), nearly smooth, sparse tubercles almost invisible through hairy coating; usually a row of 5 tubercles paralleling anterolateral and orbital margins, others scattered. Anterolateral margins with 4 anteriorly directed teeth, first or outer orbital small; small subhepatic spine between latter and second tooth. Front depressed, deeply notched in middle, and with smaller notch near eye. Orbital margin occasionally a bit uneven but not tuberculate.

Chelipeds dissimilar in size but otherwise nearly alike, stout, velveted, sparsely long setose and somewhat tuberculate above, but naked and polished below and on ventral half or ⅔ of both inner and outer surfaces of chelae; merus with 2 similar

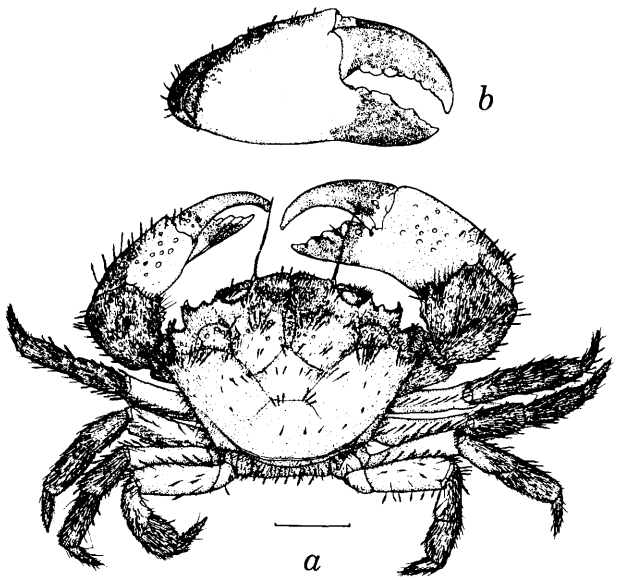

Fig. 337. *Pilumnus lacteus* Stimpson. *a*, Animal in dorsal view; *b*, major chela in external view; 5 mm indicated (from Williams 1965).

curved spines on upper margin distally; carpus with stout spine on inner angle.

Measurements in mm.—Carapace: male, length 12, width 15; female, length 7.5, width 11.1.

Color.—Gray or pinkish, with plumose hairs whitish or cream colored; hands and tips of legs light red. Small black under-hairs on anterior ⅓ of carapace (Rouse 1970).

Habitat.—This crab may be found on wharf pilings or in seaweed. It has been taken from buoys both in sounds and at sea in South Carolina (Lunz 1937a). Rathbun (1930a), Tabb and Manning (1961) and Rouse (1970) reported it from a variety of situations farther south. Near low-tide mark to about 32 m (Wenner and Read 1982).

Type-localities.—Cruz del Padre, Cuba, and Key West, Fla.

Known range.—Near Beaufort, N. C., to Florida; Cuba.

Remarks.—Ovigerous females are known yearround in southern Florida (Rouse 1970) where this is the commonest of three species of *Pilumnus* associated with sponges in salinities ranging from 15 to 45‰. They are reported also in May from Cuba (Rathbun 1930a) and South Carolina (Lunz 1937a).

***Pilumnus pannosus* Rathbun**

Figs. 338, 340*d*

Pilumnus pannosus Rathbun 1896b:142.—Rathbun 1930a:514, figs. 4–5.—Williams 1965:181, figs. 157F, 162.—Felder 1973:64, pl. 9, fig. 12.

Recognition characters.—Carapace about ¾ as long as wide, almost entirely covered with unevenly distributed, soft, thick, velvety pubescence, with scattered longer club-shaped setae giving ragged appearance. Anterior half of carapace and upper surface of chelipeds and legs dotted with beadlike tubercles; these tubercles and anterior lobulations of carapace showing through pubescence. Anterolateral margin with 4 triangular spines (outer orbital small) having slender forward-projecting tips; subheptic spine between first and second tooth well developed. Frontal lobes (when well formed) broadly subtriangular, granulate on margin, separated by V-shaped notch; outer tooth of front almost triangular, acute (blunt at tip in some specimens). Upper margin of orbit with truncate teeth covered by pubescence, lower margin with row of short, stout, truncate teeth or tubercles.

Chelipeds with upper surface tuberculate but usually large; part of outer surface smooth and naked; small hand with outer surface often rough with rows of spines; dactyls with a few tubercles near articulation. Male with shallow grooves on fingers, female with well-defined grooves on minor fingers and fixed major finger. Walking legs pubescent, fringed with club-shaped setae mixed with long fine hair.

Measurements in mm.—Carapace: male, length 9, width 12; female, length 11.6, width 16.5.

Color.—Carapace under pubescence and bare part of palms bright red (Milne Edwards *in* Rathbun 1930a). Tan, red tubercles, dark fingers on orange-brown hands.

Habitat.—Pearse and Williams (1951) listed this species as taken from a submerged rock reef, and

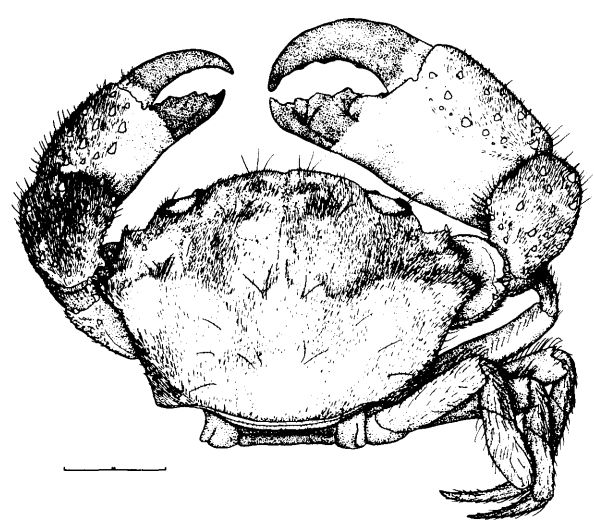

Fig. 338. *Pilumnus pannosus* Rathbun. Male in dorsal view, walking legs of left side not shown, 2 mm indicated (from Williams 1965).

Rathbun (1930a) listed it from similar situations as well as from sponges and corals. About 1 to 20 m.

Type-locality.—Key West, Fla.

Known range.—Bogue Sound off Beaufort, N. C., to Port Aransas, Tex.; West Indies to Virgin Islands.

Remarks.—Rathbun (1930a) listed ovigerous females in December and January from Florida, and they are known from April to August between South Carolina and Cuba.

Pilumnus sayi Rathbun

(Hairy crab)

Figs. 339, 340*e*

Cancer aculeatus Say 1818:449.

Pilumnus sayi Rathbun 1897b:15.—Hay and Shore 1918:440, pl. 35, fig. 4.—Rathbun 1930a:484, pl. 200, figs. 1–2; pl. 201, figs. 4–7.—Williams 1965:177, figs. 157A, B, 158.—Felder 1973:61, pl. 9, fig. 6.

Recognition characters.—Carapace about ¾ as long as wide, anterior half semicircular, strongly deflexed, sparsely covered with long filiform and plumose hairs. Anterolateral border with 4 marginal spines including outer orbital; 2 curved spines on hepatic region with sometimes 1, 2, or 3 supplementary spines; 1 long spine and sometimes spiniform tubercles between first and second marginal spines below margin. Orbit armed with 3 long spines above, and 4 long and 2 to 4 short spines below. Front advanced, deeply notched in center, less so on each side, armed with about 4 spines on each side.

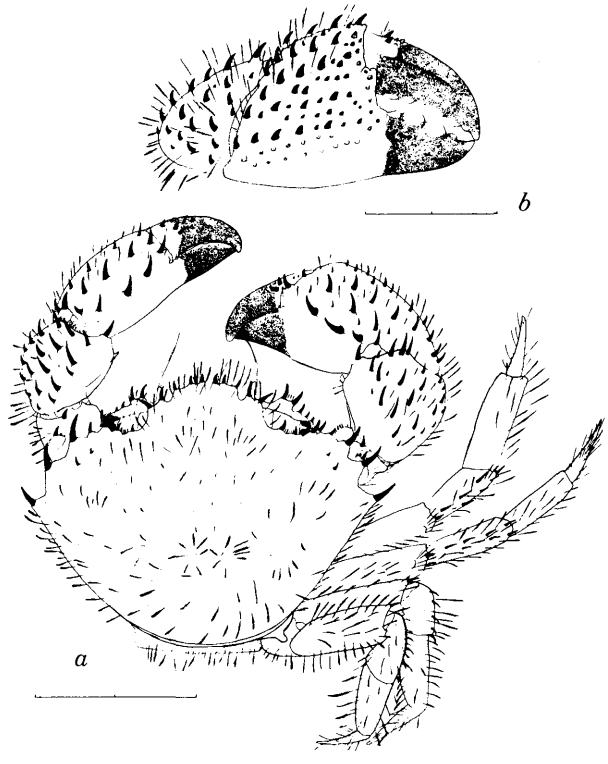

Fig. 339. *Pilumnus sayi* Rathbun. *a*, Male in dorsal view, walking legs of left side not shown; *b*, major chela in external view; 1 cm indicated (from Williams 1965).

