to those of other dromiids and of the Brachyura and Anomura generally, concluding that Hypoconcha along with other dromiids is an anomuran, not a brachyuran, while recognizing that this placement has long been controversial.

In temperature tolerance experiments, specimens collected from an offshore reef southeast of Cape Lookout, N. C., in September and October died after 17 h of exposure to $4^{\circ} \mathrm{C}$ (F. J. and W. B. Vernberg 1970).

## Hypoconcha sabulosa (Herbst)

Fig. 189
Cancer sabulosa Herbst 1799:57, pl.48, figs. 2-3. Hypoconcha sabulosa.-Hay and Shore 1918:418, pl. 31, fig. 3.-Rathbun 1937:44, pl. 8, figs. 3-4, pl. 9, figs. 1-5.—Williams 1965:145, fig. 120.Coelho and Ramos 1972:178.-Felder 1973:44; pl. 6, fig. 5 (key).-Powers 1977:20.

Recognition characters.-Body short, broad, flattened; surface nodulose, granulate, and marked by strong ridges ventrally. Carapace in old individuals pubescent above; margin densely hairy; armed anteriorly with 4 curved spines having sharp tips pointed obliquely downward followed by a few other smaller spines or raised tubercles; front between submesial pair of spines subtruncate or sloping slightly backward toward short, narrow, median fissure. Antennal fossae limited in front by pair of strong, oblique ridges arising between 2 of spines on anterior border, meeting each other in midline in front of epistome; epistome with posterior border raised into prominent ridge continuing on either side across front and some distance along


Fig. 189. Hypoconcha sabulosa (Herbst). Anterior part of animal in ventral view, detail of right side shown, 5 mm indicated (from Williams 1965).
sides of buccal area. Basal articles of antennae tuberculate; proximal article with strong inwardly directed tooth, distal article with tooth on each side of base of flagellum. Fissure in posterolateral margin of orbit prominent owing to development of strong ridge on either side.

Carpus of cheliped with granulate ridges, hand covered with more or less pointed tubercles. Other legs and abdomen much as in H. arcuata.

Measurements in mm.-Carapace: male, length 24, width 23; ovigerous female, length and width 22.

Variation.-The anterior spines may be obsolescent or in some cases doubled or tripled. The anterolateral spines vary in spacing.

Color.-Gray; or as described by Schmitt in Rathbun (1937), coral sand above with whitish-gray hairs, ground color beneath, red; rounded bosses on legs and subfrontal region reddish brown; eyes black or reddish brown; eggs orange.

Habitat.-About 3 to 82 m .
Type-locality.—Listed as "Africa" (probably an error).

Known range.-Off Cape Hatteras, N. C., through Gulf of Mexico to Bahia, Brazil.

Remarks.-Ovigerous females are known from Florida in February and June, and from North Carolina in October (Rathbun 1937, in part).

## Hypoconcha spinosissima Rathbun

Fig. 190
Hypoconcha spinosissima Rathbun 1933a:185.1937:46, fig. 14; pl. 10, figs. 1-2.-Felder 1973:44, pl. 6, fig. 4 (key).-Powers 1977:21.

Recognition characters.-Body short, broad, flattened; parchmentlike dorsum covered with short pubescence, solid ventral surface as well as legs usually densely hairy, especially in old individuals, and bearing tufts of coarse setae in hollow behind frontal notch, on eminence lateral to buccal angle, on distal edge of third maxillipeds and eminences elsewhere. Front subtruncate between antennae and divided by short, wide, median fissure followed by shallow furrow; anterolateral margin somewhat sinuous and densely hairy. Ventral surface beneath pubescence granulate and spiny, granules sparser on carapace than on appendages; spines erect and distributed as follows: 5 or 6 on anterolateral margin, longer spine at juncture of epistome with front; 1 very strong on posterior side of orbit, 1 strong curved above orbit; 1 or 2 on eminence lateral to buccal angle; row of small acute spines along anterior margin of buccal frame; 9 or 10 in irregular rows of palm of cheliped and 3 on carpus; 1 on


Fig. 190. Hypoconcha spinosissima Rathbun. Female in ventral view, USNM 55957, holotype, 5 mm indicated (from Rathbun 1937).
coxa and ischium of cheliped and first walking leg; row of short spines and tubercles on border of epistome; 6 or 7 slender spines on third maxilliped at outer angle of merus.

Legs and abdomen hairier but shaped much as in H. arcuata.
Meaurements in mm.-Carapace: male, length 27, width 28 ; largest female, length 27 , width 31 ; ovigerous female, length 25 , width 26 .

Variation.-Some specimens (USNM 55955 male) have a smoothly arched anterior border completely lacking marginal spines, and some nearly lack the ventral hairy covering.

Color.-Generally pinkish buff, darker parts salmon, fringing hairs primrose yellow (Rathbun 1937).

Habitat.-Sand and coarse bottom, 21 to 110 m .
Type-locality.—Off Cape Hatteras, N. C., 89.6 m.
Known range.-Off Cape Hatteras, N. C., to Gulf of Mexico off Mississippi Delta and Yucatan; Jamaica.

Remarks.-Ovigerous females are known from near Cape Hatteras, N. C., and Cape Canaveral, Fla., in October.

## Family Tymolidae

Carapace circular or subquadrate. Third maxillipeds greatly elongated, leaving no appreciable part of buccal cavern uncovered. Legs 2-3 long, slender, subequal, articles cylindrical; legs 4-5 small, filiform, dorsal in position. Female with genital openings on coxa of third leg (second walking leg); sternal grooves well developed. Abdomen of both sexes 6- or 7 -segmented. (Adapted from Gordon 1963; Sakai 1976; see also Wear and Batham 1975 for discussion of family placement.)

## Genus Clythrocerus Milne Edwards and Bouvier 1899

Rathbun 1937:109.
Carapace rounded, sternal plastron reduced. First and second maxillipeds lacking exopods. Antennules small, completely retractile in orbito-antennal cavity. Antennae short, peduncle valviform. Walking legs short. Abdomen of female broad, cupped; that of male slender.

## Key to Species

1. Front with 2 broad, platelike teeth on plane with flat, finely granulate carapace; posterolateral margin not spinulous
C. perpusillus

Front with 2 widely separated, fairly acute teeth depressed below level of coarsely granulate carapace; posterolateral margin spinulose
C. granulatus

## Clythrocerus granulatus (Rathbun)

Fig. 191
Cyclodorippe granulata Rathbun 1898a:293, pl. 9, fig. 1.
Clythrocerus granulatus.-Rathbun 1937:119, fig. 31; pl. 33, figs. 5-8.-Williams, McCloskey, and Gray 1968:45, fig. 3.

Recognition characters.-Surface of body and legs closely and coarsely granulate; front and posterior
orbital region depressed; remainder of carapace somewhat swollen, broader than long, lateral borders regularly rounded, narrowed in front and behind; a short, sharp spine above and near widest part; lateral margins, especially posterior half, fringed with slender spinules and some plumose hairs; branchiocardic sutures deep. Each half of bilobed front somewhat subdivided and edged with short, fine spinules; central notch partly occupied by extension of buccal cavity; cupped orbits oblique and deeply cut by a $V$-shaped notch above, at least
partly edged with fine spinules; eyes short.
Ischium of outer maxilliped with parallel margins, almost twice as long as merus, latter a little wider posteriorly than ischium; exognath as long as merus and widest at middle. Chelipeds rather slender, rough; both carpus and palm spinulose on inner margin in females and young males, smoother in mature males, fingers bent downward. First and second walking legs slender, cylindrical, second pair less than twice length of carapace, dactyl and propodus subequal; third and fourth walking legs shorter than carapace, propodus and dactyl of each slightly curved, dactyl flexed for grasping.

Abdomen of mature female broad, cupped; that of male slender.

Measurements in mm.-Carapace: male, length 4.4, width 4.6 ; ovigerous female, length 3.14 , width 3.8 .

Variation.—Old males in this species develop greatly elongate chelipeds which, along with the anterior parts of the carapace, are granular but less spinulose than in females or smaller males.

Habitat.-128 to 567 m .
Type-locality.—Off Trinidad, B. W. I.
Known range.-ESE Cape Lookout, and SE Cape Fear, N. C.; Honduras; southern Florida through Antilles to Venezuela and Trinidad.

Remarks.—Williams, et al. (1968) thought that variation in development of spinules in specimens from off North Carolina compared with that in specimens from tropical parts of the range might


Fig. 191. Clythrocerus granulatus (Rathbun). Male in dorsal view, legs of left side not shown, 1 mm indicated (from Williams, et al. 1968).
be sufficient to indicate specific differences between populations. Subsequent study of more material shows that there is considerable individual variation in ornamentation, the young being relatively more spinulose than adults.

Ovigerous females are known from North Carolina in January and October.

## Clythrocerus perpusillus Rathbun

Fig. 192
Clythrocerus perpusillus Rathbun 1901:90, fig. 14.1937:111, fig. 28; pl. 33, figs. 3, 4.-Williams, McCloskey, and Gray 1968:44.

Recognition characters.-Surface of body finely granulate. Carapace flat dorsally, slightly broader than long, part behind orbits almost equally narrowed anteriorly and posteriorly, regions slightly marked, margins lightly pubescent; small, sharp spine just anterior to middle of lateral margin preceded by finely granulate, slightly indented margin. Two triangular, blunt frontal teeth in same plane as dorsal surface separated by sinus about equal to reverse of either tooth, sinus partly occupied by extension of buccal cavity slightly exceeding frontal teeth. Orbits roughly quadrilateral and oblique, preorbital angle flat, inconspicuous, postorbital angle variably dentiform, eye projecting beyond orbit.

Outer maxillipeds long and narrow. Chelipeds stout and short, about 1.5 times length of carapace, palm and dactyl with inner superior crest, fingers bent strongly inward, opposed edges meeting, propodal finger strongest; carpus with prominent anteroexternal lobe. Second walking leg exceeding first by length of dactyl; propodus and dactyl of third and fourth walking legs curved, dactyl flexed for grasping.

Measurements in mm.-Carapace: ovigerous female (Barbados), length 2.56, width 2.75; ovigerous female (North Carolina), length 2.72, width 3.04 .

Variation.-Three females (2 ov) and a fragment of a fourth from North Carolina differ from Caribbean specimens in having the body slightly more rounded laterally, less granulate along margins of the carapace, the lateral spine less developed and not set off by an indented margin, and postorbital angles obsolete. These northern specimens may represent variants with spinous features less developed than in tropical members of the group, as seen in certain other brachyurans.

Habitat.-27 to 110 mm .
Type-locality.-OOff Vieques [Puerto Rico], 27.4 m.


Fig. 192. Clythrocerus perpusillus Rathbun. Female in dorsal view, fifth leg only of left side shown, 1 mm indicated (UNC-IMS 2076).

Known range.-SE Cape Fear, N. C.; Bahama Banks; Vieques; Barbados.

Ovigerous females are known from North Carolina in January and from the Bahama Banks and Barbados in May.

## Superfamily Homoloidea

## Family Homolidae

Crabs with carapace rectangular, ovoid or urnshaped, longer than broad. Eyes incompletely sheltered by orbits when retracted, terminal article of eyestalks either longer or shorter than slender basal article. External maxillipeds pediform, subpediform or suboperculiform. Sternum of female without longitudinal grooves. Gills $8,10,13$ or 14 on each side (Rathbun 1937, modified after Gordon 1950).

## Genus Homola Leach 1815

Rathbun 1937:62.-China 1966:204.-Zariquiey Alvarez 1968:304.-Manning and Holthuis 1981:25.

## Homola barbata (Fabricius)

Fig. 193
Cancer barbatus Fabricius 1793:460.
Homola barbata.-Hay and Shore 1918:419, pl. 30, fig. 10.-Williams 1965:146, fig. 121.-Zariquey

Alvarez 1968:304, figs. 12g, 106c.-Coelho and Ramos 1972:178.-Powers 1977:22.-Manning and Holthuis 1981:25.
Thelxiope barbata.-Rathbun 1937:63, fig. 16, pl. 15, figs. 1-2.

Recognition characters.-Carapace about $1 / 4$ longer than wide; surface granulate, spinulose, and sparsely setose; linea anomurica distinct and dorsal; sides nearly straight, only slightly convergent posteriorly, and extending almost vertically downward from spiny ridge running backward from behind strong spine situated at extremities of suture separating gastric and hepatic regions. Rostrum small, bifurcate at tip; 1 spine on each side at base of rostrum, 1 at outer orbital angle, transverse row of 2 behind rostrum, behind these a transverse row of 8, and farther back a small median spine. Anterolateral parts below and behind orbits with small spines. Eyestalks long, slender at base, and abruptly enlarged below cornea.
Chelipeds of moderate size, surface granulate and hairy; merus and carpus with rows of spines. Bases of legs grouped behind midlength of carapace, placed in a dorsally curving arc on each side with fifth not only dorsal but slightly anterior to fourth. First to third walking legs with flattened articles, long, hairy and spinulose along margins. Last legs folded forward over back and subchelate.

Second segment of abdomen with large, median, conical tooth.
Measurements in mm.-Carapace including rostrum: male, length 30 , width at base of lateral spines 22 , posterior width 16 ; female, length 33 , width at spines 25 , posterior width 20 .
Color.-"Body covered with tawny or yellowishbrown or reddish-brown hair; spines red or partly red" (Rathbun 1937).

Habitat.-55 to 682 m .
Type-locality.-Bay of Naples.
Known range.-Off southeastern Massachusetts to Rio de Janeiro, Brazil; eastern Atlantic Ocean from Portugal and Azores to Cape Verde Islands and Angola; South Africa; Mediterranean Sea.

Remarks.-Gordon (1950) discussed the anatomical structure of the spermathecae of females and copulatory apparatus of males in the genus Thelxiope (=Homola) and remarked upon the evolutionary sequence shown by these structures in the Dromiacea.

Hartnoll (1970) observed and filmed swimming individuals collected and held in the laboratory at Naples. The first, second and third walking legs beat in the frontal plane of the crab, successively stroking and feathering in planes above each other. Duration of the backward propulsive stroke is the


Fig. 193. Homola barbata (Fabricius). Animal in dorsal view, 1 cm indicated (from Smith 1887).
same as that of the forward recovery stroke. Legs of each side beat in sequence, 3-2-1, with a lag of about $1 / 3$ of a cycle between successive legs. The opposite legs of a pair beat about half a cycle out of phase. The crab swims quite rapidly and in a controlled manner, but only for short periods since it appears to fatigue rapidly. Both chelipeds and fifth legs are held in a folded position during swimming. Observation in a tank suggests that swimming is an escape reaction from benthic predators, in which case short bursts would be adequate.

In the western Atlantic Ocean ovigerous females are known nearly year round: off Nicaragua in February; Cape Canaveral, Fla., in April, and variously North Carolina to Yucatan Channel from May to September; Martha's Vineyard, Mass., in August, Delaware Bay in October, and Surinam in September.

Larvae are described from both plankton and rearing experiments. Rice and Provenzano (1970) reared seven zoeal stages in plastic trays at $20^{\circ} \mathrm{C}$ and $36.2 \%$ salinity from a female taken in Yucatan Channel. None of the larvae reached the megalopa stage, and molts were more variable than is usual in such experiments, with peaks at about 9.5 , 17.5, 26.5, 37 and 48 days after hatching. The specimen that molted to 7th stage did so on the 67th day after hatching and it is estimated that it might have molted to megalopa in another two weeks, although the bizarre-shaped last stage may have been an extra stage induced by unfavorable conditions. The zoeal stages lasted about 11 weeks. Earlier, Rice (1964) described large zoeae and a
megalopa held through one molt from plankton taken in the Straits of Florida which were identified as $H$. barbata. This megalopa lived 27 days before transforming. Thus, total larval development of this species may last 15 weeks.
Differences between the western Atlantic larvae and others from the Mediterranean Sea and South Africa (Rice and Levetzow 1967) suggest that the east and west Atlantic may harbor separate species of Homola, differing more as larvae than as adults. Further, the views of Williamson (1965; 1967) were confirmed by the rearing experiments, indicating that the Homolidae appear to be related to the Raninidae and are close to the line of descent of the true crabs, but that the family Homolidae is well separated from the much more primitive Dromiidea and from typical Anomura.
In temperature tolerance experiments, specimens collected from a reef area SE of Cape Lookout, N. C., in September and October died after 7h exposure to $4^{\circ} \mathrm{C}$ (F. J. and W. B. Vernberg 1970).

## Family Latreilliidae

Carapace pyriform, extremely narrowed anteriorly and drawn into elongate gastric region, not covering bases of legs; basal article of ocular peduncle much longer than terminal article; each supraocular spine very long, divergent, with short deflexed rostrum between; linea homolica absent; 8 gills on either side; walking legs extremely long and slender; female abdomen with broadened segments 4-6 fused into cupped plate. (Wright and Collins 1972; Guinot 1978).

## Genus Latreillia Roux 1830

Rathbun 1937:73.-China 1966:256.

## Latreillia manningi Williams

Fig. 194
Latreillia elegans-Smith 1881:419.—1883:23.1884:35 [7], pl. 2, figs. 2, 2a; pl. 3, fig. 1.1886:637 [33].-Hay and Shore 1918:419 (part).-Rathbun 1937:73, fig. 18, pl. 21, figs. 18 (part).-Chace 1940:10.-Williams, McCloskey and Gray 1968:43, figs. 1A-D (part). Powers 1977:23 (part).
Latreillia manningi Williams 1982:233, figs. 1b-c, $2 a-$ $e, 3 a, 8$.

Recognition characters.-Carapace pyriform, finely granulate; front drawn out into 2 long, divergent
horns between which a small, spinelike rostrum projects obliquely downward; each horn variably spinulose, with spine on lower side near proximal third; anterior margin of carapace with acute spine projecting downward at base of eyestalks. Eyes large, pyriform, at end of slender stalks about as long as supraorbital horns. Third maxillipeds slender and somewhat pediform.

Legs long, almost filiform, with ischial and propodal articles spinulose. Chelipeds about twice as long as body and about half as long as third walking legs, hand slightly longer than carpus, dactyl slightly less than half as long as palm. Last legs dorsal in position but not folded over back.

Abdomen in both sexes broad; female having first segment with median tubercle, second with strong median spine, third with stout spine on each lateral margin, third and remaining segments fused; abdomen of male with 6 distinct segments, spines lacking except for median spine on second segment.

Measurements in mm.-Carapace: male, length 6.510.9 , width $3.9-6.6$; female, length $8.25-12.25$, width 5.6-7.25 (Williams 1982).

Habitat.-Mud, sand, shell, sponge, and fine coral bottoms, $82-474 \mathrm{~m}$ (Williams 1982).

Type-locality.-American Shoal Light, Florida, about 10 mi . N by $\mathrm{W}^{1 / 2} \mathrm{~W}, 192-201 \mathrm{~m}$.

Known range.-Nantucket Shoals off Massachusetts to off Havana, Cuba; Venezuela; Ascension I.; Frost (1936) reported a megalopa off Newfoundland.

Remarks.-Williams (1982) revised the genus Latreillia sensu lato, finding that L. elegans Roux, formerly considered to range through the Atlantic and Mediterranean, is restricted to the eastern Atlantic while the western Atlantic form was unde-


Fig. 194. Latreillia manningi Williams. $a$, Body of male in dorsal view, 5 mm 'indicated; $b$, cheliped; $c$, first walking leg; $d$, fourth walking leg; 5 mm indicated (from Williams, et al. 1968).
scribed. The latter, named L. manningi, is a less robust species, though there is some overlap in all features examined except in relative length of the legs.

Ovigerous females are known in February and May off Florida, April and August off Massachusetts, and October off Venezuela.

Cano (1893) described two larval stages of a La treillia which can be attributed to elegans, a metazoea and a megalopa with branched horns, and he compared these to the Thalassinidea and Paguridea. Frost (1936) described a megalopa from 100$m$ depth off Newfoundland that was identified by R. Gurney. This was taken in a year marked by reduced Arctic current and a consequent influx of warm water.

## Superfamily Raninoidea

Anterior thoracic sterna broad, posterior thoracic sterna narrow and keel-like. Posterior thoracic epimera largely exposed by reduction of branchiostegite. Female openings on coxae. Last pair of legs dorsal in position, normal or reduced in size. Posterior abdominal appendages absent in males, pleopods absent from first abdominal segment of females, uropods absent (in adults). Last thoracic segment fused with others. Sternal canal present. Thoracic nerve ganglion-chain elongate. Antennary sternum triangular, spout-shaped. Gills 8 on each side (Bourne, 1922; modified from Števčić, 1973).

## Family Raninidae

Carapace remarkably elongate but not covering abdominal terga, first 4 or 5 terga lying exposed in dorsal plane of body. Last pair of legs also raised in dorsal plane of body. Antennae and antennules large, not folding into fossettes. Vasa deferentia protruding through bases of fifth pair of legs; oviducts piercing coxa of third pair of legs. Sternum broad anteriorly, narrow or linear posteriorly. A pair of respiratory orifices between tergum of first abdominal segment and coxae of last pair of legs. External maxillipeds completely covering buccal cavity, with palp concealed in repose; exopod but little longer than ischium. Gills less than 9 in number on each side. Hand flat, fixed finger extremely bent allowing dactyl to close against anterior border of hand. (Modified after Alcock 1896, and Rathbun 1937.)