Superior surfaces of chelipeds and walking legs with many filiform and plumose hairs; carpal and propodal articles most thickly covered and with several strong spines as well. Chelipeds large, unequal; carpus with 15 or 20 erect dark spines; spines of hand strong and acute above but becoming smaller on external surface, spines tending to arrangement in rows on large hand; fingers ribbed, dark, and with obtuse teeth; dactyl spiny above at base.

Measurements in mm.—Carapace: male, length 23, width 32; female, length 20, width 28.

Variation.—The specimen taken on Frying Pan Shoal off North Carolina (Charleston Museum No. 38.228) reported by Lunz (1939) appears to be an aberrant specimen of *Pilumnus sayi* rather than *P. marshi*. The specimen lacks superhepatic spines on the carapace but otherwise more nearly resembles *P. sayi* than any other western Atlantic species of *Pilumnus*. Reduced superhepatic spines are not unusual.

Color.—Grayish brown irregularly suffused with red or purple on body and legs; spines black, horn color, or purple; fingers of chelae black or brownish purple.

Habitat.—This species is fairly common from the Carolinas southward, and is often taken on shelly bottom. It has been taken from wharf piles, buoys (Lunz 1937a), the sponge *Stematumenia strobilina* (see Pearse 1934), and from offshore reefs (Pearse and Williams 1951; Cain 1972). From low-water mark to 90 m.

Type-locality.—Georgia and east Florida.

Known range.—North Carolina through Gulf of Mexico and West Indies to Curaçao.

Remarks.—Ovigerous females occur in the Carolinas from May to August, and in Florida perhaps year round (Gore, et al. 1978; Rouse 1970; Wass 1955). Chamberlain (1961) reported four zoeal stages and a megalopa in the larval development of the species, but did not describe the stages in detail. He found that larval development time varied with temperature (18 days at 30°C, 28 at 21°C) and with food. Larvae matured most rapidly when fed *Artemia salina* nauplii, did moderately well on

Artemia and algae, but did not transform at all when fed algae alone. Amplifying these experiments, McDonald and Lang (1976) found that larvae reared at 20°C took twice as long to develop to crab stage II and exhibited higher mortality during metamorphosis from megalopa to crab stage I than larvae reared at 25°C. Mortality in the latter peaked at an earlier time in development. The difference in development time under the two conditions reflects tropical affinities of the species. Comparisons of the larval development of *P. sayi* and *dasypodus* were given by Sandifer (1974a) and Bookhout and Costlow (1979).

Dudley and Judy (1971) found larvae in plankton at 1–8 m depth 1.6 km off Beaufort, N. C., from July to September, and from June to August 6.5 km offshore where they were more abundant at 8-m than at 1-m depth. None were found at stations 10–13 km from shore.

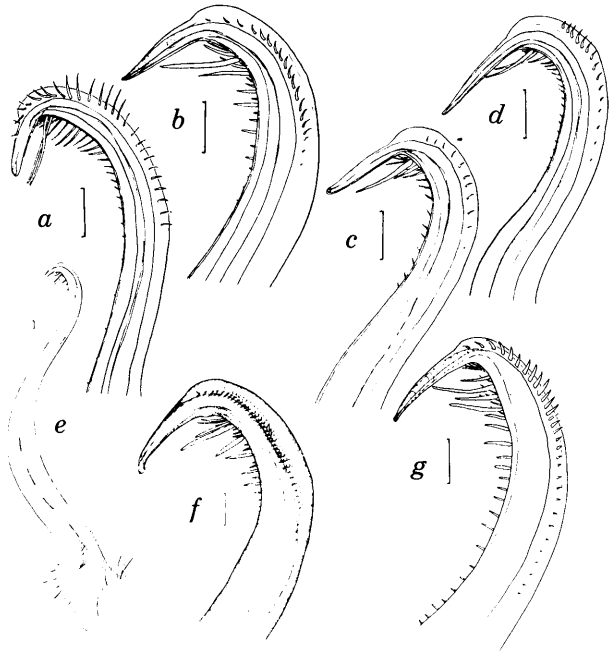

Fig. 340. Male first pleopods in mesial view: *a, Pilumnus dasypodus* Kingsley, tip; *b, P. floridanus* Stimpson, tip; *c, P. lacteus* Stimpson, tip; *d, P. pannosus* Rathbun, tip; *P. sayi, e,* entire pleopod, *f,* tip in detail; *g, Lobopilumnus agassizii* (Stimpson), tip; *a-g,* 0.125 mm indicated (from Williams 1965).

Genus *Lobopilumnus* A. Milne Edwards 1880

Rathbun 1930a:525.

Lobopilumnus agassizii (Stimpson)

Figs. 340*g*, 341

Pilumnus agassizii Stimpson 1871a:142.
Lobopilumnus agassizii.—Hay and Shore 1918:441, pl. 34, fig. 5.—Rathbun 1930a:526, pl. 211.—Williams 1965:181, figs. 157G, 163.

Recognition characters.—Regions of carapace protuberant, surface pubescent, except naked and thickly granulate on anterior and anterolateral regions; depressions between regions broad, occupying as much area as regions themselves. Front consisting of 2 large lobate masses deeply separated from each other and from orbits. Orbital region protuberant and granulate, margin crenulated with granules, with 2 fissures above and 2 very narrow ones below. Anterolateral margin with 3 triangular, spine-tipped teeth of moderate, equal size; subhepatic tooth distinct.

Chelipeds short, stout; carpus rough, tubercles thickly studded with forwardly directed granules, confluent laterally forming transverse ridges; superior and outer surfaces of hands covered with small prominent mammiliform tubercles, arranged largely in rows on outer surfaces and having apices directed forward. Walking legs pubescent and hairy, carpal and propodal articles with minute spines above.

Measurements in mm.—Carapace: female from North Carolina, length 16, width 21; male from Florida, length 23, width 31; female, length 20, width 27.

Variation.—Rathbun (1930a) stated that this species is variable as to the number and prominence of regions on the carapace, and she recognized four environmental forms within the species. Because only one specimen has ever been reported from North Carolina, and this is no longer extant, it is not possible to assign a form or forms to this area.

Color.—Gray above with granules and knobs yellowish red and reddish brown; legs white or with whitish spots (Schmitt *in* Rathbun 1930a).

Habitat.—In Bermuda, Verrill (1908a) found the carapace and legs of this species often thickly covered, sometimes almost concealed, by a coating of calcareous mud and sand adhering to hairs on the back. He found it most frequently under stones and dead corals at low tide. Pearse (1934) reported this crab from loggerhead sponge *Speciospongia vespara*. Low-tide mark to 51 m.

Type-locality.—Typical form: East and Middle Keys, Tortugas, Fla.

Known range.—North Carolina; eastern Gulf of Mexico; Yucatan; Cuba; Venezuela and Trinidad; Bermuda.

Remarks.—Ovigerous females are known from

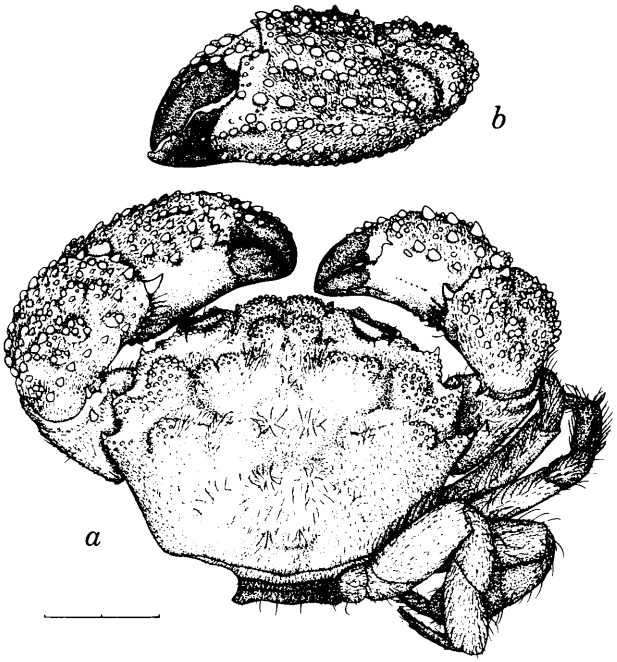

Fig. 341. *Lobopilumnus agassizii* (Stimpson). *a*, Male in dorsal view, walking legs of left side not shown; *b*, major chela in external view; 1 cm indicated (from Williams 1965).

February to July in Florida and Cuba (Rathbun 1930a, in part).

Genus *Melybia* Stimpson 1871

Rathbun 1930a:561.

Melybia thalamita Stimpson

Fig. 342

Melybia thalamita Stimpson 1871a:144.—Rathbun 1930a:562.—Coelho and Ramos 1972:194.—Powers 1977:96.