Because of aberrant shape and organization, the systematic position of raninids as well as their phy-
logeny has been interpreted in various ways (Glaessner 1969). The group has many specializations in structure and function related to burrowing in substrate, consequently it is difficult to establish which characters are primitive and which are derived. In his very readable review, Števčić (1971) regarded as secondary features the elongated body, prolonged mouthparts, narrow sternum and incompletely flexed abdomen, all related to the burrowing habit. He concluded that these are crabs which branched off the brachyuran ancestral lineage after the primary organizational level of crabs was reached. He pointed out that their larvae (citations in individual accounts below) combine brachyuran and anomuran features that tend to
link them with the homolid crabs, placing them, in his view, in an isolated position within the Brachyura near or somewhat above the Dromioidea within the Dromiacea rather than in the Oxystomata as arranged by Glaessner (1969). The first raninids occur in the Lower Cretaceous. The group as a whole rose to a peak in numbers during the Tertiary, later declining to the living forms, but the fossil forms are remarkably similar to the modern ones (Glaessner 1960, 1969). Ancestors of the raninids are not known with certainty, but according to Števčić must have been at a higher level of organization than recent forms, thus the raninids are products of regressive specialization. (See also Wear and Batham 1975.)

## Key to Subfamilies, Genera, and Species

1. Frontoorbital border more than half width of carapace; carapace smooth or partly covered with transverse lines; 8 pairs of gills . . . . . . . . . . . . 2
Frontoorbital border less than half width of carapace; carapace eroded on anterior half; 7 pairs of gills . . . . . . . . . . . . . . . . . . . [Subfamily Symethinae] Symethis variolosa
2. Orbits of moderate size, slightly oblique and situated on anterior border of carapace, ocular peduncle folded almost transversely or longitudinally; last pair of legs slender . . . . . [Subfamily Ranininae] Raninoides loevis Orbits large, deep cavities in lower side of carapace forming inverted $V$ with point at rostrum, ocular peduncles folded strongly and obliquely downward and backward; last pair of legs not slender.
[Subfamily Notopodinae; Ranilia] 3
3. Hand of cheliped with spine on upper margin . . . . . . . . . . . R. muricata

Hand of cheliped without spine on upper margin. . . . . . . . R. constricta

## Subfamily Symethinae

## Genus Symethis Weber 1795

Rathbun 1937:24.
This genus is known as fossil from the Paleocene of Alabama (Glaessner 1969).

## Symethis variolosa (Fabricius)

Fig. 195
Hippa variolosa Fabricius 1793:476.
Symethis variolosa.—Rathbun 1937:26, fig. 10; pl. 5, figs. 7-8.—Gomes Corrêa 1970:10, pl. 5, figs. 3847; pl. 6, figs. 48-55; pl. 7, figs. 61-62.-Coelho and Ramos 1972:179.-Powers 1977:25.

Recognition characters.-Body almost entirely covered with densely packed, tiny granules. Carapace irregularly narrow-ovate, convex from side to side and anteroposteriorly, abruptly elevated transversely behind frontal region with edge of
shoulder thus formed drawn into 5 anterior processes more or less separated by eroded depressions, floor of latter and other symmetrically arranged depressions on anterior half more coarsely but sparsely granular than other surfaces; frontoorbital border less than half width of carapace, front proper trilobate and produced anteriorly, median lobe largest, a few stiff submarginal hairs along its sides; rounded tooth at outer side of orbit separated from anterolateral tooth by concave depression. Eyes short and rudimentary but with pigmented cornea. Antennules small and concealed by massive antennal peduncles meeting along midline; latter having first article partly fused with carapace, second article with prominent, triangular prolongation longer than mesial ramus terminating in short flagellum.

Chelipeds fairly long; palm swollen, fingers longer than palm, bent mesioventrally, cutting edges sharp and armed with widely separated acuminate teeth progressively stronger distally, tips hooked. Articles of remaining legs intricately modeled and


Fig. 195. Symethis variolosa (Weber). $a$, Female in dorsal view, walking legs of left side not shown; $b$, tip of rostrum; $a, 5 \mathrm{~mm}$, $b, 0.5 \mathrm{~mm}$ indicated (USNM 155091).
densely fringed with hair except for thinner, sic-kle-shaped dactyls, last one least strongly curved.
Abdomen short and relatively narrow.
Measurements in mm.-Carapace: male, length 25 , width 15.5 ; female, length 31 (est.), width 20.
Variation.-The pattern of erosion on the carapace varies and the chelipeds become somewhat more sculptured with age.

Color.-General color white; 2 pink spots in front, 2 light brown spots at middle and 2 green spots behind. Splotched with vinaceous-cinnamon. (Henderson and Schmitt in Rathbun 1937.)
Habitat.-Calcareous algae, occasionally sand (Coelho and Ramos 1972); shell hash (Goeke 1981); 18 to 137 m .

Type-locality.—"In oceano Indico."
Known range.-SE Cape Lookout, N. C., $34^{\circ} 10^{\prime} \mathrm{N}, 76^{\circ} 10^{\prime} \mathrm{W}$, through western Gulf of Mexico (Goeke 1980) to Bahia, Brazil; Fernando de Noronha.

Remarks.-Both Cain (1972) and Cerame-Vivas and Gray (1966) listed this species from reef structures in tropical water off North Carolina, and F. J. and W. B. Vernberg (1970) found that animals
collected from this reef in September and October succumbed after $17-\mathrm{h}$ exposure to $4^{\circ} \mathrm{C}$ water. Coelho (1966c) corrected the impression that the species is extremely rare in the Brazilian part of its range, finding 13 specimens at 8 stations in 27-90 m depths. Goeke (1981) further discussed the species, separating it from an east Pacific congener, described the spermathecal pits as most primitive in a series progressively coalesced in other raninids, remarked on the structure of the male pleopods and the reduced gill count, and placed the genus in a distinct subfamily.
Ovigerous females are known from southeastern Florida in July.

## Subfamily Notopodinae

Serène and Umali 1972:24, 29.-Manning and Holthuis 1981:7.

## Genus Ranilia H. Milne Edwards

Rathbun 1937:17.
Carapace broadly oval. Orbits invisible from above, together forming inverted V directed obliquely ventrad from rostrum; eyes stout. Antennae directed forward, basal article somewhat dilated mesially. Outer maxillipeds with third article longer than second. Sternal plastron linear between second legs, broadened to slightly concave, hexagonal disk between third and fourth pairs. Last (fifth) legs not remarkably reduced.

This genus has a fossil record dating from the Eocene of Hungary and the Tertiary of EuropeNorth America, but neither of the living species from the Western Atlantic has been reported as fossil (Glaessner 1969).

## Ranilia constricta (A. Milne Edwards)

Fig. 196
Raninops constrictus A. Milne Edwards 1880:35.
Ranilia constricta.-Rathbun 1937:20, pl. 4, fig. 5; pl. 5, figs. 1-2.-W. E. Pequegnat 1970:180.Powers 1977:24.-Manning and Holthuis 1981:7, figs. 1-2.
Ranilia atlantica.—Monod 1956:631, figs. 17-18.
Recognition characters.-Resembling R. muricata. Carapace oval, strongly convex from side to side, drawn to a rounded midsagittal peak anteriorly but more arched posteriorly, slightly convex from front to back; smooth posteriorly but microscopically granulate and with numerous faint, transverse,
lightly granulose wrinkles anteriorly. Rostrum slender, extending beyond innermost anterior spine; beaded anterior border of carapace with 4 spines, innermost overhanging base of orbit and fourth slightly behind external angle of front strongest, second and third reduced. Eyestalks strong, about 4 times as long as rostrum and capable of being turned back into deep, oblique orbits. Antennules small. Antennae directed forward, slightly longer than eyestalks.

Bases of legs grouped behind midlength of carapace, arranged in a dorsally curving arc on each side with fifth anterodorsal to fourth. First pair of legs subchelate, stout, flattened dorsally; merus squamous denticulate above with strong spine on superodistal margin; palm almost smooth above; distal margin of hand perpendicular, toothed; dactyl strong, smoothly curved; articles except dactyl with granulose wrinkles laterally. Dactyl of second and third pairs of legs flattened triangular, of fourth leg irregularly falciform, and of fifth narrowly and asymmetrically ovate.

Abdomen short and narrow.


Fig. 196. Ranilia constricta (A. Milne Edwards). $a$, Female in dorsal view, walking legs of right side only shown; $b$, right cheliped and first walking leg, external view; 3 mm indicated (UNC-IMS 2506).

Measurements in mm.-Carapace: female, length 22.8, width 15.7 (Rathbun 1937).

Variation.-In some specimens the rostrum extends slightly beyond the innermost anterior spines of the front but in others it exceeds these spines by fully half its length. There is also variation in the eyestalks, those of some larger specimens being relatively more slender than those of smaller ones. These ill-defined differences may be attributable to growth.

Habitat.-Shallow reef water to 365 m .
Type-locality.—Near Sombrero (Florida?), 86 m (see Rathbun 1937).

Known range.-SE of Cape Fear, N. C., $33^{\circ} 42^{\prime} \mathrm{N}$, $76^{\circ} 39.5^{\prime} \mathrm{W}, 140 \mathrm{~m}$; Palm Beach, Fla., to Florida Straits and Yucatan Channel; Cuba; off Barbados; Ascension Island; eastern Atlantic from Sierra Leone and Annobon Island (Manning and Holthuis 1981).

Remarks.-A specimen from Cuba (USNM 48642) was caught with a handline on a reef. There appears to be great resemblance between this species and $R$. fornicata from the Pacific.

## Ranilia muricata H. Milne Edwards

Fig. 197
Ranilia muricata H. Milne Edwards 1837:196.-Hay and Shore 1918:420, pl. 31, fig. 1.-Rathbun 1937:18, pl. 3, figs. 3-6, pl. 4, figs. 1-4.-Williams 1965:142, fig. 117.-Powers 1977:24.

Recognition characters.-Carapace strongly convex from side to side, slightly so from front to back, smooth posteriorly but with numerous transverse, ciliated granulose wrinkles anteriorly. Rostrum slender; anterior border of carapace with 4 strong spines on each side, innermost overhanging base of orbit, third surmounting external angle of orbit, fourth at external angle of front. Eyestalks strong, about 4 times as long as rostrum and capable of being turned back into deep, oblique orbits. Antennules small. Antennae directed forward, slightly longer than eyestalks.

Bases of legs grouped behind midlength of carapace, arranged in a dorsally curving arch on each side with fifth anterodorsal to fourth. First pair of legs subchelate, stout, flattened distally, squamousdenticulate above with strong spine on superodistal margin of merus and palm; distal margin of hand perpendicular, toothed; dactyl strong, curved; members except dactyl with granulose wrinkles laterally. Second, third and fourth pairs of legs with flattened, triangular dactyls. Fifth pair of legs with flattened, narrowly ovate, asymmetrical dactyl.


Fig. 197. Ranilia muricata H. Milne Edwards. Ovigerous female in dorsal view, first to fourth legs of right side shown, only fifth leg of left side shown, 5 mm indicated (from Williams 1965).

## Abdomen short and narrow.

Measurements in mm.-Carapace: male, length 39, width 28 ; female, length 28 , width 22.

Color.-Porcelain white with red, vermiculate, tranverse lines on cephalothorax, and red dots and blotches on legs. Gibbes in Rathbun (1937) gave the color of dry specimens as purplish mixed with yellow and orange in places, particularly about the articulations and spines, with the latter having white tips and the chelipeds, remaining legs and abdominal segments with purplish markings.

Habitat.-This species appears to be confined to sand bottoms offshore. Specimens have been obtained in dredge hauls, and fragments of others have been taken from fish stomachs off North Carolina; 12 to 102 m .

Type-locality.—Unknown.
Known range.-Off Cape Lookout, N. C., $34^{\circ} 43^{\prime} \mathrm{N}$, $76^{\circ} 40^{\prime} \mathrm{W}$, to northwestern Gulf of Mexico (Goeke 1980) and Colombia; Swan Island.

Remarks.—Rathbun (1937) reported ovigerous females in April from Florida, and in September from North Carolina.

Individuals collected from a reef SE of Cape Lookout, N. C., in September and October withstood experimental exposure to temperature of $4^{\circ} \mathrm{C}$ for 7 h but died after 17-h exposure (F. J. and W. B. Vernberg, 1970).

Randall (1967) reported $R$. muricata from stomach contents of the mutton snapper, Lutjanus analis.

## Subfamily Ranininae

Serène and Umali 1972:25, 34.

## Genus Raninoides H. Milne Edwards 1837

Rathbun 1937:7.

## Raninoides loevis (Latreille)

Fig. 198
Ranina loevis Latreille 1825:268.
Raninoides loevis.-Rathbun 1937:8, fig. 3, pl. 1, figs. 1,2.-Guinot-Dumortier 1959:426, figs. 2a-b.Powers 1977:25.
Raninoides laevis.-Knight 1968:164-168 (passim), pl. 4, figs. a, b.-Glaessner 1969:502, fig. 3135a, b.-Goeke 1980:147.

Recognition characters.-Carapace elongate obovate, strongly arched transversely, nearly twice as long as broad, surface mostly smooth, regions undefined; frontoorbital border slightly less than greatest width; 4 sinuses of front continued on carapace as narrow, cilia-outlined grooves, those bordering 3-toothed rostrum slightly convergent posteriorly; tooth lateral to rostrum shorter than submedian tooth; lateralmost sinus slightly divergent; outer orbital tooth bifid, its inner branch short, dentiform, outer branch with long, slender, inward curved tip not reaching level of intermediate tooth; hepatic spine slender, slightly curved. Eyes with small, distinct stalks broadly dilated at base, orbits slightly oblique. Antennules about equal to antennae; latter with stout peduncle not concealing that of antennules, flagellum slender. External maxillipeds with merus usually shorter than ischium and edges slightly thickened and raised. Sternum broad to level of third legs, narrowed between third to fifth legs.
Chelipeds with spine near distal inner end of ischium; curved spine at inner end of ischium; curved spine at inner distal extremity of merus; carpus with


Fig. 198. Raninoides loevis (Latreille). a, Anterior part of carapace in dorsal view; $b$, distal half of right cheliped, upper surface (from Rathbun 1937).

2 unequal spines placed obliquely-transversely on distal half, outer one largest; similar spine distally on outer margin of palm and 4 irregular spines on inner margin; about 13 small spines on prehensile edge of fixed finger and a small proximal spine on outer margin of slender, slightly curved dactyl. Last (fifth) legs short, slender, arising in advance of fourth pair. Dactyls of walking legs flattened, second and third curvilinearly triangular, fourth broadly falcate, reduced fifth lobate.

Abdomen of both sexes with 7 separate segments. (Modified after Rathbun 1937.)
Known range.-S Cape Hatteras, $35^{\circ} 03.2^{\prime} \mathrm{N}$, $75^{\circ} 35.1^{\prime} \mathrm{W}$; around Gulf of Mexico and southern Caribbean Sea, including Leeward Islands, to Bahia, Brazil (Coelho and Ramos 1972; USNM).

Remarks.-Glaessner (1969) listed fossil Raninoides from the Oligocene-Miocene of northwestern North America, Chile and the East Indies. Raninoides loevis (the ligatured oe in Latreille's monograph is distinct from ae) resembles $R$. benedicti Rathbun, the characters upon which Rathbun separated the species being superficial ones that change with age, but male gonopods of the two are distinct, indicating a clear separation. Moreover, specimens from the Pacific formerly determined as $R$. loevis have been shown to be $R$. benedicti (see Guinot-Dumortier 1959; Knight 1968), thus the former is confined to the western Atlantic, the latter to the eastern Pacific.

Ovigerous females are known from west Florida in December and Dominica in March. Larvae of $R$. benedicti collected in September off Mexico were reared through four zoeal and a megalopa stage in about two months, each of the two major developmental steps requiring about a month for completion. From these and other plankton samples ranging from Baja California to Colombia, Knight (1968) described and illustrated larval development. Development of the Atlantic species is undoubtedly similar.

## Section Oxystomata

Epistome reduced or absent. Efferent branchial channels terminating at middle of buccal area, buccal cavern produced forward and generally elongate-triangular in shape, efferent channels enclosed by elongate lamellar process of exopods of first maxillipeds. Afferent branchial openings either in front of bases of chelipeds, or at sides of endostome. Gills 6 to 9 on each side. Antennules folding either longitudinally or obliquely, rarely transversely. Male genital ducts protruding through bases of fifth legs or through fifth thoracic sternum nearby. (Modified after Alcock 1896 in Rathbun 1937.)

## Superfamily Dorippoidea

## Family Dorippidae

Carapace typically flat, not hiding much more than half of abdominal terga. Antennae large. First 2 pairs of walking legs remarkably long and stout; last 2 pairs of legs reduced and subdorsal in position. Genital opening of female sternal, male coxal. (Adapted from Rathbun 1937; Sakai 1976.)

## Subfamily Ethusinae

## Genus Ethusa Roux 1828

Rathbun 1937:77.—China 1966:255.
Carapace flat, truncate-oblong, broadest posteriorly, covering little more than first 2 thoracic sterna; tooth or spine at anteroexternal angle; hepatic region small; front consisting of 2 laminar teeth, each bifid. Large antennules folding obliquely and projecting beyond fossae. Antennae with basal article inserted between eyestalk and basal antennular article but at slightly lower level, flagellum long. Buccal cavern elongate-triangular, not reaching front; its basal $3 / 4$ covered by third maxillipeds having completely exposed palp, but its distal $1 / 4$ covered by stout, foliaceous processes of first maxillipeds. Efferent openings widely open in front of bases of chelipeds. Chelipeds in male often unequal. First and second walking legs long and usually rather stout; last 2 pairs short, rather slight, arising dorsal to other legs and bearing small hooklike dactyls. Abdomen of male narrow with segments 3-5 fused or partly so; that of female triangular with 7 free segments, first 3 visible in dorsal view. (After Rathbun 1937.)

## Key to Species and Subspecies

1. Eyestalks long, extending beyond anterolateral spine

> . E. mascarone americana

Eyestalks short, not extending beyond anterolateral spine
.....-2
2. Dactyls of first and second walking legs flattened . . . . . E. microphthalma Dactyls of first and second walking legs not flattened. . . . . . . E. tenuipes

## Ethusa mascarone americana A. Milne Edwards

Fig. 199
Ethusa americana A. Milne Edwards 1880:30.
Ethusa mascarone americana.-Rathbun 1897c:109.— 1937:78, pl. 22, fig. 2; pl. 23, fig. 2.-Williams, McCloskey, and Gray 1968:43, fig. 2.-Coelho and Ramos 1972:179.-Powers 1977:28.
Ethusa mascarone.-Bouvier 1898:65 (part).
Recognition characters.-Carapace longer than broad, regions well marked, branchial and cardiac regions equally raised; surface of body very finely granulate. Front between orbits 0.4 times as wide as distance between anterolateral angles and divided into 4 sharp, well-separated spines equally advanced, median notch deeply V-shaped; anterolateral angles broad at base but tapering to slender, acute spine; projecting obliquely forward. Eyes prominent, rather slender, directed obliquely for-


Fig. 199. Ethusa mascarone americana A. Milne Edwards. Male in dorsal view, legs of left side not shown, 5 mm indicated (from Williams, et al. 1968).
ward beyond anterolateral spine, cornea dilated; orbit broadly oblique, dorsal margin sinuous.

Chelipeds of male very unequal; major carpus and chela inflated and ovate in external view but hand compressed; fixed finger about $1 / 8$ length of palm, longer dactyl closing obliquely, opposed edges of fingers gaping and toothless; minor chela smaller and slender, hand scarcely stouter than carpus, slightly compressed fingers grooved, bent inward and downward, opposed edges toothless. Chelipeds of female equal and shaped as smaller one in male.

Measurements in mm.-Carapace: male, length 7.0, width 5.8 ; female, length 10.7 , width 9.4 (Rathbun 1937).

Habitat.-Shallow water to 95 m .
Type-localities.-West Florida, 23.7 m , and West Florida, $26^{\circ} 16^{\prime}$ N, 36.6 m .

Known range.-S of Cape Lookout, N. C. $\left(34^{\circ} 06^{\prime} \mathrm{N}, 76^{\circ} 15^{\prime} \mathrm{W}\right.$ ) to Gulf of Mexico and West Indies; Maranhão to Bahia, Brazil; Golfo de California; Taboga Island, Panama.

Remarks.-Ovigerous females are known from Key West, Fla., in June.

## Ethusa microphthalma Smith

Fig. 200
Ethusa microphthalma Smith 1881:418.—Rathbun 1937:82, pl. 22, fig. 3; pl. 23, fig. 3.-Chace 1940:10.-Pequegnat 1970:175.-Powers 1977: 28.