Recognition characters.—Surface finely granulate and covered with short, thin pubescence. Carapace subelliptical, slightly convex, regions faintly marked. Frontoorbital width about 5/6 greatest width of carapace; front about 2/5 width of carapace, depressed, divided by median V-shaped notch and separated by notch from inner orbital angle. Large orbits filled by stout eyes with cluster of spinules on anterior surface of stalk; orbital margin minutely crenulate, 2 notches above with space between arcuate, inner angle subtriangular. Anterolateral margin short, bearing 4 spiniform acuminate teeth, first (outer orbital angle) and fourth small, middle 2 teeth larger, first occasionally bifid, but absent in juveniles. External maxillipeds broadly separated and densely hairy mesially.

Chelipeds unequal, long and strong, reaching far beyond carapace; merus armed with spines on upper and inner margins; carpus slightly spinulous above and laterally, 3 strong spines along inner margin; palm with double row of spines above; fingers 1/4–2/3 length of palm, heavy, broad, compressed, grooved, prehensile edges shallowly toothed; dactyl with superior carina roughened proximally. Walking legs long and slender, tapered and flattened, with sparse, long hairs; merus with superior row of spines and spine (sometimes smaller second) near distal end of lower margin in first 3 pairs; dactyl nearly length of propodus, spiny.

Measurements in mm.—Carapace: male, length 7.25, width 11.3; ovigerous female, length 4.9, width 7.3.

Variation.—Some specimens are smooth (Rathbun 1930a), old males may lack the distal lower spines on the merus of walking legs 1–3 (USNM 99731), and still others may have supernumerary spines as noted above.

Habitat.—Under *Sargassum*, coral and broken shell; beach to about 80 m, but also as deep as 368 m.

Type-localities.—Off French Reef, 27.4 m, and west of Tortugas [southern Fla.], 64–76.8 m.

Known range.—About 30 mi. SSE Cape Lookout, N. C. (34°11'N, 76°09'W); SW of Mississippi River Delta, through West Indies to Bahia, Brazil.

Remarks.—Ovigerous specimens are known from Puerto Rico in February, Barbados in March, and Florida in July.

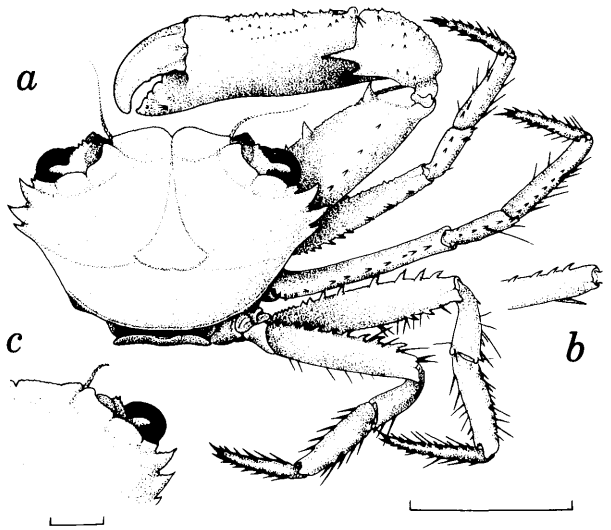

Fig. 342. *Melybia thalamita* Stimpson. *a*, Male in dorsal view, legs of left side not shown; *b*, distal end merus of first walking leg; *c*, portion of female in dorsal view; *a-b*, 5 mm, *c*, 1 mm indicated (USNM 7774).

Family Goneplacidae Dana 1852

Carapace usually quadrate. Orbit indistinctly divided into 2 hollows. Inner antennular septum a thin plate. Palp of third maxilliped articulating on or near anteromesial corner of merus; exognath of normal form and not concealed. Male genital openings either on sternum or, if coxal, with genital duct extending into groove on sternum. Marine forms, not sharply separated from the Xanthidae. (After Balss 1957.)

Guinot (1969a, b, c) tentatively regrouped a number of goneplacid genera into subfamilies that are more restricted than the groupings set forth by Balss (1957) or listed by Serène (1968). The family is still not completely revised, and Guinot's preliminary work emphasizes Balss's statement that the Xanthidae and Goneplacidae merge. Her studies show this transition partly through changes in the male genital apparatus; the subfamilies as they stand now are based largely on structure of the male pleopods. Since a subfamily key based mainly on cryptic male characters has limited utility in a faunistic handbook, I list the subfamilies recognized by Guinot that are pertinent to this study, with the similarly pertinent genera of each, and give a key to the few species considered here.

Key to Subfamilies, Genera, and Species

1. Carapace xanthoid, anterior margin consisting of front, orbits, and anterior part of arched, toothed, anterolateral border 2
   Carapace subquadrate, anterior margin almost completely occupied by front and elongate orbits 5
2. Posterolateral borders obviously convergent; eyestalks rather thick and not conspicuously hairy 3
   Posterolateral borders imperceptibly convergent (almost parallel); eyestalks tapering to reduced cornea and conspicuously hairy . . . . . [Pseudorhombilinae] ***Speocarcinus carolinensis***
3. Front prominent and almost straight, with small median notch; usually 4 anterolateral teeth, second tooth largest; carpus of chelipeds smooth. . . . . [Eucratopsinae] ***Glyptoplax smithii***
   Front with lobes convex; usually 5 anterolateral teeth; carpus of chelipeds roughened with rugae or lines of granules 4
4. Anterolateral teeth with smooth margins, first 2 coalesced, third largest, obtuse, with strongly curved lateral margin . . . . . [Eucratopsinae] ***Panoplax depressa***
   Anterolateral teeth with granular margins, first 2 low and coalesced, third and fourth strong and acute . . . . . [Pseudorhombilinae] ***Nanoplax xanthiformis***
5. Two anterolateral spines including outer orbital 6
   Three anterolateral spines including outer orbital . . . . . [Euryplacinae] ***Euryplax nitida***
6. Chelipeds with conspicuous tufts of dense hair . . . . . [Euryplacinae] ***Frevillea hirsuta***
   Chelipeds without conspicuous tufts of dense hair . . . . . [Goneplacinae] ***Goneplax sigsbei***

Subfamily Euryplacinae

Front with outer lobe more or less developed; strong projection extending ventrad to rest on basal antennal article. Orbit closed by antennal article or ventral projection from outer frontal lobe, or remaining open. Male abdomen basically triangular with segments 4–7 slender and progressively narrowed. Sternites much broadened, variable part of sternite 8 visible at level of second abdominal segment. Genital opening of male either on coxa of fifth legs with genital duct tending to lie in sternal groove, or on sternum with genital duct passing mesially from coxa through involute groove between sternites 7 and 8 to emerge where groove flares. Male first pleopod long, rather slender, tapering to filiform tip, bearing small tubercles along length; second pleopod short. (Adapted from Guinot 1969b.)

Genus *Euryplax* Stimpson 1859

Rathbun 1918b:34.—Hemming 1958b:32.—Guinot 1969b:512.

Euryplax nitida Stimpson

Fig. 343

Euryplax nitida Stimpson 1859:60.—Rathbun 1918b:34, fig. 11, pl. 7.—Williams 1965:202, fig. 185.—Guinot 1969b:512, figs. 39, 41, 47, 56–57.—Felder 1973:70, pl. 10, fig. 1.

Recognition characters.—Carapace smooth and shining, convex, noticeably broader than long. Front with interantennal margin nearly straight but deeply notched on each side at insertion of antenna; wide ventral extension from front lateral to antenna overlapped by narrower infraorbital expansion from ventral side to close orbit. Anterolateral margin converging anteriorly, less than half as long as posterolateral margin and armed with 3 strong teeth including outer orbital, carapace widest at level of third tooth.

Merus of chelipeds in male with deep round pit at anterior distal corner of lower surface, pit surrounded by fringe of long hairs and with sharp curved spine near distal end of upper surface; carpus with inner surface pilose and bearing sharp spine. Walking legs slender.

Male abdomen basically triangular, concave sides of distal segments tapering to rather narrowly rounded telson; first segment barely visible, second widest and meeting coxa of fifth legs at each side by leaving triangular, posterolateral corner of sternite 8 exposed between it and third abdominal segment at each side; exposed part of sternite 8 with involute edge meeting counterpart of sternite 7 to form short, closed groove housing genital duct opening sternally. Male first pleopods stout proximally but tapering to slender, darkened tip grooved mesially and bearing minute, sharp tubercles near tip.

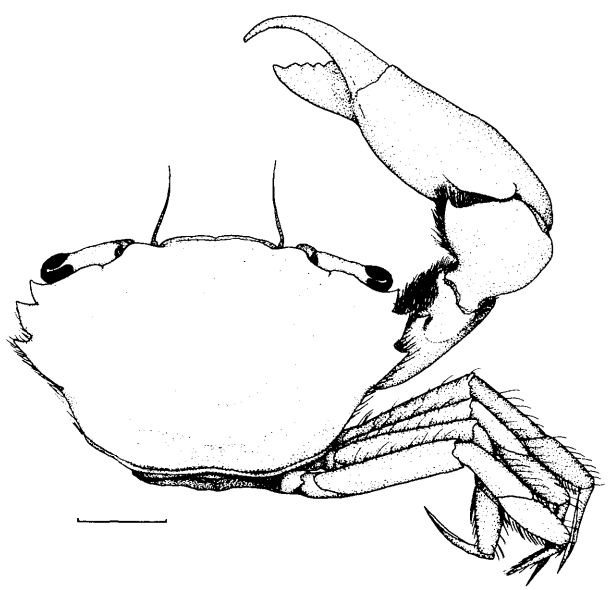

Fig. 343. *Euryplax nitida* Stimpson. Male in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

Measurements in mm.—Carapace: male, length 15, width 25; female, length 15, width 24.