Recognition characters.-Carapace with anterior part less than half as broad as posterior swollen branchial region; dorsal surface slightly convex, pubescent, regions not deeply separated but cervical groove well marked; body microscopically granular. Front between orbits half or less than half as wide as distance between prominent anterolateral angles and divided into 4 similar and nearly equidistant, spiniform teeth, less advanced than spiniform anterolateral angles, V-shaped median sinus deeper than submedian sinus. Eyes small,
barely visible in dorsal view, cornea terminal, not expanded, pigment black.

Chelipeds of males very unequal. Major cheliped with stout, swollen hand about 4 times higher and 2.5 times thicker than minor one; fingers much shorter than palm, tapering to tips, opposed edges oblique and unarmed. Minor cheliped and those of female small and slender, hand scarcely stouter than carpus, basal part smooth and nearly cylindrical, fingers alike, as long as palm, strongly compressed, longitudinally grooved, slightly curved mesially, opposed edges nearly straight, very finely and regularly toothed. First 2 pairs of walking legs twice as long as minor cheliped and nearly naked; dactyl longer than propodus, slightly curved, strongly ribbed, much compressed laterally, of nearly uniform breadth to short distance from acuminate tip. Third and fourth walking legs nearly alike, less than half length of first and second, slender, covered with short pubescence except on short, strongly curved dactyls.

Measurements in mm.-Carapace including spines: male, length 26 , width 28 ; female, length 26 , width 27 (Rathbun 1937). Unsexed specimen, length of carapace 65 mm [?] (Fowler 1951).

Variation.-Southern specimens are (generally) much larger than northern, have the carapace thickly covered with a short, soft pile, and the edge of the front concealed by a fringe of short hair


Fig. 200. Ethusa microphthalma Smith. Male in dorsal view, second to fifth legs of right side not shown completely; 1 cm indicated (USNM 66829).
walking legs subequally 4 -sided, ribbed, not compressed. Third and fourth walking legs shorter and (Rathbun 1937). Chace (1940) pointed out that his specimens from Cuba had anterolateral spines not reaching as far forward as the frontal spines.

Color.-Carapace salmon under dense cream-buff pubescence; cornea gray; tips of fingers white, legs light flame scarlet, darkest on dactyls to lightest on proximal half of back of merus (Schmitt in Rathbun 1937).
Habitat.-Rarely $20 \mathrm{~m} ; 83$ (Wenner and Boesch 1979) to 752 m (W. E. Pequegnat 1970).

Type-locality.-Off Martha's Vineyard, Mass, 260.6 m, Stn. 878, Fish Hawk, $39^{\circ} 55^{\prime} \mathrm{N}, 70^{\circ} 54^{\prime} 15^{\prime \prime} \mathrm{W}$.
Known range.-Off Martha's Vineyard, Mass., to Cuba and around Gulf of Mexico (Pequegnat, et al. 1971).
Remarks.-Chace (1940) pointed out allometric changes in proportions of the carapace. The shallowest known occurrence is that documented by Fowler (1951) off Atlantic City, N. J., along with a figure of the specimen. Ovigerous females are known in June off the Mississippi River Delta, and in July, October and November near the Florida Keys.

## Ethusa tenuipes Rathbun

Fig. 201
Ethusa tenuipes Rathbun 1897c:11.-1937:87, pl. 24, fig. 3; pl. 25, fig. 3.-Williams, McCloskey, and Gray 1968:44.-Powers 1977:28.

Recognition characters.-Carapace with anterior part much narrower than posterior swollen branchial region; dorsal surface nearly smooth, slightly convex, cardiac region slightly raised, variably hairy, especially on marginal areas. Front between orbits half as wide, or less, than distance between prominent anterolateral angles and divided into 4 nearly similar and equidistant, slender teeth slightly exceeding anterolateral angles. Eyes visible from dorsal view in V -shaped orbits, cornea shorter than eyestalk but of good size.

Chelipeds of males very unequal. Hand of major cheliped with upper and lower margins convex, fingers much shorter than palm, tapering to tips, opposed edges oblique and toothless, lower margin of fixed finger straight. Minor cheliped small and slender; hand scarcely stouter than carpus, slightly compressed, a shallow groove along upper external surface; fingers compressed, grooved, with slight proximal gape and regularly dentate opposed edges. Chelipeds of female equal and shaped


Fig. 201. Ethusa tenuipes Rathbun. $a$, Female in dorsal view, legs of left side not shown completely; $b$, male right chela and carpus, external view. $a$, USNM 66815, 5 mm ; $b$, USNM 19855 , holotype, 2 mm indicated.
as smaller one in male. Dactyls of first and second more pubescent, dactyls extremely short.

Measurements in mm.-Carapace: male, length 7.1, width 5.6 ; ovigerous female, length 11 , width 11.1 (Rathbun 1937).

Variation.-Proportions of the carapace change noticeably with age, and relative lengths of frontal teeth and anterolateral angles vary individually.

Habitat.-25 to 216 m .
Type-locality.—Off Key West, 91.5 m .
Known range.—ESE Cape Lookout, N. C. (94-77 m ); East Florida to Gulf of Mexico E of Mississippi River Delta; Cuba (Chace 1940).

Remarks.-Ovigerous females are known in April from Cuba (Chace 1940), May from Florida, and July from North Carolina and Florida.

## Superfamily Calappoidea

## Family Calappidae

Oxystomata of normal crablike form with abdomen hidden beneath thorax. Antennae small. Afferent openings of gill chambers in front of chelipeds. Outer maxillipeds not completely closing buccal cavity. Male openings coxal on fifth pair of legs.

Calappid species are known from the Cretaceous to the present in North America (Rathbun 1935).

## Key to Genera and Some Species

1. Chelae dissimilar; large tooth on dactyl and pair of protuberances on propodus of major chela [Subfamily Calappinae] 2
Chelipeds essentially symmetrical, no unusually enlarged teeth or protuberances.
[Subfamily Matutinae] 4
2. Posterolateral region of carapace expanded into dentate, winglike projection

Calappa
Posterolateral region of carapace not expanded into dentate, winglike projection
3. Merus of cheliped bispinous on distal outer surface with lower spine strong and greatly extended laterally

Acanthocarpus alexandri
Merus of cheliped not bispinous on distal outer surface; carapace subcircular, small spine at lateral angle

Cycloes bairdii
4. Carapace considerably broader than long, regularly convex above

Hepatus
Carapace nearly as long as broad, dorsal surface uneven . . . . . . Osachila

## Subfamily Calappinae

Merus of external maxillipeds almost never elongate and acute, never concealing palp in repose. Legs adapted for walking (Alcock in Rathbun 1937).

## Genus Acanthocarpus Stimpson 1871

Rathbun 1937:220.

## Acanthocarpus alexandri Stimpson

Fig. 202
Acanthocarpus alexandri Stimpson 1871a:153.-

Rathbun 1937:221, pl. 69, figs. 1-2.-Chace 1940:26.-Williams 1965:156, fig. 137.-W. E. Pequegnat 1970:177, fig. 6-3.-Coelho and Ramos 1972:181.—Felder 1973:42, pl. 5, fig. 9.— Powers 1977:29.

Recognition characters.-Carapace ovate, regularly convex, widest in anterior half; surface uneven, granulate and punctate, with protuberances arranged longitudinally in roughly 5 rows centrally, and 2 shorter, intercalated rows behind orbits; all rows formed into ridges, those adjacent to midline each terminating in a spine on posterolateral margin. Posterior margin arcuate bearing low eminence at middle; inferior margin of pterygostomian region with row of 7 to 11 strong, widely spaced, oblique ridges of varying length. Orbits large, margins ciliated.

Chelipeds strong, dissimilar; merus bispinose on distal outer surface, inferior spine strong and a little longer or shorter than half width of carapace, superior spine about $1 / 4$ to $1 / 3$ length of inferior spine; hand with superior crest of 7 closely placed teeth, and oblique 6 -toothed crest on outer surface extending from base of dactyl to posteroinferior angle, scattered tubercles between crests; inner surface of hand with stridulating ridge composed of about 45 oblique, closely placed striae which can be played against oblique ridges of pterygostomian region. Walking legs smooth. Sternal plastron with conical tubercle on either side of first article.


Fig. 202. Acanthocarpus alexandri Stimpson. Male in dorsal view, walking legs of left side not shown, 1 cm indicated (from Williams 1965).

Measurements in mm.-Carapace: male, length 41, width 42.2; female, length 39, width 41 (Chace 1940).

Color.-Dorsal surface of carapace and chelipeds pale reddish orange, deepest in hue on elevations of carapace and bases of meral spines of chelipeds; underparts white, slightly tinged with red (Rathbun 1937).

Habitat.-68 to 476 m .
Type-locality.—Off the Quicksands, Florida Keys, 135 m .

Known range.-Georges Bank off Massachusetts to west coast of Florida; Puerto Rico to Grenadines; Rio de Janeiro, Brazil (Coelho and Ramos 1972).

Remarks.-W. E. Pequegnat (1970) stated that this is by far the most abundant calappid that he collected in deeper water of the Gulf of Mexico. Ovigerous females are known off Florida in June-July (Rathbun 1937), and elsewhere in the Gulf of Mexico off northwest Florida in July-August, Mississippi Delta in October, and Texas in November (W. E. Pequegnat 1970).

The stridulatory apparatus was described in detail by Hansen (1921) and reviewed along with that in other members of the genus by Guinot-Dumortier and Dumortier (1960).

## Genus Calappa Weber 1795

Rathbun 1937:197.—China 1966:254.
Carapace strongly convex, rounded in front; posterolateral, clypeiform expansions or wings concealing flexed walking legs beneath. Front small, somewhat triangular, bilobed, projecting little if at all beyond level of small, circular orbits. Eyestalks short, thick. Antennules nearly vertical. Basal article of antennae broad, filling hiatus at inner angle of orbit. Outer maxillipeds gaping, exposing mandibles and lamellar processes of first maxillipeds. Chelipeds very large, subequal, closely fitted internally to carapace; merus with transverse winglike external expansion; compressed palms with dorsal crest, fingers of major chela with stout projecting lobule. Abdomen of adults with segments 3-5 fused. (Modified after Rathbun 1937.)

## Key to Species

1. Orbits not separated from antennular sockets; surface may be moderately ridged or roughened. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2 Orbits completely separated from antennular sockets; surface quite rough, covered with rounded protuberances and granulate . . . . . C. angusta
2. Carapace without flattened tooth or spine at either end of posterior margin; intermediate area on lower half of palm of cheliped concave, smooth or
moderately granulate, not directed obliquely upward distally
Carapace often with flattened tooth or spine at either end of posterior margin; intermediate area on lower half of palm of cheliped smooth or moderately granulate, somewhat narrow proximally but widening and continued obliquely upward distally
C. sulcàta
3. Darker part of color pattern on carapace in interlacing bands on anterior half, becoming obliquely longitudinal stripes and fading somewhat on posterior half
C. flammea

Darker part of color pattern on anterior of carapace becoming reticular in pattern at midlength but fading posteriorly
C. ocellata

## Calappa angusta A. Milne Edwards

Fig. 203
Calappa angusta Milne Edwards 1880:8.-Hay and Shore 1918:421, pl. 31, fig. 7.—Rathbun 1937:210, pl. 64, figs. 1-6.-Williams 1965:154, fig. 134.-Türkay 1968:251.-W. E. Pequegnat 1970:177.—Powers 1977:30.

Recognition characters.-Carapace 0.75 to 0.9 times as long as wide; anterolateral margins finely granulate with larger granules at intervals; surface covered with protuberances, granulate between. Tooth at posterolateral angle of winglike extension of carapace largest, preceded anteriorly by 4 teeth successively diminishing in size, and followed posteriorly by 2 or 3 smaller teeth successively diminishing in size, all with beaded edges. Orbit completely separated from antennular cavity.

Chelipeds with outer surface of palm not divided into 3 zones as in succeeding species, only lower and upper zones evident; upper margin with 6 to 8 teeth. Abdomen of either sex with sixth segment subquadrate; telson subtriangular, slightly longer than wide.

Measurements in mm.-Carapace: male, length 34, width 45 ; female, length 28 , width 33.

Variation.-Posterior part narrower than middle of carapace in juveniles, wider than middle in adults.

Color.-Ground color buff to buff yellow; high spots or lumps on carapace and chelipeds red. Marginal spine of carapace, crest of chela and lumps on crest drab. Hairs of carapace, especially those of hind margin, light olive yellow; those of walking legs light citrous yellow. Merus of chelipeds practically colorless. Underparts whitish, pterygostomian region and maxillipeds suffused with pale purple (Schmitt in Rathbun 1937).

Habitat.-More abundant offshore than in inshore waters; 14 to 210 m , rarely deeper.

Type-locality.—Barbados.
Known range.-Off Cape Lookout, N. C., through eastern and southwestern Gulf of Mexico, to Venezuela (Türkay 1968) and Grenada.


Fig. 203. Calappa angusta A. Milne Edwards. Animal from North Carolina in dorsal view, 1 cm indicated (from Williams 1965).

Remarks.-Ovigerous females have been taken from southern Florida in March.

Calappa angusta is the most unevenly granulate and tuberculate of the four species of Calappa treated here, having a central longitudinal ridged area but lacking other definite dorsal ridges. The roughness tends to be retained in adults. The teeth on the posterolateral wing of the carapace are rather blunt and there are three progressively smaller teeth behind these on the posterior margin. Flattened submesial spines or teeth on the posterior margin over the abdomen are lacking. The outer face of the chelae is rough and not zoned as in C. flammea.
In temperature tolerance experiments, specimens collected from an offshore reef southeast of Cape Lookout, N. C., in September and October died after 17 h of exposure to $4^{\circ} \mathrm{C}$ (F. J. and W. B. Vernberg 1979).

## Calappa flammea (Herbst)

Figs. 204-205
Cancer flammeus Herbst 1794:161, pl. 40, fig. 2.
Calappa flammea.-Hay and Shore 1918:421, pl. 31, fig. 8.-Holthuis 1958:148, figs. 28-35.—Wil-
liams 1965:152, figs. 130-131.-Felder 1973:43, pl. 5, fig. 11.—Powers 1977:30.

Recognition characters.-Carapace 1.14 to 1.42 times broader than long, varying from smaller to larger ratio with increasing size; surface granular, less conspicuously so in posterior half, tuberculate anteriorly, becoming obsolescent in adults; branchiocardiac grooves distinct. Front deeply notched anteriorly, projecting somewhat beyond orbits; anterolateral borders together forming semicircle in younger individuals, less strongly arched in adults. Posterolateral winglike expansions of carapace distinct, consisting of 5 broad teeth with beaded edges, fourth and fifth largest.

Chelipeds with outer surface of palm divided into 3 horizontal zones: lower zone with many large granules; intermediate zone, slightly sunken, with no large granules but with scattered small ones, more in some males than females; third zone occupying whole upper half of outer surface of palm, separated from intermediate zone by row of small, granules, bearing many small granules and some large low granular tubercles, more densely granulated than intermediate zone in females, same in both in males. Upper margin of large hand with about 7 teeth, 6 on small hand; proximal teeth broad, low, and bifurcated. Palm with strong tooth on outer lower surface near carpus, apex of tooth approximately rectangular with sharp tip. Fingers of crushing hand somewhat stouter than on cutting hand, and with prominent projecting lobule near base of each. Merus with strong 4-toothed crest parallel with outer distal border.

Male with abdomen narrow; third to fifth segments fused, fifth segment with basal width twice median length, sixth with width greater than length, telson with length about 1.5 times width. Female with few granulations near lateral border of fourth


Fig. 204. Calappa fammea (Herbst). Female from Tortugas, Fla., in dorsal view, approx. $\times 0.66$ (from Holthuis 1958).
segment; length of telson equal to or slightly greater than width.

Measurements in mm.-Carapace: male, length 99, width 136 ; female, length 106 , width 135.

Variation.-Juveniles may look quite unlike adults, having five low longitudinal crests on the carapace interrupted by irregularly spaced elevations; elsewhere there is uneven granulation and tuberculation. On the posterior border there are two low teeth between the submesial elevations and the posterolateral spines on each side. In juveniles, teeth with beaded edges on the winglike posterolateral expansions have acute tips; in adults, the second and third teeth may be sharp but lack pointed apices, and the fifth develops a shoulder on the inner basal part.

Color.-Ground color of carapace gray behind, shading to drab mottled with white over greater portion; reddish blue on outer surface of chelipeds becoming almost white on lower half of palm and on fingers; inner surface of chelipeds, pterygostomian regions, anterior surface of first walking legs, and small part of second walking legs reddish hued. Carapace with color pattern variable, purplish brown in interlacing bands on anterior half, obliquely longitudinal stripes on posterior half becoming lighter posteriorly. Merus, carpus, and proximal upper portion of palm striped with purplish brown, 2 distinct round spots of same color in middle of palm; upper half of palm with spots and patches of sulphur yellow on teeth and tubercles and same color mixed with ground color of merus, carpus, and part of carapace; 2 or 3 orange spots on hands near base of dactyls and spots of same near articulation of palm and carpus. Third to fifth legs, and underparts whitish. (Adapted from R. L. Barney in Rathbun 1937.)

Habitat.-This strikingly colored crab does not often occur within estuaries, but is often brought up from a few meters depth in the ocean. Those obtained in sounds or lagoons are usually small. Hildebrand (1955) listed the species as common from 10 to 30 m on the Campeche Banks. The species may spend much time buried in sand (Pearse, et al. 1942). Surface to 73 m , rarely to 262 m (Wenner and Read 1982).

Type-locality.—America.
Known range.-Woods Hole region, Mass., to Florida Keys: Gulf coast of United States and Mexico; Bahamas; Bermuda.

Remarks.-This species has a fossil record in North America dating from the Oligocene (Rathbun 1930b; Ross, et al. 1964).

The breeding range of the species extends as far northward as Cape Hatteras, but larval stages often drift beyond to southern New England. Some of


Fig. 205. Calappa flammea (Herbst). $a$, Male first pleopod in abdominal view, $\times 3$; $b$, male second pleopod in sternal view, $\times 3$; $c$, abdomen of male, approx. $\times 0.8$; $d$, abdomen of female, approx. $\times 0.8$; $a-c$ from Tortugas, Fla., $d$ from Bahama Islands (from Holthuis 1958).
these larvae are supposed now and then to survive a mild winter and develop by the next summer into the small individuals which have at intervals been taken on the coast of Massachusetts, Rhode Island, and New York. Some of the larval stages have been figured by Lebour (1944). Smith (1880b) gave a description of the megalopa of this species.

Members of the subfamily Calappinae, particularly Calappa, possess a large tooth on the dactyl and a pair of protuberances on the propodus of the right cheliped. With these modifications and an associated behavior pattern, these crabs can efficiently open shells of gastropods and other mollusks and feed on soft parts of enclosed hermit crabs (Shoup 1968). The crab moves over sand searching with the ambulatories, especially the first two. Intensity of search increases near food. The crab grasps the shell of a mollusk, usually trapping it between the chelipeds and the body. Using the chelae and first two pairs of legs, the crab rolls the shell over several times, frequently inserting dactyls into the aperture. The shell is normally held on the crab's right side, oriented with the aperture directed dorsally and supported by the first two pairs of walking legs. The crab grasps the edge of the aperture with the chela and positions the shell for insertion of the large tooth of the right dactyl, then inserts the tooth in the aperture, with the outside edge of the shell bridging the gap between the two heavy teeth on the propodus. The dactyl is then closed on the propodus and the bridging portion of the shell is broken. The shell is rolled and the breaking motion repeated until the contents are exposed and removed by the chela or maxillipeds.

Shoup, in his account of this process, pictured C. flammea but also mentioned other species of $C a$ lappa as well as Cycloes.

Complete reversal of symmetry, observed on both chelipeds of a number of specimens, has been attributed to simultaneous and approximately equal regeneration of the appendages following autotomy (Lewis 1969). Differences between these and normal chelipeds were described; the regenerated chelae are usually smaller and ornamentation is less prominent. If only one cheliped is regenerated, it becomes a minor chela no matter which side is involved.

Camp, et al. (1977) found the barnacle Octolasmis hoeki on the afferent branchial openings and $O$. mulleri in the gill chambers.

Randall (1967) reported C. flammea from stomach contents of the Nassau grouper, Epinephelus striatus.

## Calappa ocellata Holthuis

Figs. 206-207
Calappa ocellata Holthuis 1958:158, figs. 36-40.Williams 1965: 153, figs. 132-133.-Fausto-Filho 1967b:42, fig. 1, pl. J, figs. 1-2.-Coelho and Ramos 1972:180.-Powers 1977:31.

Recognition characters.-Carapace similar in size to C. flammea, having width to length ratio of 1.15 to 1.4 , varying from smaller to larger ratio with increasing size; granulations much coarser than in C. flammea, granules larger, fewer, and more widely separated. Posterolateral winglike projections distinctly set off from anterolateral margin, teeth with slender pointed tips, more slender than in C. flam-


Fig. 206. Calappa ocellata Holthuis. Male from Curaçao in dorsal view, approximately natural size (from Holthuis 1958).