Variation.—Females have more nearly equal chelipeds lacking the meral pit with surrounding hair.

Color.—Distal half of fingers white (Rathbun 1918b).

Habitat.—Sandy shell, grass and mud bottoms; 3.5 to 90 m (Rathbun 1918b).

Type-locality.—Florida Keys.

Known range.—Off Beaufort, N. C., to Heald Bank, Tex. (USNM); West Indies to St. Thomas; Bermuda; specimen from "Bresil, Dertero" [sic] (= Florianopolis?) figured by Guinot (1969b).

Remarks.—Ovigerous females have been taken in June from southern Florida.

Randall (1969) reported *E. nitida* from stomach contents of the longspine squirrelfish, *Holocentrus rufus*.

Genus *Frevillea* A. Milne Edwards 1880

A. Milne Edwards 1880:15.—Guinot 1969b:513.

Frevillea hirsuta (Borradaile)

Fig. 344

Goneplax hirsuta Borradaile 1916:99, fig. 11.—Rathbun 1918b:28, fig. 7.—Williams 1965:201, fig. 184.

Frevillea hirsuta.—Guinot 1969b:513.—Coelho and Ramos 1972:194.

Recognition characters.—Carapace finely granulate, approximately ⅔ as long as broad, greatest width between tips of outer orbital spines; regions faintly marked except for H-shaped depression in middle. Sides converging backward from prominent, sharp outer orbital spines each followed by sharp spine close behind. Front almost straight, with low prominence in broad, shallow median notch. Frontoorbital notch turned toward base of orbit, orbital hiatus open. Orbital margin sinuous, sloping backward, width of orbit and front nearly equal; ocular peduncles enlarged with globular cornea fully visible ventrally; infraorbital tooth present. Remarkably large basal antennular article lodged

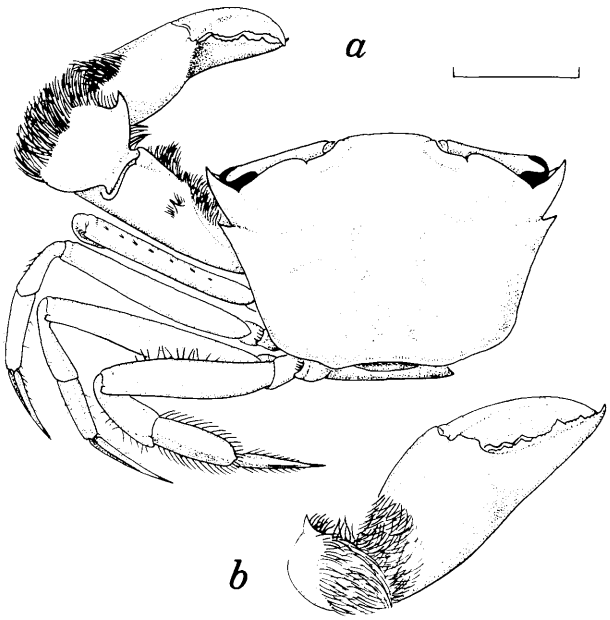

Fig. 344. *Frevillea hirsuta* (Borradaile). *a*, Male in dorsal view, legs of right side not shown; *b*, right chela and carpus in external view, 1 cm indicated (USNM 92361).

in more or less transverse fossa; following articles folding transversely and covering base of antenna.

Chelipeds almost equal; merus about ⅔ length of carapace, deep, with spine a little beyond middle of upper edge; carpus broader than long, with stout internal spine. Hand longer than remainder of limb; fingers about equal to palm, irregularly toothed, not gaping; external base of hand and distal half of carpus with long dense tuft of hair, fringe of similar hairs along inner side of merus. Walking legs slender, meri smooth or fringed with light pubescence, distal articles fringed with hairs.

Male abdomen basically triangular, concave sides of distal segment tapering to rather narrowly rounded telson; first segment barely visible; second meeting coxa of fifth legs at each side but leaving tiny, uncovered posterolateral part of sternite 8 at each side between it and broader third abdominal segment. Lateral adjacent parts of sternites 7 and 8 separated by broad groove containing genital duct emerging from coxa of fifth leg. Male first pleopods stout proximally but tapering to slender tip, and bearing minute, sharp tubercles.

Measurements in mm.—Carapace: male, length 22, width 33; ovigerous female, length 19.3, width 29.

Habitat.—73 to 155 m.

Known range.—North Carolina to Rio de Janeiro, Brazil.

Remarks.—Ovigerous females have been taken in the Gulf of Mexico off Yucatan in January and Florida in June (USNM).

Subfamily Goneplacinae

Carapace subquadrate, widest between postorbital angles because of width of front and elongate orbits. Male genital openings on coxa of fifth leg but genital duct lying in groove between sternites 7 and 8. Male first pleopod stout along all of length, tapered toward apex; second pleopod longer than first.

Genus *Goneplax* Leach

Rathbun 1918b:25.—Hemming 1958b:32.—Guinot 1969b:520.

Goneplax sigsbei (A. Milne Edwards)

Fig. 345

Frevillea sigsbei A. Milne Edwards 1880:16.
Goneplax sigsbei.—Rathbun 1918b:26, pl. 4, figs. 2, 4.—Williams, McCloskey, and Gray 1968:54, fig. 10.—Guinot 1969b:520, figs. 63, 68, 71, 72.

Recognition characters.—Carapace subrectangular, broader than long; moderately convex, regions faintly indicated; anterolateral angles acute, outer orbital spine directed obliquely forward, second spine smaller, angled more outward; lateral borders posteriorly convergent. Frontoorbital complex occupying whole anterior border of carapace; front equal to or shorter than either orbit; slight depression behind orbital margin; eyestalks long, cornea enlarged. Antennules folding transversely, almost covering short basal article of antenna at either side, antennal flagellum in orbital hiatus. Buccal area anteriorly widened, well separated from prominent epistome.

Chelipeds with merus projecting well beyond carapace, occasionally with small tooth at middle of outer margin; carpus with small, blunt tooth at inner angle; palm with longitudinal groove on outer surface just above lower margin and more oblique shorter groove on inner surface; fixed finger much broader than dactyl, shallow irregular teeth on prehensile edges. First 3 walking legs with slender dactyls longer than propodi, distal 3 articles of reduced last leg relatively broader than in preceding legs.

Abdomen of male rather broadly triangular, sides concave, all segments free, second segment broadest; small lateral part of sternite 8 uncovered between abdominal segments 2 and 3. Genital duct emerging from male opening on coxa of last leg, lying in groove between sternites 7 and 8. Male first

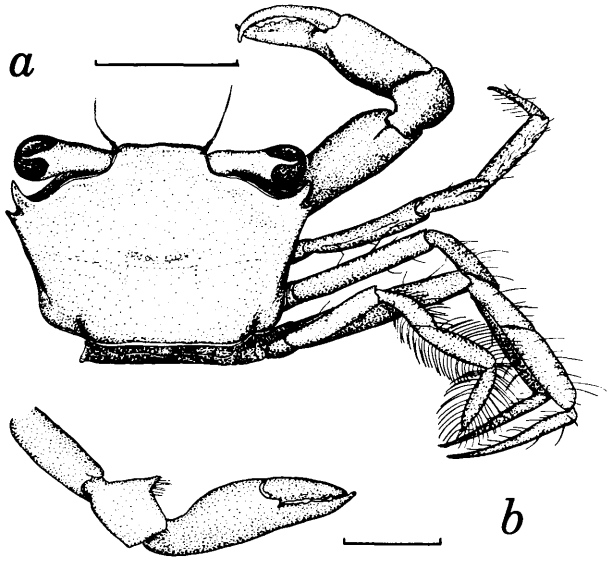

Fig. 345. *Goneplax sigsbei* (A. Milne Edwards). *a*, Male in dorsal view, legs of left side not shown; *b*, cheliped of immature specimen showing carpal spine; *a*, 5 mm, *b*, 1 mm indicated (from Williams, et al. 1968).

pleopod stout but tapered toward tip; slender second pleopod longer than first.

Measurements in mm.—Carapace: male, length 7.5, width 11.5; ovigerous female, length 10, width 12.5 (Williams, et al. 1968).

Habitat.—137 (Wenner and Read 1982) to 300 m.

Type-locality.—Grenada.

Known range.—E Cape Fear, N. C., 33°56′N, 76°26′W to 33° 55.3′N, 76°28.8′W, 130–120 m, *Eastward* Stn. 3213; Grenada, 11°27′N, 62°11′W, and 11°25′N, 62°04′15″W (Williams, et al. 1968).

Subfamily Eucratopsinae (= Prionoplacinae)

Carapace xanthoid, greatest width not at outer orbital corner; tendency to elongation of orbits and development of ocular peduncles. Sternum broadened behind chelipeds. Lateral part of sternite 8 variable, well covered by basal abdominal segments or broader and well exposed between edge of abdomen and coxa of fifth leg. Male genital openings coxal, with genital ducts extending onto sternum in a groove, or sternal, with ducts passing through involute sternal groove. Male first pleopods moderately stout, usually terminating in foliaceous lobe flanked by 2 processes, reminiscent of *Panopeus*. (Adapted from Guinot 1969a.)

Genus *Glyptoplax* Smith 1870

Rathbun 1918b:48.—Hemming 1958b:32.—Guinot 1969a:258.

Glyptoplax smithii A. Milne Edwards

Fig. 346

Glyptoplax smithii A. Milne Edwards 1880:336, pl. 61, figs. 4, 4a-d.—Rathbun 1918b:51, pl. 14, figs. 3–4; pl. 158, figs. 7–10.—A. Milne Edwards and Bouvier 1923:328, pl. 5, fig. 5.—Williams, McCloskey, and Gray 1968:55, fig. 11.

Glyptoplax smithi?.—Guinot 1969a:359, fig. 24a-c.

Recognition characters.—Carapace xanthoid in form, narrow, hexagonal, slightly convex, distinctly areolated, slightly granulate anteriorly and in patches on areoles. Front prominent, lobes squared, somewhat deflexed, separated by tiny median notch and from inner orbital angle. Eyes of moderate size, median lobe on anterior margin of stalk. Anterolateral border usually with 4 teeth, rarely 5, tooth following outer orbital either completely obsolete or reduced; second of first 3 teeth present largest, last tooth much smaller. Basal antennal article just touching front, flagellum in orbital hiatus. Mouth area divergent anteriorly.

Chelipeds rather large; merus with superior granulate crest ending in tubercle or obsolescent spine; carpus occasionally nodulous as well as granulated, low internal spine or blunt projection; palm deep distally, lobe projecting inward from proximal upper margin; fixed finger of minor hand slightly deflexed, major less so and with large tooth at base of prehensile tooth row; fingers dark brown.

Male abdomen with broadest, conspicuous first segment reaching nearly to coxa of fifth leg at each side, its dorsal surface transversely grooved and granular, especially on slightly elevated lateral parts; second segment somewhat rectangular, much narrower than first, visible part of sternite 8 between it and coxa of fifth leg; segments 3–5 fused, sides slightly concave, posterolateral corner well rounded. Exposed lateral part of sternite 8 with involute anterior edge meeting counterpart from sternite 7 to form short, closed groove housing genital duct opening sternally. Male first pleopod fairly stout, terminating in 3 projections, opposite, divergent slender and obtuse projections exceeded by central, folded, membranous hood; shaft with tracts of spinules.

Measurements in mm.—Carapace, male, length 5.6, width 7.1; ovigerous female, length 4.75, width 6.5.

Variation.—In most individuals there are 4 prominent anterolateral teeth, but in a very few there is indication of the suppressed second tooth, and in others all of the teeth are poorly developed. Terminal elements of the male first pleopod are

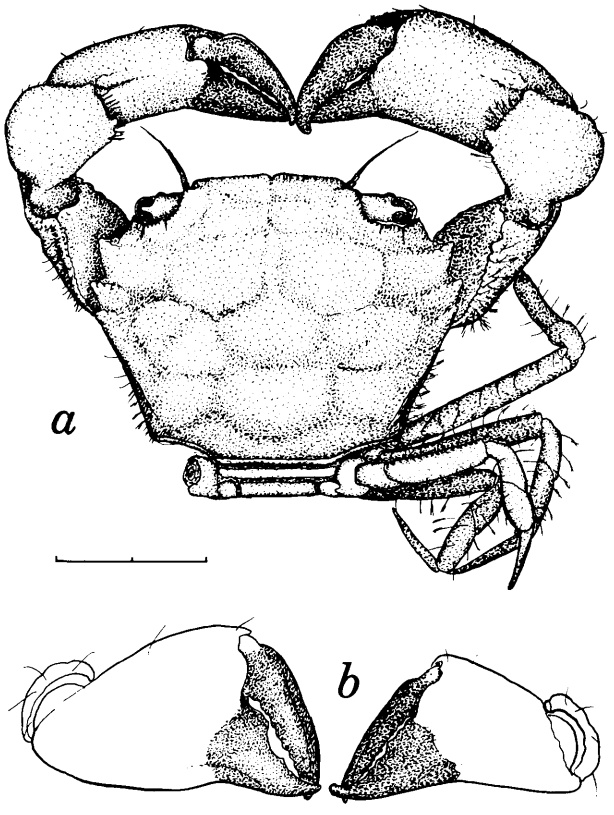

Fig. 346. *Glyptoplax smithii* A. Milne Edwards. *a*, Male in dorsal view, walking legs of left side not shown; *b*, chelipeds of same in frontal view; 2 mm indicated (from Williams, et al. 1968).

subject to some variation in size and folding of the central hood.

Habitat.—24 to 110 m.

Type-locality.—Reefs west of Florida, 23.8 m.

Known range.—From Cape Hatteras, N. C., to Gulf of Mexico and Yucatan Channel.

Remarks.—Guinot (1969a) pointed out differences between this species and *G. pugnax* Smith, the type-species of the genus, namely in male first pleopods and the visible part of sternite 8, suggesting that the two species probably do not belong in the same genus. Though these differences exist, the two are constructed on the same general plan, and I let the generic placement stand.

Ovigerous females are known from off North Carolina in January, May, and November, and off Yucatan in January.

Genus *Panoplax* Stimpson

Rathbun 1918b:47.—Guinot 1969a:264.

Panoplax depressa Stimpson

Fig. 347

Panoplax depressa Stimpson 1871:151.—Rathbun 1918b:47.—Guinot 1969a:264, figs. 3, 28a, b.
Eucratoplax elata A. Milne Edwards 1880.
Eucratopsis elata? A. Milne Edwards and Bouvier 1923:341, pl. 7, figs. 4, 5.
Micropanope levimanus Chace 1940:35; figs. 13, 14.
Micropanope laevimanus.—Guinot 1969a:265, figs. 29a, b.

Recognition characters.—Carapace depressed, arcuate anteriorly, much broader than long; finely punctate, granulate along anterolateral teeth and orbital margins, 2 oblique epigastric lobes. Frontal lobes convex, deflexed, well separated from inner orbital angles, margin often flanked by transverse, submarginal row of hairs. Orbit as wide as frontal lobe, frontoorbital margin ⅔ width of carapace; superior orbital margin with 2 notches; eyes moderate. Anterolateral border with 5 teeth; outer orbital tooth separated from shallow second tooth by shallow sinus; third tooth large, blunt, outer margin strongly arcuate; fourth triangular, acute, located at greatest carapace width; fifth reduced, usually not projecting beyond general outline. Posterolateral margins moderately converging.

Chelipeds with merus and carpus granulate toward margins; merus dentate on upper margin; carpus oblong, stout tooth at inner angle and few tubercles below it, anterior transverse groove; palms smooth and rounded, punctate; fingers not gaping, prehensile teeth low and broad, color not extending on palm. Walking legs with meri roughened, distal articles hairy, carpi and propodi broadened, especially on last leg.

Abdomen of male broadest at segment 1; posterolateral corner of sternite 8 conspicuous lateral to abdominal segment 2 and wedged between lateral parts of segments 1 and 3; segments 3–5 fused, basically triangular but concave laterally. Exposed lateral part of sternite 8 with involute anterior edge meeting counterpart from sternite 7 to form short, closed groove housing genital duct opening sternally. Male first pleopods gently curved, tapering to twisted tip terminating in membranous, irregular, minutely spinulate lobe; tiny, short spines on shaft distally.

Measurements in mm.—Carapace: male, length 7.5, width 10.9; female, length 8.2, width 12.7.

Variation.—Granulation of the carapace and chelipeds is most distinct in larger males; the carpus of the chelipeds is occasionally rugose distally. Acuteness of the third and fourth anterolateral teeth varies from acute to obtuse; in juveniles to subadults these teeth may be spine tipped. The terminal lobe of the male first pleopod is mostly elon-

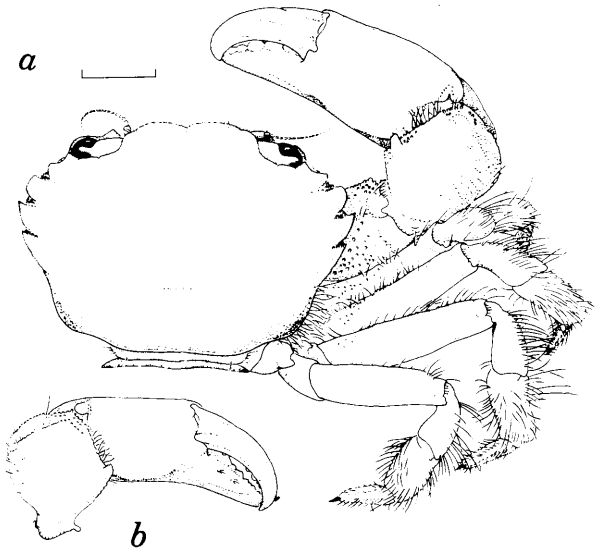

Fig. 347. *Panoplax depressa* Stimpson. *a*, Male in dorsal view, legs of left side not shown; *b*, same, left chela and carpus in dorsal view; 2 mm indicated (USNM 24556).

gate but occasionally shorter, as noted by Guinot (1969a, figs. 29a, b, c), and rarely somewhat folded distally. This last may be an artifact of preservation. The fused male abdominal segment 3–5 becomes more concave sided as the body broadens with age.