Fig. 207. Calappa ocellata Holthuis. a, Male first pleopod in abdominal view, $\times 3$; $b$, male second pleopod in sternal view, $\times 3$; $c$, abdomen of male, approx. $\times 0.8 ; d$, abdomen of female, approx. $\times 0.8 ; a-d$ from Dutch West Indies (from Holthuis 1958).
mea, notch in basal part of fifth tooth inconspicuous.

Chelipeds similar to C. flammea, though second and third zones of outer palm nearly alike in both males and females. Upper margin with teeth narrower proximally than in C. flammea, and with bifurcation indistinct or absent. Palm with strong tooth on outer lower surface near carpus, apex sharply pointed with an acute tip. Teeth on crest of merus more sharply pointed than in C. flammea.

Male with abdomen narrower than in C. flammea; third to fifth segments fused, fifth segment with basal width less than twice median length, sixth with width equal to or less than length; seventh more slender than in C. flammea. Females with no granules near lateral border of fourth segment; length of seventh segment distinctly greater than width.

Measurements in mm.-Carapace: male, length 86, width 119; female, length 54, width 89.
Color.-Dark parts predominantly purple or wine red, varying from almost black to light violet or red; dark anterior portion lightening almost imperceptibly toward median transverse line in reticular pattern, but fading abruptly on posterior half, radiating lateral lines of color being continuous posteriorly but central lines interrupted on each side by superior and inferior spot of color near posterior border and base of winglike expansion, lateral lines ending in purplish spots. Areas between anterior reticulations forming ocellated light green spots which become elongate and radiate between line of color to margins, becoming nearly white posteriorly. Color varies with age and substrate (Fausto-Filho 1967b).

Habitat.-Shallow water to 80 m .

Type-locality.-Klein Bonaire, Dutch West Indies. Known range.-Cape Hatteras, N. C., to Rio de Janeiro, Brazil; Bermuda.
Remarks.-This species is much less common than C. flammea from Tortugas northward and it is easily confused with that species, which it closely resembles (Holthuis 1958). The resemblance is so close that colors are useful in distinguishing the two forms. In addition to the characters given above, the terminal aperture in the male first pleopod is more widely open in C. ocellata than in flammea and the subterminal crook in the second pleopod has a narrower arc in ocellata than in flammea.
Difference in granulation of the female fourth abdominal segment in the two species is a character of limited utility.

Randall (1967) reported $O$. ocellata from stomach contents of the eyed flounder, Bothus ocellatus.

## Calappa sulcata Rathbun

Figs. 208-209
Calappa sulcata Rathbun 1898a:289, pl. 9, figs. 3-4.-Hay and Shore 1918:422, pl. 31, fig. 6.Holthuis 1958:179, figs. 51-54.-Williams 1965:156, figs. 135-136.-Fausto-Filho 1967b:46, fig. 3, pl. 2, figs. 5-6.-Coelho and Ramos 1972:180.-Felder 1973:42, pl. 5, fig. 10.Powers 1977:32.

Recognition characters.-Carapace somewhat wider than long, covered with uniform granulations giving appearance of being smooth; 5 prominent longitudinal rows of tubercles on low to obsolescent ridges. Anterolateral margins crenulate and granulate, grading into inconspicuous posterolateral wings; teeth triangular, pointed. Posterior margin with tooth at each end near base of abdomen, sharper in males than in females, very low in adults, most slender and sharp in juveniles; third tooth of posterolateral wings extremely sharp and slender, pointed in juveniles.

Chelipeds with outer surface of palm divided into 3 zones as in preceding species; large tubercles of lower zone low and inconspicuous; zones 1,2 , and 3 each separated by row of sharply pointed tubercles; middle zone minutely granulate, extending horizontally but curving dorsally in distal part; upper zone smooth, except for 2 low, inconspicuous, granular tubercles near upper margin of palm; granulations on palm more distinct in females than in males; tooth on outer, lower, proximal surface of palm nearly rectangular in large individuals, slender and acute in smaller ones. Meral articles of


Fig. 208. Calappa sulcata Rathbun. a, Large chela in external view; $b$, female in dorsal view; 30 mm indicated (from Williams 1965).
walking legs with granules on lower surface.
Measurements in mm.-Carapace: male, length 90, width 122; female, length 92 , width 119.

Color.-Varying from dark beige to light vermilion and pink. Color diminishing in intensity from front to back, becoming yellowish white or ivory at posterior margin. Three well-marked spots on carapace, one central a little behind median transverse line, and two somewhat smaller ones laterally a little anterior to it. Central spot intense ocher with an even darker ring inside it; lateral spots having lunate darker anterior and posterior lighter parts. In dark beige specimens the three spots are nearly the same color as the carapace, but somewhat wine red with lighter shades. Dorsal part of orbit with round or elongate dark vermilion punctations (Fausto-Filho 1967b).

From a large male taken at Oregon II Stn. 17696 off mouth of Amazon River, frozen May 12, 1975, by B. B. Collette and thawed June 24 when color notes were made: Color generally as Holthuis (1958)


Fig. 209. Calappa sulcata Rathbun. a, Male first pleopod in abdominal view, approx. $\times 3 ; b$, male second pleopod in sternal view, approx. $\times 3$; $c$, abdomen of male, approx. $\times 0.8$; $d$, abdomen of female, approx. $\times 0.6$; $a-c$ from near Margarita Island, Venezuela; $d$ from Surinam (from Holthuis 1958).
and Rathbun (1937) recorded it. A $1.5-\mathrm{cm}$, round, reddish-brown spot in center of carapace and paired smaller lunate spots of similar color on each branchial region anterior to posterolateral wings in which cavity of each lunule has a yellowish hue. Many small spots on orbits, along anterior margin and crest of chelae and distalmost upper corner of cheliped carpus of granular, almost reticulated, deep reddish brown, but some tiny areas within spots showing white. Chelipeds with irregular dark area in center of each carpus and shadowy large spot with suggestion of smaller ones on upper, outer side of each palm. This surface also bears a suggestion of iridescence.

Habitat. - 22 to 183 m (Cerame-Vivas, personal communication).

Type-locality.—Off Louisiana $29^{\circ} 24^{\prime} 30^{\prime \prime} \mathrm{N}, 88^{\circ} 01^{\prime} \mathrm{W}$, 64 m .

Known range.-Cape Hatteras, N. C., through Gulf of Mexico to Sergipe, Brazil.

Remarks.-Hildebrand (1954) reported this species (under the name C. springeri) as conspicuous but never abundant in the western and northwestern Gulf of Mexico at depths off 22 to 64 m . One ovigerous female was found in May off Padre Island, Tex.

Meiss and Norman (1977a, b) compared the stomatogastric ossicles and musculature to that in penaeideans, astacideans and anomurans, finding the structure to reflect generally accepted concepts of the phylogenetic position of the brachyurans.

## Genus Cycloes De Haan 1837

Rathbun 1937:225.-Chace 1968:610.

# Cycloes bairdii Stimpson 

Fig. 210
Cyclois bairdii Stimpson 1860a:237.
Cycloes bairdii.-Rathbun 1937:225, pl. 69, figs. 3-4.-Fausto-Filho 1967b:54, fig. 7, pl. 4, figs. 16-17.-Williams, McCloskey, and Gray 1968:49, fig. 6.-Chace 1968:607(remarks).-Coelho and Ramos 1972:181.—Powers 1977:32.

Recognition characters.-Carapace slightly broader than long, broadest anterior to lateral spine, regularly convex, median regions well defined; surface densely and coarsely granulate, uneven or tuberculate, partly in longitudinal rows. Front with subtriangular, median notch, each submesial tooth slightly expanded on outer edge. Anterolateral margin with beaded edge, 5 or 6 denticles behind orbit; short sharp tooth or spine at lateral angle.

Chelipeds strong, dissimilar; outer surface of palm granular and divided into 3 zones, lower granular zone separated from intermediate zone by interrupted row of raised granules extending distally from single-toothed proximal crest, continuing distal crest of merus bearing 2 broad teeth and smaller granules; intermediate zone smoother, concave, extending horizontally but curving dorsally in distal part; upper zone rougher and with irregular larger granules trending in 3 obscurely oblique rows; upper margin with 9 teeth; dactyl of major chela with stridulating band of transverse ridges on inner surface. Fourth walking legs more flattened than preceding ones.

Measurements in mm.-Carapace: male, length 40,


Fig. 210. Cycloes bairdii Stimpson. Male in dorsal view, walking legs of left side not shown; 1 cm indicated (USNM 171465).
width 43 ; female, length 45.8 , width 49 (Rathbun 1937); fragment, width 53.5 (Chace 1968).

Variation.-Chace (1968) discussed differences in size, color pattern, granulation, extension of frontal lobes and width of abdomen, pointing out that Pacific specimens generally have more pronounced elevations than do those from the western Atlantic but that there is considerable variation even in a single locality. He also discussed possible subspecific differences between the Atlantic and Pacific populations, suggesting also that when the distributional ranges are better known, C. deweti from Saint Helena may prove to be a variant at the periphery.

Color.-Variable. Bright pale yellow, cream-buff or whitish with varied spots depending on color of crab-lemon yellow in irregular rows; bright red or crimson, especially laterally; white with posterior $2 / 3$ of each margined with purple; or with faint cinnamon or pale hazel markings. Eyestalks cream buff to purple. Chelipeds yellow or white outside with red to purple spots and a spot inside at articulation of dactyl; carpus with 1 or 2 dark spots at middle of outer side near upper margin. Walking legs yellow with bands of red and purple (Verrill and Schmitt in Rathbun 1937).

Habitat.-Burrows in sand or on reefs; 2.7 to 228 m .

Type-locality.—Cape St. Lucas, Mexico.
Known range.-Bermuda; ESE Cape Lookout, N. C., to Espírito Santo, Brazil, in west Atlantic; tip of Baja California to Ecuador and Galapagos Islands, including Clarion, Socorro and Cocos islands, in eastern Pacific.

Remarks.-Chace (1968) gave a key to the species and a nomenclatural history of the genus. Cyloes bairdii is relatively abundant off northern Brazil (Fausto-Filho and Neto 1976).

## Subfamily Matutinae

Merus of external maxillipeds elongate and acute, entirely concealing palp in repose (Alcock in Rathbun 1937).

Guinot (1966, 1967), in a revolutionary approach to relationships among the genera Aethra, Osachila, Hepatus, Hepatella, and Actaeomorpha, only two of which occur in the western Atlantic, proposed that they be united in a subfamily, Aethrinae Dana or Hepatinae Stimpson, a taxonomic unit which would bridge the parthenopid and oxystomatid lines and give some coherence to their lineages that is not accounted for in arrangements adopted by Rathbun, and modified by Glaessner (1969). While this viewpoint has merit, in a manual
of this kind which seeks to simplify complexities, it is best to retain the standard classification, leaving resolution of novel or classical approaches to the test of time.

## Genus Hepatus Latreille 1802

Rathbun 1937:234.-Holthuis 1959:173.
Carapace broad, convex, regularly arcuate anteriorly, strongly narrowing posteriorly; hepatic regions large, branchial regions small. Front nar-
row, straight or nearly so, rather prominent and situated above level of lateral border continued beneath orbits to margin of buccal cavity. Orbits small, circular, level with front. Antennules oblique. Antennae at inner angle of orbit. Buccal cavity triangular, extending to level of lower border of orbits and entirely covered by external maxillipeds, with triangular merus concealing articles distal to it. Chelipeds fitting closely against lower body surface; palms with superior crest, fingers inclined downward and inward. (Modified after Rathbun 1937.)

## Key to Species

1. Carapace covered with large, usually discrete spots (spots may be interconnected or form irregular, transverse stripes, proportionately small in juveniles); front noticeably tuberculate and truncate; Chesapeake Bay south
H. epheliticus

Carapace covered with small spots often aligned in transverse rows; front slightly tuberculate and obtusely bidentate; Georgia south, rare

## H. pudibundus

## Hepatus epheliticus (Linnaeus)

(Calico crab, Dolly Varden crab)
Fig. 211
Cancer epheliticus Linnaeus 1763:414.
Hepatus epheliticus.-Hay and Shore 1918:422, pl. 37, fig. 1.-Rathbun 1937:238, pl. 70, figs. 3-4; pl. 71, figs. 1-4.-Williams 1965: 158, fig. 140.Felder 1973:43, pl. 5, fig. 14.-Powers 1977:33.

Recognition characters.-Carapace covered with large spots, about $2 / 3$ as long as wide, convex above, regularly arcuate in front, strongly narrowed behind, almost smooth, with indistinct lines of low granules on gastric region and posterior part of branchial region. Front narrow, truncate, tuberculate, not dentate, and placed higher than continuation of anterolateral borders of carapace; anterolateral borders dentate with denticles more prominent than in $H$. pudibundus, middle denticle of each tooth projecting.

Chelipeds moderately strong; carpus and hand with lines of coarse tubercles on outer face and 3to 4-toothed crest on superior margin of hand. Dactyls of walking legs with coating of short, dense pubescence except for tip and a narrow smooth line on each side.

Measurements in mm.-Carapace: male, length 53, width 79 ; female, length 60 , width 88 .

Variation.-In a series representing successive ages a great deal of variation is shown, the granulations
being relatively much coarser and the spots more numerous and variable in color among juveniles.

Color.-Dark gray or brownish with numerous, rather large, round or irregular spots of light red (muddy lavender to light red in young) with darker borders scattered over carapace. Spots may be coalesced in transverse rows or reticulate patterns.

Habitat. - This species is often found in depths of a few meters in channels of Beaufort, N. C., harbor, though such individuals are not so numerous or large as those taken in the ocean outside. Gunter (1950) found the species in water ranging from 28.7 to $35.2 \%$ salinity. Normally buried in sandy substrate (Anonymous 1975), 2-91 m (Franks, et al. 1972).

Type-locality.-Carolina.
Known range.-Chesapeake Bay to western Bay of Campeche, Mexico (Rickner 1977); Cuba; Jamaica; Dominican Republic.

Remarks.-Though this species has been recorded in depths to 91 m , Franks, et al. (1972) found it most abundant shoreward around 22 m off Mississippi, and Hildebrand $(1954,1955)$ found it most common shoreward of the latter depth in Texas and Mexico. Hildebrand found ovigerous females rarely in July, and Rouse (1970) found one ovigerous female in southwest Florida in January. Dudley and Judy (1971) in the vicinity of Beaufort, N. C., found females with orange eggs in August and with black eggs from May to October; larvae from June to October at 1 - to 8-m depths 1.6 and 6.5 km offshore, and at 1 m in November at the latter sta-
tion; larvae present at 1 - to $8-\mathrm{m}$ depths from July to September $10-13 \mathrm{~km}$ offshore.

Earlier, Costlow and Bookhout (1962b) described five zoeal stages and a megalopa from individuals hatched and reared at $25^{\circ} \mathrm{C}$ in an array of salinities ranging from 20 to $40 \%$. Complete development took place only at 30 to $35 \%$, though some growth occurred in the other salinities. They pointed out that the adults are usually found in waters with salinity in the $30-35 \%$ range. Curiously, Kalber and Costlow (1968) and Kalber (1970) found that all the larval stages are good osmoregulators, but adults lose the ability.

Several authors noted the occurrence of the sea anemone Calliactis tricolor (Lesueur) on the carapace of this crab (Carlgren and Hedgpeth 1952; Hildebrand 1954, 1955), and Cuttress, et al. (1970) reviewed the association with this and other crabs. Calliactis tricolor lives more commonly in Puerto Rico as a commensal on Turbo and Fasciolaria shells, less commonly on Murex shells, inhabited by Dardanus venosus. Besides D. venosus, which is active toward the anemone, Petrochirus diogenes and Stenocionops furcata display extremely effective behavior patterns in transferring it. Hepatus epheliticus, on which C. tricolor lives in the Gulf of Mexico, occasionally showed rearing and rubbing of its carapace on the tentacles in response to $C$. tricolor. This led the anemone to transfer to the crab. Calliactis tricolor also transferred to $H$. epheliticus without such activity by the crab. In discussing results, the authors emphasized the variety of tactile stimuli used by different crabs. This is reflected in a flexible response pattern in the anemone.


Fig. 211. Hepatus epheliticus (Linnaeus). Male in dorsal view, legs of left side not shown, 2 cm indicated (from Williams 1965).

Gray (1957) found that H. epheliticus has a large gill area in relation to its weight. He related this large respiratory area to its active nature as compared to activity of other strictly aquatic crabs with smaller gill area. In studies of metabolic tolerance, F. J. and W. B. Vernberg (1970) showed that H. epeliticus from the Cape Hatteras area placed in $25^{\circ} \mathrm{C}$ water at $10 \%$ o salinity died within 24 h , at $20 \%$ o were moderately active after 24 h , and in $30 \%$ o were very active after 24 h . W. B. and F. J. Vernberg (1970) also showed that this species has metabolic adaptations to temperatures relating it to other species with southern affinities.

Johnson (1964) studied the histology of the male reproductive system.

## Hepatus pudibundus (Herbst)

Figs. 212-213
Cancer pudibundus Herbst 1785:199.
Hepatus princeps.-Rathbun 1937:235, pl. 70, figs. 1-2.-Guinot-Dumortier 1960:510, fig. 10.
Hepatus pudibundus.-Holthuis 1959:167, figs. 3638a, b.-Williams 1965:157, figs. 138-139.-Fausto-Filho 1967b:50, fig. 5, pl. 2, figs. 9-10.Coelho and Ramos 1972:182.-Felder 1973:43, pl. 5, fig. 13.-Powers 1977:33,34.

Recognition characters.-Carapace between $2 / 3$ and $3 / 4$ as long as broad, relatively narrower in juveniles than in adults, covered with transverse lines or small spots, strongly convex. Surface smooth in adults; juveniles with 8 distinct rows of tubercles, 3 in a transverse line in broadest part of carapace, 2 others anterior and 3 posterior. Front thick, obtuse, slightly bidentate and tuberculate (and placed higher than continuation of anterolateral borders of carapace). Anterolateral margin divided into 12 or 13 more or less rectangular teeth, denticulate on margins and not projecting; anterior portion of posterolateral margin consisting of 2 rows of tubercles placed side by side with no space between, a small blunt tooth in middle of rows and another in posterior portion of this margin.

Outer face of hands with 5 rows of tubercles exclusive of marginal ones. Dactyls of walking legs with coating of short, dense pubescence, except for tip, and a narrow smooth line on each side.

Measurements in mm.-Carapace: males, length 16-60, width 21-76; females, length $14-46$, width 18-62 (Holthuis 1959).

Color.-Light roseate to violet depending on quantity and size of spots, the pattern varying individually. Spots usually small, especially in center of carapace, but varying from scattered to ar-


Fig. 212. Hepatus pudibundus (Herbst). Female in dorsal view, approximately natural size (from Holthuis 1959).
rangement in closely ranked transverse rows whose lateral ends bend posteriorly and coalesce along lateral margin of carapace. Chelipeds with upper and external parts of palm roseate, granules varying from faded to dark vermilion spots. Walking legs banded with vermilion and orange spots (Fausto-Filho 1967b).

Habitat.-Beach to 49 m .
Type-locality.-Martinique.
Known range.-Georgia to Santa Catarina, Brazil (Coelho and Ramos 1972).

Remarks.-Fausto-Filho (1967b) gave great detail on coloration as well as a figure showing the transversely banded pattern on the carapace. The figure here shows the more scattered pattern of spots. Nomura and Fausto-Filho (1966) calculated the regression coefficient of carapace width on length for males and females, pointing out no difference between the sexes although their sample of females was much smaller than that of males.

Ovigerous females are known from Guyana and


Fig. 213. Hepatus pudibundus (Herbst). $a$, Male first pleopod; $b$, male second pleopod; $a-b$ approx. $\times 8$; $c$, abdomen of male; $d$, abdomen of female; $c$ - $d$ approx. $\times 2$ (from Holthuis 1959).

Surinam in April and September. Several of the specimens Holthuis (1959) studied carried one or more sea anemones on the carapace and one bore barnacles.

## Genus Osachila Stimpson 1871

Rathbun 1937:248.—Hemming 1958b:17.—Guinot 1966:748.-1967:828-841 (passim).

Near Hepatus in all essential characters, but differing in narrower, octagonal carapace, more or less depressed and expanded at sides; very uneven surface having usually 6 chief protuberances; and much produced front forming true rostrum. (Modified after Rathbun 1937.)

## Key to Species

1. Posterolateral margin of carapace shorter than anterolateral, thickened and raised, bearing 3 lobes including lateral angle, third lobe obsolescent . .
O. semilevis

Posterolateral margin of carapace about as long as anterolateral margin, not thickened and raised, bearing 4 lobes including angle, second lobe smallest
O. tuberosa

## Osachila semilevis Rathbun

Fig. 214
Osachila semilevis Rathbun 1916:652, pl. 36, fig. 1.Hay and Shore 1918:422, pl. 31, fig. 9.-Rathbun 1937:251, pl. 77, fig. 1.-Williams 1965:159 (not fig. 142).-Powers 1977:34.