Habitat.—Recorded from coral rock, 5 to 95 m.

Type-locality.—East and Middle Keys, Tortugas, [Fla.], 9.1. to 12.8m.

Known range.—SE of Cape Lookout, N. C.; off Jacksonville and Cape San Blas, Fla., through West Indies to Barbados.

Remarks.—Guinot (1969a) suggested the above synonymy for this species on the basis of preliminary study. Following examination of a series of identified material in the USNM and type-material of *Eucratoplax elata* and *M. levimanus*, I agree with her analysis.

Ovigerous females are known from Puerto Rico in March and Dry Tortugas in July.

Subfamily Pseudorhombilinae

Carapace xanthoid, anterolateral border arched and armed with 5 teeth. Male with lateral part of sternite 8 variably covered by basal abdominal segments but always exposed between edge of abdomen and coxa of fifth legs; adjacent exposed edges of sternites 7 and 8 involute, forming tube housing genital duct opening sternally. Male first pleopods strong, twisted and often ornamented with spinules following twist of shaft, terminated by rolled lobe; second pleopod short. (Adapted from Guinot 1969c.)

Genus *Nanoplax* Guinot 1967

Guinot 1967:362.

Nanoplax xanthiformis (A. Milne Edwards)

Fig. 348

Panopeus xanthiformis A. Milne Edwards 1881:353, pl. 53, figs. 4–4b.

Micropanope xanthiformis.—Rathbun 1930a:442, pl. 180, figs. 7–8.—Lunz 1937:13.—Williams 1965: 193, figs. 176, 183I.

Nanoplax xanthiformis.—Guinot 1967a:362, fig. 16.—Coelho and Ramos 1972:192.

Recognition characters.—Carapace much broader than long, hexagonal, convex anteroposteriorly; regions well defined, depressed coarse granulations on anterior and anterolateral portions, oblique ridge parallel to margin on hepatic region. Front slightly deflexed, shallow, lobes separated by shallow notch; margin sinuous, outer corner rectangular. Anterolateral margin arched, bearing 5 teeth with sharply granulate margins; first small; second small, lobiform, and separated from preceding by slight notch; third strong and triangular; fourth more spiniform; fifth small and pointed.

Chelipeds rather strong, unequal, rugose with coarser granules than on carapace; merus with row of spines above; carpus with prominent anterior groove, strong internal spine and often a smaller spine or spiniform tubercle below it; major hand slightly roughened on upper and proximal parts; minor hand rougher on outer surface; fingers deeply grooved, major dactyl with large basal tooth. Walking legs elongate, merus with row of spines above, other legs spinulous.

Male abdomen rather short; third segment concealing sternum, narrower second segment with posterolateral corner obliquely truncate revealing small portion of sternum; first pleopod strong, tightly twisted on long axis, opening apical.

Measurements in mm.—Carapace: male, length 9.9, width 14.5; female, length 8.1, width 11.2.

Variation.—There is considerable individual difference in roughness of chelipeds; the major hand, especially, is relatively smoother in older individuals.

Color.—"Anterior portion of carapace light yellowish orange. Fingers of major chela brownish black, of minor chela black. Spines and tubercles of both chelipeds light salmon" (Rathbun 1930a).

Habitat.—Various types of bottom in deeper water; 11 (Wenner and Read 1982) to 340 m.

Type-locality.—Off Grenada, 168.3 m.

Known range.—Cape Hatteras, N. C.; through

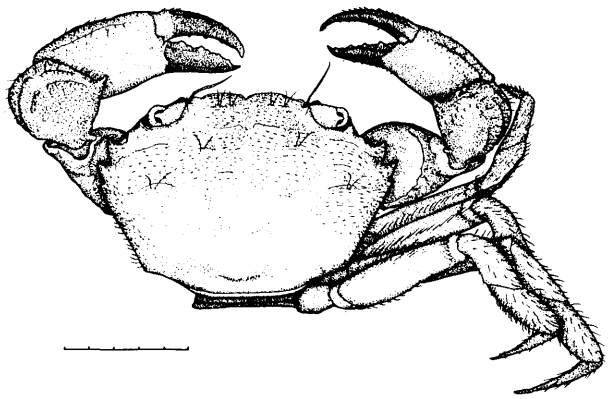

Fig. 348. *Nanoplax xanthiformis* (A. Milne Edwards). Animal in dorsal view, walking legs of left side not shown, 5 mm indicated (from Williams 1965).

Gulf of Mexico and West Indies to Cabo Frio, Rio de Janeiro, Brazil.

Remarks.—Ovigerous females are known in June, August, and November from Florida, and in October from North Carolina (Rathbun 1930a, in part; Camp, et al. 1977).

Guinot (1967a; 1971) placed *Nanoplax* in both the Xanthidae and the Goneplacidae, leaving its status uncertain.

Genus *Speocarcinus* Stimpson 1859

Rathbun 1918b:38.—Hemming 1958b:37.—Guinot 1969c:706.

Speocarcinus carolinensis Stimpson

Fig. 349

Speocarcinus carolinensis Stimpson 1859:59, pl. 1, figs. 1–3.—Rathbun 1918b:39, pl. 8, pl. 159, fig. 6.—Williams 1965:202, fig. 186.—Guinot 1969c:707, figs. 119–122, pl. 4, fig. 1.

Speocarcinus coralinensis Fausto-Filho and Neto 1976:69.

Recognition characters.—Carapace convex longitudinally, gastrocardiac and mesogastric regions faintly outlined; surface punctate, obscurely granulate near margin, faintly rugose, varyingly pubescent; anterior and anterolateral margins beaded. Front straight, projecting and deflexed, ¼ width of carapace, median notch. Orbital margin with faint lobe between dorsal fissures; infraorbital tooth pointed; ocular peduncles hairy, narrowing from thickened base to cornea, not filling orbit. Anterolateral border with 5 teeth including outer orbital; second tooth rounded and poorly separated from first by shallow concavity, third lobiform but pointed, fourth more acute and directed forward; fifth smaller, acute and directed slightly more laterad. Posterolateral margin almost parallel. Third maxillipeds divergent anteriorly.

Chelipeds strong, short, unequal; merus with strong spine on upper border; carpus granulate internally and with blunt internal spine; hands with outer surface smooth, microscopically granulate, 2 rows of small tubercles on upper surface (often most prominent on minor), diminishingly continued on dactyls; fingers with low, irregular teeth on prehensile edges, stronger on major hand with stout tooth at base of dactyl. Walking legs with hairy margins, tapered to very slender dactyls.

Male with large part of sternite 8 exposed lateral to abdominal segments 1 and 2; abdominal segments 3–5 fused, broadest at base, concave sided. Exposed lateral part of sternite 8 with involute anterior edge meeting adjacent counterpart of sternite 7 to form closed groove housing genital duct opening sternally. Male first pleopods rather slender, twisted and tapering to terminal lobe bent mesially at right angle to shaft; second pleopods short.

Measurements in mm.—Carapace: male, length 23, width 29; female, length 17, width 27 (most individuals smaller).

Habitat.—Burrows of worms, *Squilla, Callianassa,* and other crustaceans in mud (Stimpson *in* Rathbun 1918b); near low-tide mark to 149 m (150 m according to Fausto-Filho and Neto 1976).

Type-locality.—Charleston Harbor, S. C.

Known range.—S Cape Hatteras, N. C., 35°3.5′N, 75°25.7′W, through West Indies to Amapá, Brazil.

Remarks.—Guinot (1969c) regarded *S. carolinensis* as recognized until that time to be a composite

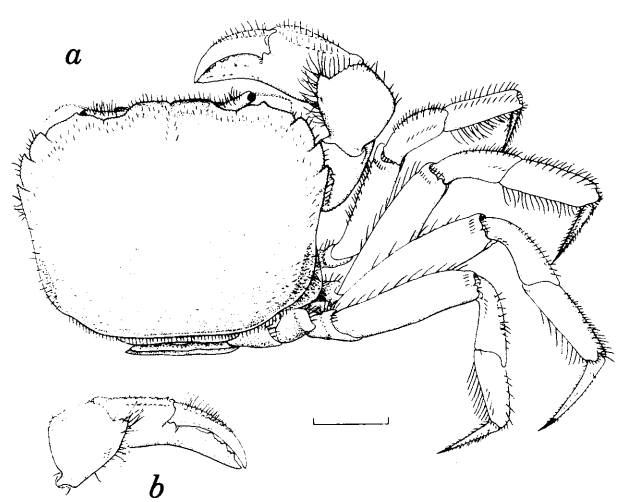

Fig. 349. *Speocarcinus carolinensis* Stimpson. *a*, Female in dorsal view, legs of left side not shown; *b*, same, left chela and carpus in dorsal view; 5 mm indicated (USNM 45951).

species. She restricted *S. carolinensis*, recognized specimens from off Texas in the Gulf of Mexico, and Surinam, as *S. lobatus* Guinot, and described a probable third species from Puerto Rico.

An ovigerous female is known from North Carolina in August.

Superfamily Pinnotheroidea

Family Pinnotheridae

Carapace often somewhat membranous. Anterolateral margins entire or very slightly dentate. Front, orbits, and eyestalks very small, cornea often rudimentary. Buccal cavity usually wide, often semicircular in outline. Merus of third maxilliped never quadrate, and never with palp distinctly at anterointernal angle; ischium small, absent, or fused with merus and directed obliquely inward (Rathbun 1918b).

Small crabs living as commensals or parasites in bivalve mollusks, ascidians, worm tubes, and on or in echinoderms. Free-living or migratory stages are occasionally taken in open water.

Key to Genera

1. Dactyls of walking legs simple, acute 2
   Dactyls of first, second and third walking legs bifurcate . . . . ***Dissodactylus***
2. Third walking leg longer and stronger than other walking legs, often considerably so . . . . . ***Pinnixa***
   Third walking leg little, if any, longer than other walking legs 3
3. Walking legs diminishing in size from distinctly largest first to smallest last leg; carapace about twice as broad as long, oval, flattened and rather firm; buccal mass subtriangular . . . . . ***Parapinnixa***
   Walking legs similar shaped, second and third nearly equal in length; carapace suborbicular, or flattened and firm in small stages 4
4. Buccal mass subquadrate; carapace somewhat orbicular and either smooth and membranous or firm and covered with short pile . . . . . ***Pinnotheres***
   Buccal mass subtriangular; carapace firm, smooth . . . . . ***Pinnaxodes***

Subfamily Pinnotherinae

Carapace usually not markedly transverse. Ischium of external maxillipeds either rudimentary or indistinguishably fused with merus to form single piece, usually oblique, occasionally nearly transverse; palp not so large as merus-ischium (Rathbun 1918b).

Genus *Dissodactylus* Smith 1870

Rathbun 1918b:114.—Hemming 1958b:31.

Key to Species

1. Dactyls of walking legs 1–3 bifurcated less than halfway to base . . . . . ***D. crinitichelis***
   Dactyls of walking legs 1–3 bifurcated halfway to base . . . . . ***D. mellitae***

Dissodactylus crinitichelis Moreira

Fig. 350

Dissodactylus crinitichelis Moreira 1901:37, pl. 3, figs. 1–4.—Rodrigues [da] Costa 1971:260.—Coelho and Ramos 1972:196.—Schmitt, McCain, and Davidson 1973:17.—Powers 1977:120.

Dissodactylus encopei Rathbun 1901:22, fig. 5a-e.—1918b:119, text-figs. 67a-e, pl. 27, figs. 1–4.—Williams, McCloskey, and Gray 1968:56, fig. 12.

Recognition characters.—Carapace about 1.4 times wider than long, posterior width little less than greatest width. Dorsal surface nearly naked and polished, strongly convex longitudinally, slightly so transversely. Anterolateral margins and front smoothly arched, former marked by slightly raised line continued somewhat mesioposteriad on carapace beyond rounded lateral angles. Posterolateral margins slightly convergent, posterior margin sinuous. Ventrolateral margins of carapace and margin of female abdomen clothed with soft hair. Outer maxillipeds very small; inner distal angle of propodus fitting against thickened, hairy inner angle of

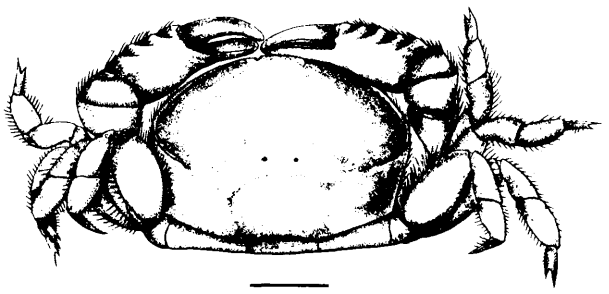

Fig. 350. *Dissodactylus crinitichelis* Moreira. Male in dorsal view, 2 mm indicated (from Moreira 1901).

merus; merus-ischium subspatulate, curved; propodus about as long as carpus, widening distally, truncate and bearing short, stumpy dactyl at distal, inner angle.

Chelipeds short, stout, upper and outer surfaces of propodus and carpus crossed by oblique rugae fringed with hair; hand elongate, subcylindrical, upper margin nearly straight, lower margin sinuous; fingers deflexed, grooved edges meeting when closed, tips acute, crossing, tooth at base of dactyl fitting in sinus of fixed finger. Walking legs lightly fringed with long hair, dactyls 1–3 curved, bifurcate less than halfway to base and acuminate; that of last leg straight, styliform.

Male abdomen with segments 1–2 fused and very slightly constricted at middle, segments 3–6 fused, sides slightly convex, telson equilaterally triangular; female with all segments free, 3–6 nearly equal in width, triangular telson broad and short.

Measurements in mm.—Carapace: male, length 4.6, width 6.6; female, length 5, width 9 (Rathbun 1901).

Habitat.—Fine white sand, coral and broken shell bottoms; sea grass (*Halodule*); commensal in various parts of its range on the echinoids *Encope emarginata*, *E. michelini*, and *Clypeaster subdepressus*; to 52 m (summarized by Schmitt, et al. 1973; Powers 1977).

Type-locality.—Estado de Rio Grande do Sul, Brazil.

Known range.—Southeast of Cape Lookout, N. C.; off northwest Florida; Caribbean Sea and South America to Rio de la Plata, Argentina (Coelho and Ramos 1972).

Remarks.—Ovigerous females are known from west Florida in March, Barbados in June, and Jamaica in September (USNM).

***Dissodactylus mellitae* (Rathbun)**

Fig. 351

Echinophilis mellitae Rathbun 1900a:590.
Dissodactylus mellitae.—Rathbun 1918b:117, text-fig. 66, pl. 28, figs. 7–8.—Hay and Shore 1918:444, pl. 36, fig. 1.—Williams 1965:209, fig. 192.—Schmitt, McCain, and Davidson 1973:18.—Powers 1977:120.

Recognition characters.—Minute. Carapace about ¼ wider than long, slightly wider at lateral angles than posteriorly, dorsal surface convex, smooth and polished except anterior parts slightly pubescent. Edge of front concave, fringed with short hairs. Anterolateral borders arcuate, with fine raised rim curving inward on carapace at lateral angles and continuing mesiopostériorly for some distance; posterior margin sinuous. Orbits opening mesially, eyes small. Outer maxilliped with fused, spatulate merus and ischium; outer edge of carpus arcuate; propodus quadrate.

Chelipeds short and stout; hand longer than other articles combined, cylindrical, upper and outer faces bearing few impressed, short, oblique lines with short appressed hairs extending distally; fingers considerably shorter than palm, bent inward and curved, opposable margins with tufts of short bristles; carpus with distal fringe of short hairs and an impressed line similar to those of chelae; merus short and stout, lower surface with oblique lines. First, second, and third walking legs stout, margins fringed with short hairs, dactyls bifurcated halfway to base; fourth walking legs with styliform dactyls, fringed with long hairs on margins.

Abdomen of male with first and second, and third to fifth segments partially fused, margins convex; telson subtriangular with convex sides. Abdomen of females with first segment linear, second to fourth fused; telson broadly triangular, half as wide as sixth segment, sides sinuous.

Measurements in mm.—Carapace: male, length 2.9, width 3.5; ovigerous females, length 3.3, width 4.5.

Color.—Light, with scanty dark mottlings which persist in alcohol and are then of purplish color (Rathbun 1918b).

Habitat.—This species clings to the outside of the keyhole urchin *Mellita quinquiesperforata* and the sand dollars *Echinarachnius parma* and *Encope michelini*. The crabs are easily overlooked because as the sand dollars are lifted from the water, the small crabs may move about and drop off. Shallow water to 124 m (Wenner and Read 1982).

Type-locality.—Pensacola, Fla., on *Mellita quinquiesperforata*.

Known range.—Western part of Vineyard Sound, Mass., to Charleston, S. C.; Hutchinson Island, east Florida (Camp, et al. 1977); western Florida; off Galveston, Tex. (Rogers 1968).