Recognition characters.-Much like O. tuberosa. Carapace octagonal, with 6 large protuberances, 1 mesogastric, paired metagastric, 1 cardiac, very prominent paired mesobranchial; protuberances eroded, depressions nearly smooth. Anterolateral margins continued toward buccal cavity, armed with tripartite teeth, each triad with strong central tooth


Fig. 214. Osachila semilevis Rathbun. Male in dorsal view, 2 mm indicated (USNM 171469).
continuing as slight ridge onto carapace and flanked on each side by minor teeth, triads separated from each other by closed or obsolescent sutures; posterolateral margin shorter than anterolateral, thickened and raised, bearing 4 lobes including lateral angle projecting laterally as far as adjacent anterolateral tooth, third lobe obsolescent, last lobe quite prominent. Front usually with narrow but-tonhole-like sinus.

Chelipeds short, thick, tuberculate on outer face and with rough margins; hand stout, upper margin with 3 simple teeth; fixed finger thick, dactyl comparatively slender and straight. Walking legs of moderate size, more or less prismatic and lightly grooved. Abdomen narrow, eroded along margins and on last 2 segments.
Measurements in mm.-Carapace: male, length 10.5 , width 11.6 ; ovigerous female, length 13 , width 15.

Habitat.-23.7 to 91 m .
Type-locality.-Gulf of Mexico, 48 m .
Known range.—Off Beaufort, N. C., to northwest Florida.

Remarks.-This species has been recorded north of Florida only a few times, most recently by Cain (1972) from offshore reefs near Cape Lookout, N. C., and is much less abundant in collections than O. tuberosa. Ovigerous females have been taken from Florida and Georgia in August.

## Osachila tuberosa Stimpson

Fig. 215
Osachila tuberosa Stimpson 1871a:154.-Hay and Shore 1918:423, pl. 31, fig. 10.-Rathbun 1937:250, pl. 77, fig. 3.-Williams 1965:159, figs.

141 and 142 (as $O$. semilevis by error).-Guinot 1966:748-755 (passim), figs. 3, 7, 15, 17.-1967:828-841 (passim), figs. 26, 31, 35.-W. E. Pequegnat 1970:178.-Powers 1977:34.

Recognition characters.-Carapace octagonal, with 6 large protuberances, 1 mesogastric, paired metagastric, 1 cardiac, paired mesobranchial; protuberances and lateral margins finely eroded. Anterolateral margins continued toward buccal cavity, armed with tripartite teeth each with strong central tooth continuing as slight ridge onto carapace and flanked on each side by minor teeth, triads separated from each other by closed or obsolescent sutures; posterolateral margins not thickened and raised, with 4 lobes, first lobe projecting laterally slightly beyond adjacent anterolateral margin, second almost obsolescent, third and fourth progressively prominent. Maxillipeds, sternum, abdomen and bases of legs eroded.

Chelipeds short, thick, tuberculate on outer face, and with rough margins; hand stout, upper margin with 3 teeth, proximal one bifid; fixed finger thick. Walking legs more or less prismatic with sharp margin and light longitudinal grooves.

Measurements in mm.-Carapace: male, length 18.0 , width 18.8 ; female, length 18 , width 20.

Color.-" "Sand color with reddish cast, white below, claws and legs white." (Henderson in Rathbun 1937.)

Habitat.- 45 to 481 m .
Type-locality.-Five stations among the south Florida reefs (see Stimpson 1871a).

Known range.-Off Cape Hatteras, N. C., to


Fig. 215. Osachila tuberosa Stimpson. Animal in dorsal view, 3 mm indicated (from Williams 1965).
northwest Florida and Yucatan Channel (W. E. Pequegnat 1970; Springer and Bullis 1956).

Remarks.-This species is now known to occur fairly commonly on the reefs off Georgia and North Carolina. Ovigerous females are known off Georgia in June and August and at unrecorded dates off southern Florida.

Guinot $(1966,1967)$, in her discussion of the genus, gave a well-illustrated discussion employing this species for comparative purposes. As she suggested, the attribution of fig. 142 to $O$. semilevis in Williams (1965) is erroneous. It is in reality O. tuberosa and is used as the illustration for that species in this paper.

Specimens collected from reefs off Cape Lookout, N. C., in September and October died within 7 h exposure to $4^{\circ} \mathrm{C}$, demonstrating the southern affinity of the species (F. J. and W. B. Vernberg 1970). In complementary salinity tolerance experiments, first zoeae maintained at $20^{\circ} \mathrm{C}$ expired within 16 h at 10 and $20 \%$ dilution, but were very active after 48 h at $30 \%$.

## Family Leucosiidae

Crabs having carapace circular, oval, or polygonal. Eyes and orbits small, front narrow but wider than orbit. Antennules folding more or less obliquely. Antennae small. External maxillipeds completely enclosing buccal cavity, except often a small crevice in front. Afferent branchial channels occupying sides of endostome on either side of deep, median, endostomal groove serving as efferent branchial channel. Afferent channels covered by exognaths of external (third) maxillipeds, efferent channels by pair of lamellar processes of first maxillipeds. Chelipeds symmetrical. Abdomen hidden beneath thorax, commonly with third to sixth abdominal terga fused, sixth sometimes free. Vasa deferentia opening on fifth thoracic sternum near bases of last pair of legs. (Modified after Alcock 1896 in Rathbun 1937.)
Manning and Holthuis (1981) discussed the complex history of the subfamilies in the family Leucosiidae.

## Key to Subfamilies, Genera, and Some Species

1. Carapace polygonal, uneven, nodular or eroded . [Subfamily Ebaliinae] 2 Carapace ovoid or hemispherical and smooth or granular . . . . . . . . . 3
2. Posterior part of carapace lacking deep cavities (viewed posteriorly)

## Ebalia

Posterior part of carapace with deep, rounded cavity on each side (viewed posteriorly). . . . . . . . . . . . . . . . . . . . . . . . . . . . . . Speloeophorus
3. Merus of external (third) maxilliped with mesial margin less than twice length of ischium . . . . . . . . . . . . . . . . . . . . . . . . . . [Subfamily Iliinae] 4 Merus of exernal (third) maxilliped with mesial margin 2 or more times length of ischium
[Subfamily Leucosiinae] 5
4. Chelipeds slender; carapace not marbled, posterior half with 5 spines . . . .
. Myropsis quinquespinosa
Chelipeds robust; carapace marbled, posterior half with 3 spines .
Persephona mediterranea
5. Posterior half of carapace with 7 spines . . . . . . . . . Callidactylus asper Posterior half of carapace with 3 spines . . . . . . . . . . . . . . . . Iliacantha

## Subfamily Ebaliinae

Surface of carapace uneven. Chelipeds of moderate length; fingers not very thin and elongate, dactyl moving in oblique plane. Anterior margin of buccal cavity arcuate, middle part projecting beyond pterygostomian region. Epistome and infraorbital lobe well developed. Pterygostomian margin extending either slightly or distinctly for-
ward, terminating in an indentation. Merus of external maxillipeds half or more than half length of ischium measured along inner border. First abdominal segment in female often under carapace (Rathbun 1937).

## Genus Ebalia Leach [1817]

Rathbun 1937:123.—Hemming 1958b: 15.

## Key to Species

1. Carapace octagonal
E. cariosa
Carapace hexagonal or subglobular.
E. stimpsonii

## Ebalia cariosa (Stimpson)

Fig. 216
Lithadia cariosa Stimpson 1860a:238.-Hay and Shore 1918:424, pl. 32, fig. 6.
Ebalia cariosa.-Rathbun 1937:125, pl. 35, figs. 6-7.-Williams 1965:147, fig. 122.-Coelho and Ramos 1972:182.-Powers 1977:35.

Recognition characters.-Carapace convex, roughly pentagonal; front truncate, lateral angles obtuse; surface uneven and covered everywhere, including other parts of body and legs, with beadlike granules, larger posteriorly and ventrally. Front narrow, upturned, and broadly notched, connected with middle protuberances by a median ridge traversing gastric region; ridge flanked on each side by sinuous, deep, broad excavation of darker color than protuberant parts. Anterolateral margin of hepatic region sinuous, hepatic region slightly prominent, delimited posteriorly by an impressed line. Pterygostomian region with large downward pointing tooth, hardly visible in dorsal view. Posterolateral margin with broad tooth, separated from bilobate intestinal region by deep sinus; cardiac and inner lobules of branchial region strongly protuberant, separated from thick intestinal lobes by deep narrow sulcus.

Chelipeds stout, a little longer than width of carapace, joints angular; merus about as broad as hand, outer margin convex and a little irregular; hands rather small, tapering to rather slender fingers. Walking legs cylindrical. Abdomen of male narrow,


Fig. 216. Ebalia cariosa (Stimpson). Animal in dorsal view, legs of left side not shown, 3 mm indicated (from Williams 1965).
triangular, with backward-projecting spine, ridge or tubercle at proximal end of penultimate segment. Abdomen of female with penultimate segment very large, nearly circular.
Measurements in mm.-Carapace: male, length 12, width 13 ; female, length 13 , width 15 .
Color.-Light gray or buff, female occasionally with two or three small red spots on abdomen; other specimens may be pale red (Rathbun 1937).
Habitat.—Below low-tide mark to 131 m (Coelho and Ramos 1972).

Type-locality.-Beaufort, N. C.
Known range.-Beaufort, N. C., to west Florida; western Gulf of Mexico (Rickner 1977); Jamaica; northeastern South America to São Paulo, Brazil.
Remarks.-This species is occasionally found in channels in the Beaufort, N. C., harbor. The species feigns death when brought on deck in a dredge haul, and thus closely resembles the pebbles and pieces of shell among which it appears to live. Ovigerous females are found at this locality throughout the summer.

## Ebalia stimpsonii A. Milne Edwards

Fig. 217
Ebalia stimpsonii A. Milne Edwards 1880:22.Rathbun 1937:124, text-fig. 33; pl. 35, figs. 1-3; pl. 37, figs. 1-3.-Williams, McCloskey, and Gray 1968:46.-Powers 1977:35.

Recognition characters.-Integument everywhere covered with crowded, depressed granules. Carapace hexagonal, length and width subequal; rather


Fig. 217. Ebalia stimpsonii A. Milne Edwards. Female in dorsal view, legs of left side not shown, 3 mm indicated (USNM 66514).
uneven, granules smaller on anterior $1 / 3$, elsewhere a few granules prominent; front bidentate, broadly emarginate; row of outstanding granules on lateral margin; hepatic region depressed, its margin forming low, blunt prominence a little anterior to branchiohepatic suture; pterygostomian prominence farther forward, subacute; cardiac region swollen, surrounded by depression; posterolateral lobe in transverse line with middle of cardiac region; posterior margin faintly bilobed. In male, 4 posterior protuberances subrectangular, rounded at tips; in female, lobes shallower, posterior pair forming nearly horizontal line.

Chelipeds with granules coarser on merus than on hand; palm inflated proximally, fingers slender, tapering, and bent at angle to long axis of hand. Walking legs slender, covered with smaller granules.
Measurements in mm.-Carapace: male, length 5.6,
width 5.4 ; female, length 7.7 , width 7.6 .
Habitat.-Sandy mud to shelly and coral bottoms; 7.3 to 160 m (Fausto-Filho and Neto 1976).

Type-locality.—Barbados, 13.72 to .91 .45 m .
Known range.-SE Cape Lookout, N. C.; west Florida to Barbados; off mouth of Amazon R., Brazil.

Remarks.-Ovigerous females are known in March from the Bahamas and May from North Carolina and the Bahamas.

Randall (1967) reported E. stimpsonii from stomach contents of the reef squirrelfish, Holocentrus coruscus.

## Genus Speloeophorus A. Milne Edwards 1865

Rathbun 1937:141.

## Key to Species

1. Lateral portions of carapace tumid, not expanded into wings; deep cavity of carapace with only 2 openings, not visible dorsally . . . . . . S. nodosus
Lateral portions of carapace expanded into broad, flattened wings; deep cavity of carapace with 4 openings, visible dorsally . . . . . . S. pontifer

## Speloeophorus nodosus (Bell)

Figs. 218-219
Oreophorus nodosus Bell 1855:307, pl. 33, fig. 8.
Speloeophorus nodosus.-Hay and Shore 1918:425, pl. 32, fig. 5.-Rathbun 1937:142, pl. 40, figs. 1-5.-Williams 1965:148, figs. 123-124.—Powers 1977:36.

Recognition characters.-Carapace convex, roughly pentagonal or hexagonal, broader than long; posterolateral angles rounded; surface nodose, evenly and thickly covered everywhere with crowded, rounded granules. Front thick, bilobed, upturned; prominent broad ridge extending backward from front to cardiac region. Hepatic region to each side with low hump, behind this, at side of gastric region, a much larger hump, and still farther back near posterior border, another of nearly equal size; posterior humps overhanging and largely containing deep cavity at either side with opening invisible in dorsal view. Subhepatic region with nodose prominence near front, and farther back 2 others of smaller size.

Chelipeds short, stout, coarsely granulate, crested along outer margin; merus with large distal and small proximal lobe; fingers thin, flat, grooved. Walking legs with dentate or narrowly lobed crests.

Measurements in mm.-Carapace: male, length
14.8, width 19.8 ; female, length 22 , width 26.

Variation.-Carapace of males much more uneven than that of females.

Color.-Pink with a few purplish spots on carapace and rusty-brown marks on legs. Rathbun (1937) described this species as looking like a dead piece of coral overgrown with purplish and greenish algae, with patches of red ones; chelae with natural greenish cast; reticulations around whitish areas


Fig. 218. Speloeophorus nodosus (Bell). Animal in dorsal view, legs of left side not shown, 3 mm indicated (from Williams 1965).


Fig. 219. Speloeophorus nodosus (Bell). Animal in posterior view, 3 mm indicated (from Williams 1965).
of green hue; fingers dull white with reddish and whitish spots; eyes not distinguishable from rest of body; underparts dirty white, abdomen green.
Male, bluish purple.
Habitat.-Among rocks; 2.7 to 18.3 m .
Type-locality.—Unknown.
Known range.-Florida; West Indies.
Remarks.-This species is rare in the northern part of its range and was reported by Pearse and Williams (1951) from reefs off Beaufort Inlet, N. C. The species readily plays dead when brought on deck.
Ovigerous females are known from North Carolina in April and Florida in July.

## Speloeophorus pontifer (Stimpson)

Figs. 220-221
Lithadia pontifera Stimpson 1871b:115.
Speloeophorus pontifera.-Hay and Shore 1918:425, pl. 32, fig 5.
Speloeophorus pontifer.-Rathbun 1937:144, pl. 39, figs. 1-3.-Williams 1965:149, figs. 125-126.Powers 1977:36.


Fig. 220. Speloeophorus pontifer (Stimpson). Female in dorsal view, 3 mm indicated (from Williams 1965).

Recognition characters.-Carapace angular, roughly trefoil shaped, from $1 / 6$ to $1 / 3$ wider than long; surface granulate, uneven. Lateral margin of each side extended into broad wing projecting over bases of legs; anterolateral margins concave, with notch near middle; posterolateral margins broad, with deep rounded cavity to each side of intestinal region, extending toward much smaller pit on dorsal surface at side of cardiac region, narrow suture connecting cavity and pit of each side. Front narrow, produced, upturned, and with deep median sinus. Orbits small. Middorsal ridge extending from front almost to posterior margin, interrupted in middle of carapace; branchial region on each side with prominent elevation more or less divided into 2 parts, one connected by ridge to anterior angle of lateral wing, other similarly connected to posterior angle. Hepatic region small, slightly elevated; pterygostomian region prominent, with conical down-ward-pointing eminence visible from above.

Chelipeds of moderate size, somewhat crested; merus with 2 large triangular teeth on outer margin; fingers slender and curved. Walking legs granulate and tuberculate.

Abdomen tuberculate; segments 3 to 5 only partially fused; sixth segment with sharp backwardpointing, proximal spine.
Measurements in mm.-Carapace: male, length 6, width 8 ; female, length 10 , width 13 .

Variation.-This small species apparently attains a width of about 15 mm , and is extremely variable. The ridges and elevations of the dorsal surface may be sharp and conspicuous or low and rounded; the lateral angles of the lateral wings of the carapace may be produced or rounded off. The female is not so wide in proportion to length as the male, and is somewhat tumid on the outer posterior part of the lateral wings.

Color.-Pale red in middle, remainder white (von Martens, et al. in Rathbun 1937).
Habitat.-Low tide to 229 m .


Fig. 221. Speloeophorus pontifer (Stimpson). Female in posterior view, 3 mm indicated (from Williams 1965).

Type-locality.—Barbados.
Known range.-Southeast of Cape Lookout and off Beaufort, N.C., to west Florida; West Indies to Barbados.

## Subfamily Iliinae

Carapace almost hemispherical, surface only slightly uneven. So-called frontal teeth often being well-developed inner orbital angles. A median frontal tooth often present. Infraorbital lobe seldom well developed, roof of efferent branchial channel usually reaching same level. Epistome usually reduced. Margins of mouth and pterygostomian region in same transverse plane. First abdominal segment in female often under carapace (Rathbun 1937, for Philyrinae).

## Myropsis Stimpson 1871

Rathbun 1937:164.

## Myropsis quinquespinosa Stimpson

Fig. 222
Myropsis quinquespinosa Stimpson 1871:157.— Rathbun 1937:164, pl. 46, figs. 1-3.-Chace 1940:24.-Williams, McCloskey, and Gray 1968:46, fig. 4.-W. E. Pequegnat 1970:179.— Felder 1973:39, pl. 5, fig. 5.-Powers 1977:38.

Recognition characters.-Body and appendages granulate except dactyls of legs; carapace subspherical, a little longer than wide, narrowed anteriorly; front subacutely bidentate, elevated, anterior extremity of septa of branchial channels not extending beyond orbits; 5 posterior spines, median spine intestinal, intermediate pair marginal (equally long and more evenly conical in adult), outer smaller pair on branchial region over insertion of last legs with strongly upturned tip; tubercle at middle of lateral margin, another on hepatic region and between these a small granulated tubercle behind hepatic suture; hepatic region slightly swollen, cervical suture partly defined at hepatic region; cardiac and intestinal regions defined by faint furrows on either side.

Chelipeds very long and slender, densely granulate; merus longer than carapace exclusive of spine; palm broader than thick, upper face nearly 3 times as long as wide; fingers longer than palm, armed with minute acute teeth of variable size. Walking legs cylindrical and microscopically granulate.

Abdomen of male with segments 3-6 fused.

Measurements in mm.-Carapace: male, length exclusive of median spine 69 , including median spine 73 , width 68 ; ovigerous female, length including median spine 49 , width 45.

Variation.-Granules on the body vary in size and the median posterior spine is relatively longest in immature specimens; the posterolateral spines occasionally exceed the other posterior spines in length (Rathbun 1937).

Color.-Buff to yellowish white with buff yellow to pinkish tint on legs, front between eyes darker, white beneath (Henderson and Schmitt in Rathbun 1937).

Habitat. - 84 to 521 m , rarely to 1048 m (Rathbun 1937). Williams, et al. (1968) reported the species to occur mainly at depths of 120 to 160 m along the edge of the continental shelf south of Cape Hatteras and W. E. Pequegnat (1970) found it mainly between 183 and 210 m in the Gulf of Mexico, noting that it was recorded at greater depths near islands.

Type-locality.-Tennessee Reef, Florida Keys.
Known range.-South of Martha's Vineyard, through Gulf of Mexico and Caribbean Sea to Surinam.

Remarks.-Ovigerous females are known throughout the year from various parts of the range: February, Bahamas; March to May, Cuba, Florida and Panama; June, Honduras; July, North Carolina and Florida; September, Colombia and Venezuela; October, NE Gulf of Mexico; December, South Carolina and Alabama.


Fig. 222. Myropsis quinquespinosa Stimpson. Female in dorsal view, legs of left side not shown, 1 cm indicated (from Williams, et al. 1968).

## Genus Persephona Leach 1817

Rathbun 1937:151.—Hemming 1958b: 18.

## Persephona mediterranea (Herbst 1794)

## (Purse crab)

Fig. 223
Cancer mediterraneus Herbst 1794:150, pl. 37, fig. 2. Leucosia mediterranea Lichtenstein 1815:142.
Guaia punctata.-H. Milne Edwards 1837:127.Gibbes 1850:185.—Desbonne 1867:53 (in part).
Persephona punctata.—Stimpson 1859:70.-Coues 1871:123.—Rathbun 1901:97.-Hay and Shore 1918:423, pl. 32, fig. 9 (part of synonymy pertaining to northern species).-Dragovich and Kelly 1964:82.—Dudley and Judy 1971:9.
Persephone punctata.-Kingsley 1878c:324 [9].— 1880:403.—Smith 1884:349.—1887:637 [33].
Persephona punctata aquilonaris Rathbun 1933a: 184.-1937:154, pl. 42, figs. 6-7.-Behre 1950: 23.-Hildebrand 1954:267.-Holthuis 1959: 183 (part giving distribution of subspecies).Williams 1965:150, fig. 127.
Persephona aquilonaris.-Guinot-Dumortier 1959: 429, figs. 7, 9.-Tabb and Manning 1961: 600.—Fausto-Filho 1968:44.—Rouse 1970:142. —Coelho and Ramos 1972:183.—Williams 1974c:24, fig. 65.
Persephona mediterranea.-Guinot-Dumortier 1959:


Fig. 223. Persephona mediterranea (Herbst). Animal in dorsal view, detail of left side shown, 5 mm indicated (from Williams 1965).

429, 433.—Grizzle 1974:135.—Williams and Wigley 1977:10.—Powers 1977:39.

Recognition characters.-Carapace hemispherical, thickly strewn dorsally and laterally with granules of various sizes, and with 3 sharp, recurved spines, 1 at each end of posterior margin and 1 median just above posterior margin. Front narrow, broadly bidentate, produced and elevated, and with dentiform angles of branchial channels projecting slightly beyond it. Anterior and lateral regions bounded externally by row of beadlike granules broken anteriorly by single tubercle of larger size, and posteriorly extending to point nearly opposite termination of posterior margin.

Chelipeds subyclindrical in adult male, approximately 1.5 times as long as carapace; merus with many large tubercles; carpus and chela nearly smooth except on margins; chela somewhat flat and dilated; fingers weak.

Measurements in mm.-Carapace: male, length excluding posterior spine 60 , width 58 ; ovigerous female, length including posterior spine 34 , width 30.

Color.-Gray to grayish brown, with darker brownish irregular spots or marmorations; granules white or tinged with red.

Habitat.-This crab is sometimes taken in otter trawls but usually by dredging in shelly mud in relatively shallow water; 3.6 to 55 m .

Type-locality.-Erroneously, Mediterranean Sea.
Known range.-New Jersey through Gulf of Mexico and Caribbean Sea to Santa Catarina, Brazil.

Remarks.-Guinot-Dumortier (1959) pointed out that Rathbun's Persephona punctata aquilonaris is specifically distinct from her P. p. punctata, and that geographic ranges of the two overlap widely. According to Guinot-Dumortier, P. punctata has never been taken in North America, ranging from Panama (Colon, Limon Bay) through the Antilles, French Guiana to Brazil (São Paulo, see Coelho and Ramos 1972). Almost in an aside at the end of her discussion, Guinot-Dumortier pointed out that the type of the crab in the Berlin Museum represented by Herbst (1794:150, pl. 37, fig. 2) as Cancer mediterraneus has the characters found in P. aquilonaris. Both shape and spotted coloration leave no doubt of this. Although inappropriately named for a mistaken locality, the name $P$. mediterranea must stand.

The species is occasionally abundant in colonies. The purselike receptacle formed by the enormously enlarged penultimate segment of the abdomen in the female may be found filled with eggs at almost any time during spring and summer in the Carolinas. Otherwise, ovigerous females are known from Florida in February (Rouse 1970),

April and July, Texas in May and September, and French Guiana in September.

## Subfamily Leucosinae

Fingers slender, almost same diameter from base to near tip, either much longer than palm or, if shorter, of filiform slenderness; either opening and closing in vertical plane or, if in a nearly horizontal plane, tip of dactyl movable through an arc of about $120^{\circ}$; palms either short, swollen and subglobular, or tapering-cylindrical with swollen base always much broader than at origin of fingers distally (Rathbun 1937).

## Genus Callidactylus Stimpson 1871

Rathbun 1937:192.

## Callidactylus asper Stimpson

Fig. 224
Callidactylus asper Stimpson 1871:158.—Rathbun 1937:193, pl. 58, figs. 1-3.-Williams, McCloskey, and Gray 1968:48, fig. 5.-Coelho and Ramos 1972:184.—Powers 1977:37.

Recognition characters.-Carapace rounded, regularly convex except near anterior margin; upper surface ornamented with scattered, prominent granules or short capitate spinules becoming less prominent and grading into granules posteriorly; furnished with 11 or more rather blunt spines, 4 on anterior half, 7 on posterior half ( 3 in midline, 2 on posterior margin and 2 on posterolateral margins). Front short, orbit longitudinal with 3 distinct sutures on outer side extending to base of orbital tube; pterygostomian channel tridentate anteriorly and exceeding orbit. Hepatic region well defined, protuberant, toothed, surrounded by depressions and with strong toothlike eminence on its posterior part. External maxillipeds sharply granulated; exognath with convex lateral margin; endognath with lateral surface of merus concave, in female with row of strong setae on submesial longitudinal ridge of ischium arching over smooth channel anterior to brood chamber under abdomen lacking in male.

Chelipeds with hand longer than merus; palm short, pyriform, much swollen within proximally and somewhat twisted so that fingers move in oblique plane; fingers longer than palm, thin; delicate, laminate, curving upward and inward toward crossed tips, serrate on outer edge and armed on opposed edges with numerous needle-shaped teeth. Walking legs almost naked; propodi com-


Fig. 224. Callidactylus asper Stimpson. Male in dorsal view, legs of left side not shown, 5 mm indicated (from Williams, et al. 1968).
pressed with moderate laminate crests above and below; dactyls of first 3 pairs 3-edged, of last pair 2-edged and shorter and broader than others.

Abdomen of male with segments 3-5 fused; female with segments 4-6 fused, smooth and glossy around middle but a transverse tuberculate ridge on fourth and sparse granules on sixth segments; telson concave.
Measurements in mm.-Carapace: male, length 13.2 , width 11 ; female, length 17.9 , width 15.5 (Rathbun 1937).

Habitat.-Calcareous algae, sand and organic bottom, 27 to 393 m (Coelho and Ramos 1972).

Known range.-S of Cape Lookout, N. C. (Williams, et al. 1968), through SE Gulf of Mexico to Panama and southeastward to Alagoas, Brazil (Coelho and Ramos 1972).

Remarks.-Ovigerous females are known in February from Florida, March from Surinam, and October from Panama and Venezuela.

## Genus Iliacantha Stimpson 1871

Rathbun 1937:183.

## Key to Species in the Carolinas

1. Fingers about half as long as palm of hand . . . . . . . . . . . . I. intermedia
Fingers longer than palm of hand. . . . . . . . . . . . . . . I. subglobosa

## Iliacantha intermedia Miers

Fig. 225
Iliacantha intermedia Miers 1886:302, pl. 26, figs. 3, 3a.-Hay and Shore 1918:424, pl. 32, fig. 3.Rathbun 1937:186, pl. 54, figs. 1-2.-Williams 1965:151, fig. 129.-Coelho and Ramos 1972: 184.-Fausto-Filho 1975:81.-Powers 1977:37.

Recognition characters.-Similar to I. subglobosa, but carapace more coarsely granulate; posterior spines shorter, flattened, triangular, connectd by prominent line of granules. Front grooved above, broadly notched anteriorly, and with angles of branchial channels extending beyond it. Margin of carapace distinctly granulate; intestinal region not protuberant above median spine.

Chelipeds slender, nearly as long as carapace; merus cylindrical and granulate with coarser granulations proximally; hand smooth, somewhat inflated proximally but tapering to slender fingers; fingers about half as long as palm, incurved at tip, and denticulate on opposed margins. Male abdomen widened at convex-sided sixth segment.

Measurements in mm.-Male: carapace length 16, width 12 ; chela, length 13 , fingers 4 . Female: carapace length 27 , width 21 .

Color.-Gray without marking of any kind.
Habitat.- 10 to 329 m.
Type-locality.—Bahia, Brazil.


Fig. 225. Iliacantha intermedia Miers. Male in dorsal view, 5 mm indicated (from Williams 1965).

Known range.—Off Beaufort, N. C., to NW Florida; St. Thomas, V. I.; Venezuela; Ceará and Bahia, Brazil.

Remarks.-The young of this species and Persephona mediterranea have a close resemblance.

## Iliacantha subglobosa Stimpson

Fig. 226
Iliacantha subglobosa Stimpson 1871a:155.-Hay and Shore 1918:424, pl. 32, fig. 2.-Rathbun 1937:185, pl. 53, figs. 1-2.-Williams 1965:150, fig. 128.-W. E. Pequegnat 1970:179.-Coelho and Ramos 1972:184.—Powers 1977:38.

Recognition characters.-Carapace orbicular, smoothly and evenly convex, finely granulate, unarmed except posterior border with 3 spines; lateral spines subtriangular, blunt; median one higher, longer, conical, and curved upward. Front grooved above, broadly notched anteriorly and with angles of branchial channels extending beyond it. Margin of carapace distinct, somewhat acute on hepatic region and anterior portion of branchial region, indistinct beyond; hepatic region swollen; intestinal region slightly protuberant above base of median spine.

Chelipeds 2.5 times as long as carapace, excluding spine, finely granulate; merus more sharply


Fig. 226. Iliacantha subglobosa Stimpson. Female in dorsal view, 5 mm indicated (from Williams 1965).
granulate than carpus and hand; fingers slender, longer than palm, denticulate on opposed margins. Walking legs slender, smooth; merus as long as 3 terminal articles; dactyls grooved, and with 2 fringes of hair on upper and posterior surfaces. Male abdomen gradually tapering from fifth to seventh segment.
Measurements in mm.-Male: carapace length 21, width 16 ; chela, length 22 , fingers 13 .

Habitat. - 16 to 915 m (Wenner and Read 1982).
Type-localities.-Three stations in Florida reefs, 73-146 m.

Known range.-Off Cape Hatteras, N. C., to northwest Florida; through eastern Gulf of Mexico and Caribbean Sea south to Alagoas, Brazil.

Remarks.-Ovigerous females have been taken in April, June and July off Florida, May off Colombia, September off Colombia and Venezuela, and in October off Venezuela.

## Section Oxyrhyncha

Carapace more or less narrowed in front and usually produced to form a rostrum; branchial re-
gions considerably developed, hepatic regions small. Epistome usually large; buccal cavity quadrate, with anterior margin usually straight. Gills almost always 9 in number on each side; efferent channels opening at sides of endostome or palate. Antennules longitudinally folded (Rathbun 1925).

## Superfamily Majoidea

## Family Majidae

Chelipeds especially mobile, usually about same size as other legs, fingers straight. Second article of antenna well developed, generally fused with epistome and often with front. Orbits generally more or less incomplete. Hooked hairs almost always present. Male openings coxal (Borradaile 1907). Palp of external maxilliped articulated either at summit or at anterointernal angle of merus (Alcock 1895). First pleopod in male greatly exceeding second pleopod in length (Garth 1958).

## Key to Subfamilies

(Modified after Garth 1958)

1. Eyes either without orbits, or with commencing orbits . . . . . . . . . . . 2
Eyes with complete or nearly complete orbits; basal antennal article broad,
expanded to form foor to to orbit . . . . . . . . . . . . Mithracinae
2. Male abdomen terminally broadened, terminal segment subquadrate and
inserted deeply into sixth segment; male first pleopod longitudinally
grooved, with rows of filamentous setae on either side of groove. . . . .

Oregoniinae
Male abdomen not terminally broadened, terminal segment subtriangular and not inserted deeply into sixth segment; male first pleopod exceedingly varied, but not as above . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
3. Eyes without orbits; eyestalks generally long, non retractile, retractile against sides of carapace, or against acute postocular spine affording no concealment; basal (fused) antennal article extremely slender and unusually long

Inachinae
Eyes with commencing orbits; basal (fused) antennal article not extremely slender $\qquad$
4. Eyes with cupped postocular process into which eye retracts, and with supraocular eave or spine. . . . . . . . . . . . . . . . . . . . . . . . . Pisinae
Eyes lacking postocular cup, but with tubelike housing . . . . . . . . . . . . 5
5. Eyestalks long; orbit partly protected by hornlike supraocular spine or eave, strong postocular tooth, or both; body truncate in front . . . . Tychinae
Eyestalks short, relatively immobile and either concealed by supraocular spine or sunk in sides of rostrum; basal antennal article truncate-triangular; body not truncate in front

Epialtinae

## Subfamily Inachinae

Eyes without orbits; eyestalks generally long, either nonretractile, retractile against sides of carapace, or against an acute postocular spine. Basal
article of antenna extremely slender throughout its extent and unusually long. First pleopod not very stout, straight or curved, apically tapering, but apex most varying (hairy; spinose, naked, etc.; acute, blunt, bifid, etc.); second pleopod short (Garth 1958).

## Key to Genera of Inachinae

(Modified after Garth 1958)

1. Seven free abdominal segments in both sexes, rostrum double.

Anomalothir
Six free abdominal segments in male, 5 in female . . . . . . . . . . . . . . . 2
2. Rostrum double . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3

Rostrum single . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 7
3. Interantennular spine present and conspicuous . . . . . . . . . . . . . . . . 4

Interantennular spine absent or inconspicuous . . . . . . . . . . . . Collodes
4. Eyestalks slender; carapace with 3 erect median spines . . . . . Arachnopsis Eyestalks not slender . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 5
5. Seven long, capitate dorsal spines . . . . . . . . . . . . . . . . . . . . . Aepinus Fewer than 7 long, capitate dorsal spines . . . . . . . . . . . . . . . . . . . . 6
6. Spine of basal antennal article equally advanced with front. . Euprognatha Spine of basal antennal article not equally advanced with front Batrachonotus
7. Merus of outer maxilliped as broad as ischium, palp of moderate size . . 8 Merus of outer maxilliped often narrower than ischium, palp large and coarse

10
8. Postorbital tooth large, curving around side of eye . . . . . . . . . Pyromaia Postorbital tooth small, or if large not curving around eye 9
9. Carapace rough with spines and tubercles; legs not subprehensile

Carapace smooth; legs subprehensile..............................
10. Rostrum considerably less than postrostral length; basal antennal article often longitudinally sulcate

Podochela
Rostrum approaching or surpassing postrostral length; basal antennal article not longitudinally sulcate

11
11. Carapace nodulose; merus of walking legs with long distal spine; rostrum sparsely spined

Metoporhaphis
Carapace smooth; merus of walking legs with distal spine no longer than other spines; rostrum multispinose Stenorhynchus

## Genus Aepinus Rathbun

Rathbun 1925:92.

## Aepinus septemspinosus (A. Milne Edwards)

Figs. 227, 241c
Apocremus septemspinosus A. Milne Edwards 1879:185, pl. 35, figs. 5-5d.
Aepinus septemspinosus.-Rathbun 1925:92, text figs. 28-29, pl. 32, figs. 3, 4; pl. 219, figs. 1-3.-Coelho and Ramos 1972:207.-Powers 1977:43.

Recognition characters.-Carapace triangular in front half, broadly semicircular in posterior half; dorsal aspect bearing 7 capitate spines, 1 gastric, 1 cardiac, 2 branchial ( 1 on each side), 2 supraorbital ( 1 on each side, shorter), 1 directed obliquely backward on first abdominal segment; scattered tubercles; gastric region narrow, high, and with triangular laminate projection on each anterolateral slope with intervening tubercles; hepatic region steeply sloping to laminate marginal tooth preceded by triangular pterygostomian tooth. Rostrum short, formed of 2 shallowly rounded, nar-
rowly separated lobes, tuft of hooked hairs at base. Triangular tooth on partition between antennules. Eyes short, flat above, tubercle situated anteriorly in corneal emargination. Postocular tooth small, easily broken, close to carapace behind orbit. Basal antennal article deep, its prominent ventral crest bifurcating near anterior end with longer outer branch continuing to epistome and terminating in a lobe.

Chelipeds small, granulations trending in longitudinal lines; palm narrow, male with fingers slightly gaping proximally. Sternum of male with prominent crest between coxae of chelipeds and minor crests converging from walking legs, less-developed granulate line in juveniles. Abdomen of adult females with terminal segment coarsely pitted or tuberculate, with smooth median carina, younger females granulate.
Measurements in mm.-Carapace: male, length 6.0, width 7.1; ovigerous female, length 5.5, width 7.0.


Fig. 227. Aepinus septemspinosus (A. Milne Edwards). a, Body of male in dorsal view; $b$, left chela, external view; $a, 2 \mathrm{~mm} ; b, 1$ mm indicated (USNM 24150).

Variation.-Specimens from the Antilles are more delicate than those from the Gulf of Mexico and North Carolina, the former having more slender and divergent spines. Beside other variations given above, the supraorbital spines vary in direction.

Habitat.-Generally on calcareous algae, occasionally on detritus or mud bottom, 12.8 to 85 m (Coelho and Ramos 1972).

Type-locality.—Florida Strait, $24^{\circ} 55^{\prime} \mathrm{N}, 83^{\circ} 25^{\prime} \mathrm{W}$, 67.7 m .

Known range.-S Cape Lookout, N. C., $34^{\circ} 10^{\prime} \mathrm{N}$, $76^{\circ} 10^{\prime} \mathrm{W}$; SW Cape San Blas, Fla., and Bahama Banks to Bahia, Brazil.

Remarks.-Only one specimen (an empty exoskeleton, UNC-IMS 2414) is known from north of the Florida Straits; it is one of the largest and most heavily spined males seen. Ovigerous females are known in February from off Cape San Blas, Fla., Vieques [P. R.], and St. Thomas.

## Genus Anasimus Milne Edwards 1880

Rathbun 1925:64.

## Anasimus latus Rathbun

Figs. 228, $241 n$
Anasimus latus Rathbun 1894:58.-1925:65, pl. 214.-Guinot-Dumortier 1960:177, fig. 18a, b.Williams 1965:240, fig. 217.-Coelho and Ramos 1972:209.-Felder 1973:49, pl. 7, fig. 5.Powers 1977:43.

Recognition characters.-Carapace broadly ovate, elevated on median line, posterior half semicircular, anterior half broadly triangular, surface covered with unequal granules. Carapace with median row of spines, 2 gastric (posterior one larger), large cardiac, 1 small backward-pointing intestinal, and long acuminate backward-projecting spine at distal end of first abdominal segment; anterior gastric spine one of transverse row of about 5; branchial region with 3 small spines or tubercles in triangular arrangement. Three anterolateral spines, 1 hepatic and 2 branchial above base of cheliped. Rostrum short, medially carinate, broadly triangular at base, ending in short, sharp, upturned spine. Eyes large; prominent supraorbital spines separated by depression, postorbital spines long, exceeding eye in large specimens. Antenna short, slightly exceeding rostrum, basal article with terminal spine and stout spine pointing downward and forward in front of eye. Pterygostomian region with row of spines and spinules continued to antennal
segment including long spine at angle of buccal cavity. Sternum of male coarsely granulate.

Chelipeds of male more than twice length of carapace, granulate; merus cylindrical; palm swollen, shorter than fingers; fingers slender, curved inward, gaping at base only, finely and evenly toothed except for larger basal tooth on dactyl. Female with chelipeds a little longer than carapace but smaller than in male, fingers not gaping. Walking legs long, slender, cylindrical, roughened except on dactyl, with numerous short, stout, appressed spinules; propodi and dactyls with double fringe of hair.

Abdomen of male with 6, female with 5 free segments; female with median tubercle on third and fourth segments.

Measurements in mm.-Male: carapace length 34, width 32 ; length of cheliped 83 , of first walking leg 145. Ovigerous female: carapace length 25 , width 25.1.

Variation.-Adults are relatively broader than the young whose rostrum and dorsal spines are relatively longer. There is some variation in count of spines but the basic pattern is recognizable. The postorbital spines are very small, pointing directly outward, being little more than tubercles in specimens 9 mm long or less.

Color.-Recently preserved specimens show dark reddish or brown rings on the legs (Holthuis 1959).

Habitat.-This species has been taken from coarse sand, coral, coral sand, and mud and shell bottom; 27 to 274 m (Wenner and Read 1982).

Type-locality.-Gulf of Mexico, east of Delta of Mississippi River, $29^{\circ} 14^{\prime} 30^{\prime \prime} \mathrm{N}, 88^{\circ} 09^{\prime} 30^{\prime \prime} \mathrm{W}, 124.4 \mathrm{~m}$.

Known range.-Off Cape Lookout, N. C., through


Fig. 228. Anasimus latus Rathbun. Male in dorsal view, legs of left side not shown, 10 mm indicated (from Williams 1965).

Gulf of Mexico (Felder 1973) to Amapá, Brazil (Coelho and Ramos 1972).

Remarks.-Ovigerous females have been recorded from the northern Gulf of Mexico and Florida in all seasons of the year, from North Carolina in June (Williams 1965) and November (Sandifer and Van Engel 1972), the Guianas from April to August (Holthuis 1959 and USNM), and Colombia in November-December (USNM).

Sandifer and Van Engel (1972) described development of hatching eggs taken from an ovigerous female off Cape Lookout, N. C., in November. The eggs were hatched at $21^{\circ}-25^{\circ} \mathrm{C}$ and larvae reared in $32 \%$ salinity sea water on a diet of Artemia nauplii. The larvae hatched as pre-zoeae in transit to the laboratory and most of them died during this stage. Survivors had become first zoeae by the time they were segregated into culture dishes and fed. Only a few of these molted to second stage, and two molted to megalopa after 21 days. In addition to describing development of this species, the authors reviewed literature on rearing majid crabs.

Boschma (1968) described a rhizocephalan parasite from a specimen of $A$. latus caught off Surinam.

## Genus Anomalothir Miers 1879

Rathbun 1925:23.