Remarks.—Hyman (1924a) described the first zoeal stage of this crab, comparing it to the zoea of

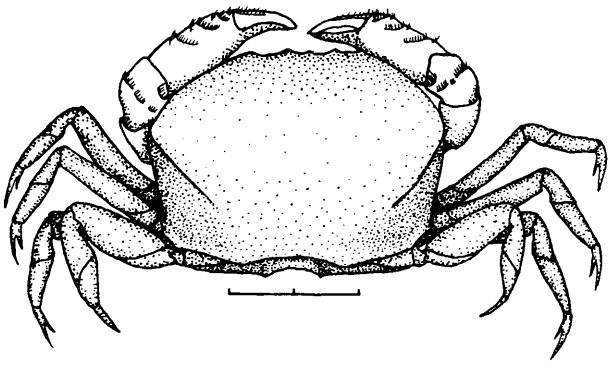

Fig. 351. *Dissodactylus mellitae* (Rathbun). Animal in dorsal view, 2 mm indicated (from Williams 1965).

Pinnotheres maculatus, and reported it as common in plankton tows in the Beaufort, N. C., area in summer. Dudley and Judy (1971) found the larvae in low concentrations off Beaufort Inlet from May to October. Ovigerous females occur there during summer, and are reported from Narraganset Bay in August (Rathbun 1918b), and in Florida from July to October (Wass 1955, in part). Sandifer (1973d) found larvae tentatively identified as *D. mellitae* only twice in plankton near the mouth of Chesapeake Bay in July and August, and Tagatz (1968) found them once in May in St. Johns River, Fla.

Dissodactylus mellitae reacts positively to host-factor of *Mellita quinquiesperforata* and also to *Encope michilini* when it is conditioned to the latter for a day or two before testing (Gray, et al. 1968). It is possible that the crab may be conditioned to any flat sand dollar, but it does not react to other echinoderms in experiments. Rate of flow of scent-bearing streams was an important factor in orienting and directing the crabs toward a host, the stronger of unequal currents being more effective. In nature, crabs dislodged from a host are seldom far from other sand dollars and can search randomly for host-factor streams. When a crab locates a host it pounces on it and scurries to the oral side. Incidence of crabs on *Mellita* in the Beaufort, N. C., area varies from 9% to 88% ($\bar{x}$ = 33%) in surveys, with a mean of 1.22 crabs per host.

Genus *Pinnotheres* Bosc [1802]

Rathbun 1918b:62.—Hemming 1958b:36.—Schmitt, McCain, and Davidson 1973:36

Key to Species

Key to Hard-stage Males and Females

1. Carapace with striking pattern of light spots on dark background of pubescence . . . . . ***P. maculatus***
   No striking color pattern . . . . . ***P. ostreum***

Key to Posthard Females (and Male *P. maculatus*)

1. Carapace nearly naked 2
   Carapace covered with short, deciduous pubescence . . . . . ***P. maculatus***
2. Third maxilliped lacking dactyl on propodus; host mollusk *Chama congregata*, little corrugated jewel box . . . . . ***P. chamae***
   Third maxilliped with dactyl inserted behind middle of propodus; host mollusk *Crassostrea virginica*, American oyster . . . . . ***P. ostreum***

Pinnotheres chamae Roberts

Fig. 352

Pinnotheres chamae Roberts 1975:238, figs. 1–2.—1975a:243–252 (passim), figs. 1–5.

Recognition characters.—Mature female: Carapace suborbicular, widest posteriorly; smooth nonpubescent, regions undefined. Front narrow, covering eyes in dorsal view; lateral margin with dense row of plumose setae. Antennules folding beneath carapace, short 4-segmented outer ramus bearing numerous long aesthetascs, inner 2-segmented ramus bearing 2 short terminal setae and 2 subterminal setae. Antennae originating in orbits, 5-segmented. Buccal mass roughly quadrangular but crescentic in outline, much broader than long; ischium and merus of external maxilliped united; carpus or first article of palp densely setose, terminal propodus smaller.

Chelipeds symmetrical, elongate, slender; propodus setose on inner surface, palm swollen at in-

sertion of dactyl; tips of both fingers calcareous and hooked almost at right angle; prehensile edges closing closely, tip of dactyl crossing inside slightly longer fixed finger; more slender dactyl with 2 or 3 small proximal teeth and larger tooth fitting between teeth on fixed finger; latter bearing 2 teeth proximally, distal one serrate. Walking legs slender, similar in length, last leg originating slightly dorsal to preceding leg; slender tips of dactyls curved sharply inward, first 3 legs with dactyls bearing scattered short setae, that of fourth with dense row of long plumose setae on inner margin.

Abdomen wider than carapace, third and fourth segments widest.

Male unknown.

Measurements in mm.—Carapace of female: length 4.3–6.8, width 3.6–5.9 (Roberts 1975).

Color.—Ivory or cream; eyes brown, ovaries bright orange (Roberts 1975).

Habitat.—"Commensal with *Chama congregata* attached to coral nodules" (Roberts 1975).

Type-locality.—North Carolina coast.

Known range.—Known only from type-locality.

Remarks.—The above data from Roberts (1975) were taken from the holotype and seven paratype females.

Roberts (1975a) reared and described larval stages that developed from eggs on six of these females. The females were placed individually in finger bowls containing 200 ml of filtered water of 31‰ salinity at 25°C and maintained with daily changes of water until the eggs hatched. Adults were not fed. After hatching, zoeae from a single female were placed individually in plastic compartmented boxes with 50 ml of filtered water of 31‰ salinity, at temperatures of 23.5°- 28°C ($\bar{x}$ = 25.3°C) over a culture period of 22 days. A mixture of post-trochophore larvae of *Arenicola marina* obtained from egg masses held in filtered seawater for 24 h, and *Artemia* nauplii were provided as food. In addition, a mass culture was established in a large finger bowl containing 1 liter of like water and fed the same food. All larvae were examined daily as they were transferred to clean water.

Three zoeal instars and one megalopa were observed, described and illustrated. Intermolt durations were: zoea I, 3.2 days; II, 3.7 days; III, 3.7 days; megalopa, 1.5 days. The first crab stages were also described. In summarizing knowledge of the morphology of two groups of *Pinnotheres* larvae, those with carapace spines and those without, Roberts pointed out that *P. chamae* and *P. ostreum* among American species lack spines but *P. maculatus* is spined.

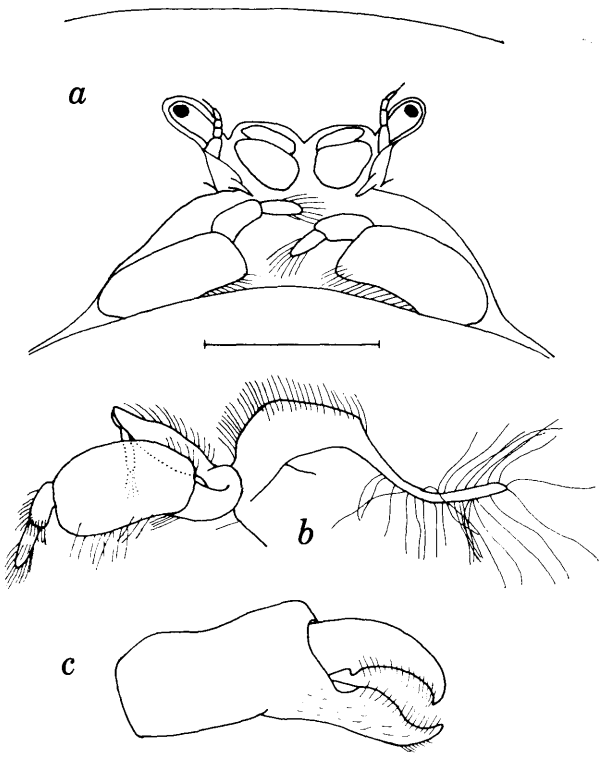

Fig. 352. *Pinnotheres chamae* Roberts. Female; *a*, Ocular and buccal regions in frontal view; *b*, third maxilliped; *c*, chela; 1 mm indicated (from Roberts 1975).

***Pinnotheres maculatus* Say**

(Mussel crab)

Fig. 353

Pinnotheres maculatus Say 1818:450.—Rathbun 1918b:74, text-figs. 35–36, pl. 17, figs. 3–6.—Hay and Shore 1918:443, pl. 35, fig. 10.—Williams 1965:206, fig. 190.—Coelho and Ramos 1972:195.—Felder 1973:74, pl. 10, figs. 10–11.—Schmitt, McCain, and Davidson 1973:53.—Fenucci 1975:167, pl. 3, figs. A, N.—Powers 1977: 123.

Recognition characters.—Mature female: Carapace suborbicular, somewhat broader than long, thick and firm but not hard, convex, smooth; surface uneven, covered with short, dense, fragile, woolly hairs. Gastrocardic area higher than, and separated by depression from, branchiohepatic area. Front slightly advanced, approximately ⅕ width of carapace, subtruncate in dorsal view, slightly bilobed. Orbits small, subcircular, eyes spherical. Antenna longer than width of orbits; antennules large, obliquely transverse. Buccal mass roughly quadrangular, crescentic, much broader than long; ischium and merus of external maxilliped united;