## Anomalothir furcillatus (Stimpson)

Figs. 229, 241a
Anomalopus furcillatus Stimpson 1871a: 125.
Anomalothir furcillatus.-Rathbun 1925:24, text-fig.
6, pl. 8, fig. 2; pl. 9, fig. 2; pl. 206.-Williams 1965:236, fig. 312.-Powers 1977:43.

Recognition characters.-Carapace much elongated, almost subcylindrical, pubescent, with regularly placed tubercles. Rostrum long, from 0.66 to 1.25 times as long as remainder of carapace, bifurcated, horns contiguous for half or more of length, slightly divergent. Eyes without orbits; preand postorbital spines small, acute. Antenna visible in dorsal view, basal article narrow. Merus of maxilliped without notch at inner angle where palp inserts.

Chelipeds in adults longer than carapace; merus subcylindrical, with row of small spines below and less distinct row above; carpus with 3 spines on outer surface; palm unarmed, elongate; fingers short, stout, less gaping in male than in female. Walking legs pubescent; first 2 pairs long, slender; third and


Fig. 229. Anomalothir furcillatus (Stimpson). Female in dorsal view, legs of right side not shown, 3 mm indicated (from Williams 1965).
fourth pairs shorter, prehensile, with dactyls spinose on inner border; third pair shortest, merus with 2 or 3 strong hooked spines beneath, propodus and curved dactyl of about equal length; fourth pair intermediate in length, nearly straight, with propodus longer than dactyl.

Abdomen of both sexes with 7 free segments.
Measurements in mm.-Carapace: male, length including rostrum 18, length rostrum to base movable antennal articles 7.5 (br.), width 5.6 ; female, length including rostrum 27.6 , length rostrum to base movable antennal articles 15.0 , width 6.6.

Color.-Light orange yellow; palms much deeper color (Henderson in Rathbun 1925).
Habitat.-Rathbun (1925) listed this form from sand, broken shell, pebbled and rocky bottom; 55 to 480 m .

Type-locality.—Off "The Samboes" [southern Florida], 225 m .
Known range.-Off Cape Lookout, N. C., through eastern Gulf of Mexico and West Indies to Grenada.
Remarks.-Though the depth range of this species is usually beyond the $200-\mathrm{m}$ mark, it may occur in shallower water in the Carolinas. Ovigerous females are known from the northeastern Gulf of Mexico in March.

## Genus Arachnopsis Stimpson 1871

Rathbun 1925:89.

Arachnopsis filipes Stimpson

Figs. 230, 241d
Arachnopsis flipes Stimpson 1871a:121.—Rathbun 1925:89, text-figs. 26, 27; pl. 32, figs. 1, 2; pl. 219, figs. 4, 5.-Williams, McCloskey, and Gray 1968:58.-Coelho and Ramos 1972:206.-Powers 1977:44.

Recognition characters.-Carapace oblong, rather narrow, somewhat truncate in front; smooth and glossy except for few hairs on anterolateral part of branchial and sides of frontal and gastric regions; dorsal aspect bearing 3 erect, slender, blunt spines, 1 gastric, 1 cardiac, and 1 on first abdominal segment; spinules and spiniform granules beneath subhepatic and pterygostomian regions; often finely denticulate along margins, lateral slopes of rostral horns, around orbits and postorbital spines. Rostrum short, formed of 2 triangular teeth widely separated at tips by shallow notch often disclosing point of interantennular spine in dorsal view. Eyes long, overreaching but capable of being drawn back beneath long postocular spine directed obliquely forward; orbital arch high, occasionally surmounted by tubercle or small spine. Basal antennal article with 2 spinulous crests on inferior surface meeting anteriorly, lateral crest continued back to angle of buccal area; small, sharp anterolateral spine directed obliquely forward with movable ar-


Fig. 230. Arachnopsis filipes Stimpson. $a$, Male in dorsal view, legs of right side not shown; $b$, left chela, external view; $a, 3 \mathrm{~mm} ; b$, 1 mm indicated (USNM 18114).
ticle of antenna interposed between it and rostrum. Sternum, abdomen and maxillipeds granulate or spinose.

Chelipeds in male moderately enlarged, somewhat longer than carapace, curved; edges of ischium, merus and surface of carpus spinulous; propodus mainly smooth but sparse spinulation proximally, its upper and lower margins convex; fingers as long as palm, gaping except near tips; cutting edges toothed, largest tooth at middle of fixed finger, slightly smaller tooth preceding it on dactyl. Walking legs filiform, nearly equal in length.

Measurements in mm.-Carapace: male, length 7.9, width 5.1 ; female, length 7.5 , width 5.1 .

Variation.-A few specimens show a sometimes setose pair of tubercles or tiny clusters of tubercles in front of the gastric spines. Still fewer individuals have in addition a low median spine in front of the gastric spine as well as one between the cardiac spine and that on the first abdominal segment.
Habitat.-Rathbun (1925) reported the species from fine sand, shell, coral and sponge bottoms, Williams, et al. (1968) from a Lithothamnion reef near the edge of the continental shelf, and Coelho and Ramos (1972) from calcareous algae and sand; 27 to 238 m (rarely 366 m ?).

Type-locality.—Off Conch, Carysfort and French reefs, Florida.

Known range.-SE Capes Hatteras and Lookout, N. C.; Gulf of Mexico off NW Florida; through West Indies to off Rio Grande do Norte, Brazil.

Remarks.-Mature females are common in collections studied but the only ovigerous one is a spiny variant from west of Puerto Rico in February. A number of specimens bear Sacculina.

In temperature tolerance experiments, specimens collected from an offshore reef southeast of Cape Lookout, N. C., in September and October died after 7 h of exposure to $4^{\circ} \mathrm{C}$ (F. J. and W. B. Vernberg 1970).

## Genus Batrachonotus Stimpson 1871

Rathbun 1925:122.

## Batrachonotus fragosus Stimpson

Figs. 231, $241 e$
Batrachonotus fragosus Stimpson 1871a:122.-Rathbun 1925:123, text-fig. 48,1 pl. 39, figs. 1-2 (not B. brasiliensis Rathbun, pl. 39, figs. 3-4).-Williams 1965:238, fig. 214.-Powers 1977:44.

Recognition characters.-Male. Carapace triangular, broadly expanded behind; gastric, cardiac, and
branchial regions strongly protuberant, each surmounted by stout spine or large tubercle; intestinal region with 2 small tubercles just above posterior margin; hepatic region angular, approximating postorbital tooth. Cervical depressions deep and broad giving carapace superior outline much like frog's back. Rostrum short, formed of rounded lobes separated by shallow notch, scarcely projecting beyond antennular fossae, margin and supraorbital margin denticulate. Basal articles of antenna with dentate margins and small tooth at anterior extremity. Merus of outer maxilliped broad with prominent outer and inner anterior angles. Abdomen and sternum granulate except for smooth area between chelipeds; abdomen with 6 free segments, last 2 fused, proximal fixed segment with prominent median spine.

Chelipeds somewhat longer than carapace, spinulose; ischium with distal spine; hand slightly compressed; fingers nearly as long as palm, gaping nearly whole length, large tooth in middle of fixed finger. First pair of walking legs more than twice length of second pair, posterior pairs short.

Female. Carapace narrower behind and wider in front than male, tuberculation more uniform, spines less frequent. First walking leg little longer than second, approximately 1.5 times length of carapace. Abdomen tuberculate or granulate, with 5 free segments, last 3 fused.


Fig. 231. Batrachonotus fragosus Stimpson. Animal in dorsal view, legs of right side shown in approximate position, legs of left side not shown, 2 mm indicated (from Williams 1965).

Measurements in mm.-Carapace: male and female, length 7 , width 6.

Variation.-Rathbun (1925) stated that this species exhibits wide variations from the type. Some specimens have the elevated regions each surmounted by a spine, some have an abdominal spine, others, mainly females, are smoother, lacking even tubercles on the elevated regions.

Habitat.-The species has been reported from mud, sand of various grades, and broken-coral and shell bottoms; shore to 247 m (Wenner and Read 1982).

Type-locality.-South of Tortugas, [Fla.], $24^{\circ}$ $36^{\prime} 40^{\prime \prime} \mathrm{N} 80^{\circ} 02^{\prime} 20^{\prime \prime} \mathrm{W}, 29.3 \mathrm{~m}$.

Known range.-Cape Hatteras, N. C., to south-
ern and western Florida; West Indies to Barbados.
Remarks.—Coelho (1971) pointed out that B. brasiliensis Rathbun is a valid species which should not be synonymized with B. fragosus. The Brazilian species has a median tubercle (female) or spine (male) on the intestinal region but lacks a median spine on first abdominal segment.

Ovigerous $B$. fragosus are known from northwestern Florida in January and Tortugas in June (USNM).

## Genus Collodes Stimpson 1860

Rathbun 1925:105.

## Key to Species

1. Carapace without median spines; basal antennal article coarsely dentate
laterally . . . . . . . . . . . . . . . . . . . . . . . . . . . . C. robustus
Carapace with median spines; basal antennal article spinulose laterally . . .
C. trispinosus

## Collodes robustus Smith

Fig. $241 g$
Collodes depressus Smith 1881:414 (not C. depressus A. Milne Edwards 1878).

Collodes robustus Smith 1883:5.-Rathbun 1925:114, text-figs. 36-41, pl. 29.-Williams, McCloskey, and Gray, 1968:58.

Recognition characters.-Carapace ovate-triangular, thickly covered with granules except on gastric region. Larger than C. trispinosus, hepatic regions more prominent, median spines reduced to tubercles hardly larger than surrounding granules in adults. Rostrum wider than in C. trispinosus, its horns more widely separated at tips. Postorbital tooth broader than in C. trispinosus, slightly exceeding eyes in adults. Lateral margin of basal antennal article dentate; interantennular spine long and slender. Sternum of male coarsely granulate.

Chelipeds much as in C. trispinosus, a low tooth on dactyl opposite that on fixed finger. Remaining legs long and hairy.
Measurements in mm.-Carapace: male, length 27, width 21; ovigerous female, length 18.2 , width 15 .

Habitat.-Rathbun (1925) reported this species from bottoms ranging from soft sticky mud to coarse shell and sponge; 27 to 682 m .

Type-localities.-Twenty-one stations off Martha's Vineyard to off Chesapeake Bay, $1-2$ to 285 m .

Known range.-North of Cape Cod, $42^{\circ} 12^{\prime} \mathrm{N}$, $70^{\circ} 13^{\prime} \mathrm{W}$, to southeast of Cape Lookout, N. C.

Remarks.—Williams and Wigley (1977) gave new distributional records from New England. Rathbun (1925), Williams, et al. (1968), and USNM records show ovigerous females off Virginia in March, off North Carolina in July, south of Martha's Vineyard in August-September, and off the mouth of Chesapeake Bay in October-November.

## Collodes trispinosus Stimpson

Figs. 232, $241 f$
Collodes trispinosus Stimpson 1871a:120.—Rathbun 1925:107, text-figs. 32a, b; pl. 36, figs. 5-6.Williams 1965:239, figs. 215, 223D.-Powers 1977:45.

Recognition characters.-Carapace ovate-triangular, covered with coarse granules except on front, anterior part of gastric region, and about bases of spines; single, slender, erect, capitate spine on gastric and cardiac regions, and first abdominal segment. Rostrum short, with 2 minute and usually well-separated horns. Eyes of moderate length, partially retractile; postorbital tooth slender, a granule on upper orbital border. Antenna with first movable article approximately as long as rostral horns; basal article of antenna twisted, with 4 or 5 spinules on outer border and with laminate crest on inner margin ending in large tooth; interantennular spine short. Merus of outer maxilliped obcordate, deeply cut on distal margin, strongly produced at inner and outer angles.


Fig. 232. Collodes trispinosus Stimpson. Male in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

Chelipeds of male moderately stout, palm thick, smooth outside; surface of carpus and margins of merus and palm spinulose; fingers widely gaping, with triangular tooth near middle of fixed finger and low molariform tooth near base of dactyl. Walking legs long; first 2 pairs variably subequal; third and fourth pairs successively shorter; dactyls as long as propodi.
Measurements in mm.-Carapace: male, length 14, width 12 ; female, length 12 , width 10 .
Habitat- - Rathbun (1925) reported this species from gray sands of varying coarseness, broken shell, and gravel bottoms; 7.3 to 247 m (Wenner and Read 1982).

Type-locality.—Off the Quicksands, Carysfort Reef, and French Reef [Fla.], 62.1 to 91 m.
Known range.-Near Cape Hatteras, N. C., to south and west Florida near Apalachicola.
Remarks.—Rathbun (1925) reported ovigerous females from North Carolina in October, and they are known from Florida in March, June and July, and Georgia in June and July (USNM).

## Genus Euprognatha Stimpson 1871

Rathbun 1925:95.

## Euprognatha rastelifera Stimpson

Figs. 233, 241b
Euprognatha rastellifera Stimpson 1871a:123.-Hay and Shore 1918:454, pl. 37, fig. 7.-Coelho and Ramos 1972:207.
Euprognatha rastellifera marthae Rathbun 1925:96,
text-fig. 30, pl. 33; pl. 34, figs. 1-2; pl. 35, figs. 3-4; pl. 216.-Williams 1965:237, figs. 213, 223B.

Recognition characters.-Carapace pyriform, granulate, tubercle or short truncate spine on gastric and cardiac regions, each branchial region, and supraorbital margin. Rostrum short, with 2 small teeth or horns. Ocular peduncles short, with tubercle at emargination of cornea. Frontal teeth short, spiniform, or triangular. Postorbital projection dentiform, triangular, tapering to slender point. Obtuse antennal spines directed obliquely forward, approximately as advanced as front; interantennular spine inclined downward, equaling or surpassing front. Sides of hepatic and pterygostomian region with few small spines. Sternum granulate except for concave part between chelipeds.

Chelipeds approximately twice as long as carapace, granulate, margins spinous; hand swollen; fingers more than half length of palm, slightly gaping. Walking legs granulate, with tufts of curled setae and often small spines; first pair longest, others successively shorter.

Abdomen of males with 6 , females with 5 , free segments.

Measurements in mm.-Carapace: male, length 14.3 width 11.5 ; female, length 9.5 , width 7.8 .

Variation.-The spines of the carapace are often capitate. Rathbun (1925) divided the species E. rastellifera into a northern subspecies, marthae (ranging from Nantucket to southern Florida), and a southern or Caribbean subspecies, acuta (ranging from Cuba to Grenada and Barbados), with a region of intergradation in the Florida Keys. The southern form (acuta) has longer, sharper, and more slender spines than marthae, and a narrower, higher, and more closely and finely roughened carapace with regions more deeply separated. Likewise, the chelipeds have spines on the border of the merus well developed and legs more spinulose than in the northern form.
Rathbun pointed out that there is considerable overlap in distribution of these subspecies, listing acuta from as far north as Martha's Vineyard. Subspecific intergradation over such a broad range of latitude in this region of the western Atlantic seems unlikely. Rather, the variation may parallel that seen in Callinectes sapidus which is apparently a polymorphic species, responding perhaps to temperature by developing spines of longer mean length in tropical than in temperate waters.
Habitat.-The species has been reported from a variety of sandy and muddy bottoms; 25.6 to 708 m .

Type-locality.-Southwest of Martha's Vineyard, Mass., $40^{\circ} \mathrm{N}, 70^{\circ} 57^{\prime} \mathrm{W}, 155 \mathrm{~m}$.

Known range.-Off Georges Bank $\left(40^{\circ} 35^{\prime} \mathbf{N}\right.$,


Fig. 233. Euprognatha rastellifera Stimpson. Male in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).
$67^{\circ} 37^{\prime}$ W) to São Paulo, Brazil (Coelho and Ramos 1972).

Remarks.—Ovigerous females are known virtually throughout the year: January and May off Cuba; February and June at Key West; March to June, and October off Chesapeake Bay; May off New Jersey; September off Long Island to Martha's Vineyard; and November off Georges Bank (USNM).

## Genus Inachoides H. Milne Edwards and Lucas 1842

Garth 1958:95.

## Inachoides forceps A. Milne Edwards

Figs. 234, 240i
Inachoides forceps A. Milne Edwards 1879:199, pl. 33, figs. 4-4d.-Garth 1958:101.-Williams, McCloskey, and Gray 1968:60, 14.—Powers 1977:45.
Inachoides laevis.-Rathbun 1925:61 (part, the Atlantic specimens), text-fig. 17.

Recognition characters.-Carapace longer than broad, nearly smooth, regions protuberant and rounded; hepatic region produced to submarginal deflexed tubercle, branchial region with small tubercle on margin above base of cheliped. Rostrum tapering from triangular base to simple extremity of variable length. Supraorbital arch without sur-


Fig. 234. Inachoides forceps A. Milne Edwards. Male in dorsal view, legs of left side and missing legs of right side not shown, 2 mm indicated (from Williams, et al. 1968).
mounting tubercle. Postorbital spine minute. Sparse branchial tubercles and pterygostomian tubercle on lateral region in front of base of each cheliped. Basal segment of antenna with 2 smooth or slightly spinulous ridges converging anteriorly, small spine at anterolateral angle. Outer maxillipeds with longitudinal, denticulate ridge on outer part of ischium; anterointernal corner of merus projecting sharply and obliquely forward.

Chelipeds of male long and heavy in comparison to body; merus subcylindrical; palm stout, margins convex, surface sparsely spinulous, more or less in rows; fingers curved, male with fixed finger strongly decurved leaving narrow, oval gape, large tooth at base. Walking legs similar in length, carpus and propodus subequal, dactyl falciform; first of these legs slenderest and with straightest dactyl.

Measurements in mm.-Carapace: male, length 10.7, width 8.2 (Rathbun 1925); ovigerous female, length 7.1 , width 4.5 .

Variation.-In restricting I. laevis Stimpson to the east Pacific, Garth (1958) remarked that studies in progress then on the named Atlantic varieties $I$. forceps and I. obtusus A. Milne Edwards, and I. intermedius Rathbun would show them to represent variations in I. forceps analogous to variants in the Pacific species which had never been named. The named varieties arose primarily from differences observed in rostral length, I. forceps as figured by Milne Edwards (1879) having the longest extremity. Most specimens from throughout the range have a short extremity on the rostrum corresponding to the variety Rathbun called I. intermedius. Only one lot of specimens from Puerto Rico (USNM 24186) seen by me approaches I. obtusus in lack of a rostral extremity (Rathbun 1925). Thorough study will probably bear out Garth's (1958) idea (based on gonopod morphology) that all these forms belong to a single species, and if so, Milne Edwards's $I$. obtusus (1879:199, pl. 33, figs. 3-3d) will fall into synonymy.

Habitat.-Shallow water to 20 m .
Type-locality.-Guiana and Desterro, Brazil.
Distribution.-SE Cape Lookout, N. C.; west coast of Florida to Desterro ( = Florianopolis), Brazil.
Remarks.-Ovigerous females are known from Puerto Rico in January, Brazil in October, and Florida in February and November. The synonymy given by Williams, et al. (1968) errs in including references to specimens from the Pacific.

## Genus Metoporhaphis Stimpson 1860

Rathbun 1925:19.

## Metoporhaphis calcarata (Say)

Figs. 235, 240h
Leptopodia calcarata Say 1818:455.
Metoporhaphis calcaratus.-Hay and Shore 1918:454, pl. 37, fig. 5.
Metoporhaphis calcarata.—Rathbun 1925:21, text-fig. 5, pls. 6-7.-Williams 1965:243, figs. 221, 223J.Coelho and Ramos 1972:209.-Felder 1973:48, pl. 7, fig. 2.-Powers 1977:46.

Recognition characters.-Carapace triangular, longer than broad, uneven, nodulose, each nodule sometimes surmounted by tubercle and this in turn usually with pencil of soft, hooked hairs. Rostrum as long as or longer than carapace, subcylindrical, tapering to point, often armed with 4 or 5 slender spines projecting outward alternately from opposite sides of lower surface, and with distal pair so close to tip as to give tip bi- or trispinose


Fig. 235. Metoporhaphis calcarata (Say). a Animal in dorsal view, legs of left side not shown, 10 mm indicated (from Williams 1965); right chela, external view, $b$, male (USNM 102001), $c$, female (USNM 73416), 2 mm indicated.
appearance. Eyes protuberant, peduncles terminating in superior spinule projecting beyond cornea. Basal antennal article with spine below at midpoint of length, another at outer distal angle, and spinule at end of next 2 articles.

Chelipeds of moderate length, twisted, stout in male and less than half as long as first walking legs; merus with sharp terminal dorsal spine and row of smaller ventral spines; carpus with sharp dorsal spine near each extremity and row of sharp spines along mesial margin; hand broad, inflated, row of widely spaced spines along dorsomesial aspect of palm, fingers about as long as palm, bent mesially. Female with chelipeds feebler, palm shorter, fingers longer and more gaping. Walking legs slender, articles cylindrical but somewhat crooked; meri with 1 conspicuous spine and 2 smaller spines at extremity; dactyls longer than propodi, fringed with hair.
Male with 6 , female with 5 , free abdominal segments.
Measurements in mm.-Carapace: male, length including rostrum 21 , rostrum 9.9 , width 8.7 ; female, length including rostrum 24 , rostrum 8.9, width 12.7.
Color.-Dirty gray to lemon yellow.
Habitat.-Often found among hydroids and fouling materials on hard substrates; ocean and high salinity estuaries; shallow water to 90 m .
Type-locality.-Bay of Charleston, S. C.
Known range.-Off Cape Hatteras, N. C., through Gulf of Mexico and Caribbean Sea to Rio de Janeiro, Brazil.
Remarks.-Ovigerous females have been taken nearly year round: November, March and April in

Georgia, March and August in Florida (Wass 1955), August in South Carolina, and October in North Carolina. Wass noted that this species can remain suspended in water by "rhythmic waving of its long, setae-lined legs."

## Genus Podochela Stimpson 1860

Rathbun 1925:31.

Carapace somewhat depressed, elongate, pyriform; gastric region narrow, swollen. Body and appendages usually ornamented with curved hairs
above, straight hairs most often below legs. Rostrum arcuate or truncate, occasionally spinelike. Supraocular margin elevated or thickened. Eyes short, stout, prominent tubercle above, cornea oblique. Postorbital tooth or lobe remote from eye when present and either well developed or reduced to granule. Sutures between sternal segments of male depressed; sternum of female deeply concave, margins elevated and laminate. Abdomen with first 2 or 3 segments visible dorsally in male, 4 or 5 in female. Chelipeds of moderate length, merus curved, trigonal. Walking legs slender, subprehensile, diminishing in length from first to last pairs. (Modified after Rathbun 1925.)

## Key to Species

1. Rostrum broad, rounded in front

Rostrum long, spiniform
P. gracilipes
2. Last 3 pairs of legs rather stout, dactyls less than $1 / 2$ length of propodi; cardiac region raised; pterygostomian region bearing broad, spinelike projection
P. riisei

Last 3 pairs of legs slender, dactyls $1 / 2$ or more length of propodi; cardiac and gastric regions raised; pterygostomian region bearing long, thin lamina . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . P. sidneyi

## Podochela gracilipes Stimpson

Figs. 236, $241 j$
Podochela gracilipes Stimpson 1871a:126.—Hay and Shore 1918:454, pl. 37, fig. 6.-Rathbun 1925:47, text-fig. 13, pl. 17.-Williams 1965:243, figs. 220, 223 I.—Coelho and Ramos 1972:208.—Powers 1977:47.

Recognition characters.-Carapace with pronounced, rounded protuberance on cardiac region and 2 much smaller median protuberances on gastric region; 2 pterygostomian tubercles; small tubercle on epistome and projecting angle of buccal frame visible in dorsal view on large specimens. Rostrum long, spiniform, hairy, unarmed. Sternum of males with thick, blunt spine mesial to base of cheliped. Crests on basal article of antenna less pronounced than in P. riisei, article long, narrow posteriorly, with diagonal ventral ridge merging with terminal spine distally.

Chelipeds in male stout, inflated, fingers widely agape to near tip, large tooth near base of dactyl. Chelipeds slender in female. Walking legs slender, first pair 3 times length of carapace; dactyls long, nearly straight, $1 / 3$ length of propodus; propodi of last 3 pairs thickened distally; dactyls slightly scythe-shaped, $2 / 5$ length of propodus on second
pair, $1 / 2$ length on third, and $2 / 3$ length of propodus on fourth pair.

Abdomen of male with 6 , female with 5 , free segments.

Measurements in mm.-Carapace: male, length 14 , width 9 ; ovigerous female, length 10.4 , width 7.1.

Habitat.-Fine sand and mud to calcareous algae (Coelho and Ramos 1972); 6 to 219 m .


Fig. 236. Podochela gracilipes Stimpson. Animal in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

Type-localities.-West of Tortugas, off Pacific and Carysfort Reefs [Fla.], 66 to 110 m .
Known range.-Off Cape Lookout, N. C., through Gulf of Mexico and Caribbean Sea to Santa Catarina, Brazil.
Remarks.-Ovigerous females are known in January from Yucatan Channel, February to July in Florida, March in Alabama and Colombia, and December in North Carolina.
Metabolic activity of first stage zoeae of this tropical species from offshore reefs near Cape Hatteras was lowest among zoeae of 6 species of Brachyura determined at $15^{\circ}, 20^{\circ}$ and $25^{\circ} \mathrm{C}$ (W. B. and F. J. Vernberg 1970).

## Podochela riisei Stimpson

Figs. 237, 241k
Podochela riisei Stimpson 1860a:196, pl. 2, fig. 6.Hay and Shore 1918:453, pl. 37, fig. 9.-Rathbun 1925:33, text-figs. 9a-b; pl. 11, figs. 1-2; pl. 208, fig. 2.-Chace 1940:56.-Williams 1965:241, figs. 218, 223G.-Powers 1977:47.

Recognition characters.-Carapace with greatest width about $2 / 3$ length, dorsal region uneven and with tufts of hairs. Rostrum broad, rounded in front, deeply excavated below for antennules, carinate above and with tuft of curled hairs. Basal article of antenna with sharp projecting ridge on each margin. Sternum of male thrown into ridge radiating to bases of legs.
Chelipeds slender in both sexes, fingers in contact throughout their length (stouter and slightly agape proximally in adult males). First pair of walking legs stouter than others, about 3 times as long as carapace; upper surface of all legs with regularly spaced tufts of stiff curled hairs.


Fig. 237. Podochela riisei Stimpson. Animal in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).

Abdomen of male with 6 , female with 5 , free segments.
Measurements in mm.-Carapace: male, length 23, width 18.6 ; female, length 23 , width 20.

Variation.-The rostrum is variable in shape and length, being nearly triangular in some specimens. Margins of the basal antennal articles are thick in old individuals but may be thin in younger ones. Sternal segments of males usually have rounded surfaces but are sometimes flattened.

Color.-Overall color light brown; legs lighter, grading to almost off-white or pale yellow; chelae and chelipeds nearly white to almost transparent; carapace darker on lateral aspects of urogastric and cardiac regions, as well as at posterolateral portions of metabranchial regions. Wass (1955) reported brick red specimens.
Habitat.-Has been taken from among hydroids on pilings, calcareous algae, on sandy bottom (Dragovich and Kelly 1974), and in rocky areas in northwestern Florida (Wass 1955); shallow water to 139 m (Wenner and Read 1982).

Type-locality.-Island of St. Thomas [West Indies].
Known range.-North Carolina to Campeche, Mexico; through West Indies to Trinidad (USNM); Rio de Janeiro, Brazil (MCZ 1832); Bermuda.
Remarks.-The largest male measured (USNM 97516) from the southeastern Gulf of Mexico bears an anemone covering all of the carapace except the "neck." The Rio de Janeiro specimen seems typical of the species, but the locality is remote from the remainder of the geographic range.
Ovigerous females are known through much of the year over the range: February in Puerto Rico, March to April in Georgia, June-July in Jamaica, September in North Carolina, June to August and November to March in Florida. Yang (1967) reared the first and second zoea, megalopa, and first crab stage in laboratory culture, and described the first zoeal stage. Hinsch (1973) found the sperm structure of $P$. riise $i$ and $P$. gracilipes to be similar.
Rouse (1970) found the species uncommon in southwestern Florida, as did Dragovich and Kelly (1964) in salinities ranging from 20 to $45 \%$ over a temperature range of $15.2^{\circ}$ to $30^{\circ} \mathrm{C}$.

## Podochela sidneyi Rathbun

Figs. 238, $241 l$
Podochela sidneyi Rathbun 1924:1.-Rathbun 1925:39, text-fig. 9c, pls. 12-13.-Williams 1965:242, figs. 219, 223H.-Felder 1973:49, pl. 7, fig. 4.-Powers 1977:48.

Recognition characters.-Closely resembling Podochela riisei, cardiac and posterior eminences more


Fig. 238. Podochela sidneyi Rathbun. Animal in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).
produced, spiniform. Rostrum narrower at base and more triangular. Pterygostomian region bearing long thin lamina either subtriangular or produced downward in a lobe. Sternal segments flat with sharp cristate margins.

Chelipeds of adult male less inflated than in $P$. riisei; first pair of walking legs 3 or more times as long as carapace; dactyls of last 3 pairs less curved, longer and relatively more slender than $P$. riisei; dactyl of second leg up to $1 / 2$ length of propodus, of third leg to $2 / 3$, and of fourth leg to $3 / 4$ length of propodus.
Abdomen of male with 6 , female with 5 , free segments.
Measurements in mm.-Carapace: male, length 23, width 19.4; female, length 19.4 , width 16.6 .

Habitat.-A variety of bottoms including reef environment; shallow water to 187 m .
Known range.-Off Cape Hatteras, N. C., to Veracruz (Ray 1974); northwestern Cuba; Yucatan Channel.
Remarks.-Hildebrand (1954) reported the carapace of this species as decorated with hydroids and ascidians. Ovigerous females are known from October to March in Georgia, March, April, June, and September in Florida (Camp, et al. 1977; Cooley 1978), and March in Alabama.

## Genus Pyromaia Stimpson 1871

Rathbun 1925:127.

## Pyromaia cuspidata Stimpson

Figs. 239, 241 m
Pyromaia cuspidata Stimpson 1871a:110.-Hay and

Shore 1918:455, p1. 38, fig. 4.-Rathbun 1925:129, text-fig. 49, pl. 41.-Boone 1927:34.Chace 1940:57.-Williams 1965:240, figs. 216, 223E.-W. E. Pequegnat 1970:181.-Powers 1977:48.

Recognition characters.-Adult male. Carapace pyriform, approximately $2 / 3$ as wide as long; regions well marked, tumid, rough, with scattered granules, sharp tubercles and spines; often 6 large median spines ( 2 mesogastric, 1 urogastric, 2 cardiac, 1 intestinal), elsewhere 1 protogastric, 2 or 3 hepatic, remainder branchial. Depressions separating branchial regions from other regions somewhat pitted. Rostrum tapering to point, trigonal; upper and lateral margins spinulose. Interantennular spine acute, triangular, pointing downward and forward. Orbits large, open; supraorbital spine almost erect, directed slightly outward and forward; postorbital tooth large, curved around end of eye; anterior margin fringed with hair. Basal article of antenna long, with terminal spine, larger spine at middle of inner margin followed by row of tubercles or spinules. Tubercle at angle of buccal cavity. Outer maxilliped spinulose, longitudinal depression on ischium, merus cordate.
Legs covered with short fur, surface underneath roughened with sharp granules or spines. Merus of cheliped armed on margins, terminal spine of upper margin longest; upper margin of carpus spinulose with few spines on outer surface; hand inflated, fingers bare, grooved, uniformly toothed distally, slightly agape at base. Walking legs spinulose; meri with distal spine; first legs longest, remainder successively shorter.
First abdominal segment long, with acute back-ward-pointing spine; 6 free segments, last 2 fused.

Adult female. Legs almost bare; chelipeds not


Fig. 239. Pyromaia cuspidata Stimpson. Male in dorsal view, legs of left side not shown, 10 mm indicated (from Williams 1965).
much stronger than walking legs, dactyl longer than palm; legs shorter than in male. 5 free abdominal segments, last 3 fused.

Measurements in mm.-Carapace: male, length 41, width 32; ovigerous female, length 27 , width 33.

Variation.-The young have pubescence resembling that in females, the postorbital tooth smaller than in adults, slender and directed outward in small specimens ( 7.5 mm long), directed outward and forward in somewhat larger forms.

Color.-Immature individuals brown, legs with lighter crossbands.

Habitat.-This species has been taken on gray mud, sand, pebble, and broken-coral bottoms; 27 to 549 m .

Type-localities.-Off Sand Key, 150 m ; Alligator Reef, 170 m ; the Samboes, 170 and 221 m ; southwest of Sand Key, 229 m [Fla.].

Known range.-Off Cape Lookout, N.C., to west Florida; Cuba and Yucatan Channel to off Nicaragua $14^{\circ} 3 l^{\prime} \mathrm{N}, 80^{\circ} 41^{\prime} \mathrm{W}$.

Remarks.-Ovigerous females are known off Florida in February, June and July, and off Cuba in April (USNM).

## Genus Stenorhynchus Lamarck 1818

Rathbun 1925:13.—Garth 1958:129.—Opinion 763.

## Stenorhynchus seticornis (Herbst)

(Arrow crab)
Figs. 240, $241 o$
Cancer seticornis Herbst 1788:229, pl. 16, fig. 91 (see Rathbun 1925).
Stenorynchus sagitarius.-Hay and Shore 1918: 455, pl. 37, fig. 8.
Stenorynchus seticornis.—Rathbun 1925:13, text-fig. 3, pls. 2-3.—Chace 1940:55.—Monod 1956:567, figs. 838-839.-Williams 1965:244, figs. 222, 223K.—Türkay 1968:254.—Felder 1973:48, pl. 7, fig. 1.—Pequegnat and Ray 1974:237, figs. 11, 12.-Powers 1977:49.

Stenorhynchus seticornis.-Coelho and Ramos 1972:209.-Opinion 763.

Recognition characters.-Carapace smooth, triangular, longer than broad, diminishing in width to level of eyes and thence produced into slender, horizontal, flattened, laterally spinulose rostrum varying from slightly longer to 2.5 times as long as carapace; rostral tip acuminate. Orbits not defined; postorbital spine small, occasionally bifid. Eyes short, not retractile. Basal article of antenna slen-
der, with strong spine at middle directed downward and forward.

Legs extremely long and slender, composed of cylindrical articles, finely spinulose and bearing in addition 2 rows of spines on merus, 2 or 3 spines on carpus, and 3 terminal spines on merus. Chelipeds slender, cylindrical; hand weak; palm of male cheliped from 2.5 to 4 times as long as dactyl. First pair of walking legs from 8 to 9 times as long as postrostral part of carapace, second, third, and fourth legs successively shorter; dactyls on each pair longer than propodi.

Abdomen in male with 6 , female with 5 , free segments.

Measurements in mm.-Carapace: male, length including rostrum 60 , width 24 , rostrum to eyestalk 33.5; female, length including rostrum 59 , width 21 , rostrum to eyestalk 35 .

Variation.-There is great variation in length of rostrum, relative length of palm and fingers, and length of legs. In old individuals the rostrum, chelipeds, and legs are pubescent.

Color.-Body ground color gray, banded dorsally with stripes of light and dark brown or black converging anteriorly as a nested series of inverted V's; one dark pair of stripes continuing united on dorsal side and another more lateral pair of like color on ventral side of rostrum. Legs reddish brown, joints darker; fingers of chelipeds bluish purple.

Rathbun (1925) summarized other color observations. The general pattern is as above, with ground color creamy white, buff, or light orange vermilion; stripes white, chestnut, brown, or black;


Fig. 240. Stenorhynchus seticornis (Herbst). Animal in dorsal view, legs of left side not shown, 30 mm indicated (from Williams 1965).


Fig. 241. Subfamily Inachinae, tips of right first pleopods of males, all sternal views except $a, i$ abdominal: a, Anomalothir furcillatus (Stimpson); b, Euprognatha rastellifera Stimpson; $c$, Aepinus septemspinosus (A. Milne Edwards), USNM 24150; d, Arachnopsis filipes Stimpson, USNM 18114; e, Batrachonotus fragilis Stimpson; f, Collodes trispinosus Stimpson; g, C. robustus Smith, USNM 10085; $h$, Metoporhaphis calcarata (Say); i, Inachoides forceps A. Milne Edwards, UNC-IMS 2078; $j$, Podochela gracilipes Stimpson; $k$, P. riisei Stimpson; $l, P$. sidneyi Rathbun; $m$, Pyromaia cuspidata Stimpson; $n$, Anasimus latus Rathbun; o, Stenorhynchus seticornis (Herbst); (a,b,e,f,h,j-o from Williams 1965); 0.33 mm indicated.
legs reddish with bright red spots at joints; chelae purple or mauve; spine on legs and rostrum orange or red; eyes maroon.

Habitat.-This form has been dredged or trawled from a variety of bottoms-rock, coral rock, pebbles, sand, or sand mixed with broken shell; also, it has been taken from wharf piling and rock jetties. Near surface to 188 m (Wenner and Read 1982) (1465 m , Young 1978).

Type-locality.—Guadeloupe (Holthuis 1959).
Known range.-North Carolina to Santa Catarina, Brazil; Bermuda.
Remarks.-Rathbun's (1925) summary of this seemingly distinctive species, which has been followed by subsequent authors, is too inclusive. Both Yang (1967) and Barr (1975) referred the eastern Atlantic records to $S$. lanceolatus (Brulle). From studies of both larvae and adults, Yang (1967)
thought that two forms may exist in the western Atlantic, a shallow-water species to which the name S. seticornis can be applied correctly, and a possibly distinct deeper water form. Yang (1967) compared the adult morphology of two forms and (1976) described larval development of S. seticornis in laboratory culture through two zoeal stages, the megalopa and first crab stage, as well as the first zoeal stage of the deeper dwelling form.

The species as currently recognized has a tremendous recorded range in depth, but Yang thought the shallow form to occur usually from near the surface to near 90 m and the deeper form to range usually from near 40 to near 135 m . The validity of Yang's ideas remains to be determined.
Ovigerous females are known year round in the western Atlantic (see also Hartnoll 1965). Eggs hatch in 12 days at $22-25^{\circ} \mathrm{C}$ (Hartnoll 1965). Hinsch (1973) described sperm structure of the male. The species changes in form at the pubertal molt, relative size of male chelipeds increasing markedly. The female develops pubescence around articulation of the dactyl; there is a tooth near its base in both sexes. Moreover, the female develops a rim around the edge of the sternum which fits inside the abdomen (Hartnoll 1965).

Individuals collected from a reef southeast of Cape Lookout, N. C., in September and October withstood experimental exposure to temperature of $40^{\circ} \mathrm{C}$ for 7 h but died after 17 -h exposure (F. J. and W. B. Vernberg 1970).

Hartnoll (1966) described an entoniscid (Achelion occidentalis) from specimens of S. stenorhynchus collected in Jamaica.
Barr (1975) studied the biology and behavior of $S$. seticornis in 22 -m depths near the Tektite underwater habitat in Lameshur Bay, St. John, Virgin Islands, from July 23 to August 12, 1970, observing crabs for about 40 h in situ plus behavior of 103 crabs in the habitat entry room. The species lives there on live coral reefs, patch reefs on sand, sand, and the edge of large reefs; crabs were more abundant on coral substrate than sand but most abundant on reef edges near the coral-sand interface, usually in direct contact with stony or soft coral. Those on sand were associated with stable objects such as sponges, anemones, etc., and were smaller than the mainly larger crabs on coral.
Counts of crabs along $1 \times 10 \mathrm{~m}$ transects in daytime, dusk, night, and dawn, showed somewhat
greater numbers at dusk and night. The crabs migrate upward at dusk, reaching heights of 1 m or more on soft coral and gorgonians by dark, and retreat at dawn, tending to hide in the same place each day. Although some small crabs may have been overlooked, proportions were $1 \delta^{\hat{2}}: 1.14$ 年; females measured $4.5-13 \mathrm{~mm}$ in carapace length (cl), males $3.5-16.5 \mathrm{~mm}$. Sexes were equal in the $8-\mathrm{mm}$ class, females dominated the $8.5-13 \mathrm{~mm}$ class, and only males exceeded this size. Both sexes are mature at $8.5-9.5 \mathrm{~mm}$ cl. Among 35 mature females, 28 were ovigerous.

Mating, observed in late afternoon-early evening and once at 0200 h , was described in detail. Males are the aggressors, but assume an inverted position during copulation with the upright females supporting the pair. Molting is no prerequisite, females copulate with or without eggs but in the former case old eggs soon hatched and new ones were deposited within 19 h . Hatched larvae seek the light.

Stenorhynchus seticornis tends to be an omnivorous, opportunistic scavenger, mainly on detrital particles. Self cleaning seems to be a chief activity. Barr theorized that the species is essentially a filter feeder, its body catching particles to be consumed later; the crabs crawl about exposing themselves to water currents at night but feed mostly in daylight. They prey little if at all on other living organisms and are not, themselves, important food to predators. The long, spiny appendages apparently make them difficult to eat, for fishes will take only the body of a legless or almost legless specimen and active crabs fend off approaching fishes with the walking legs and retreat to the protecting spines of a sea urchin.

Randall (1967) reported S. seticornis from stomach contents of the rock hind, Epinephelus adscensionis, red hind, E. guttatus, Nassau grouper, E. striatus, and sharp nose puffer, Canthigaster rostrata.

## Subfamily Oregoniinae

Male abdomen terminally broadened, last segment subquadrate or transversely ovate, invaginated into sixth segment, its outer border emarginate or introverted. Male first pleopod lanceolate, longitudinally grooved, provided with numerous filamentous setae, and having bulbous base (Garth 1958).

## Key to Genera and Species

(Adapted from Garth 1958; Rathbun 1925)

1. Carapace broader than long or very little longer than broad; rostrum short; adult male cheliped much shorter than walking legs. Chionoecetes opilio

Carapace considerably longer than broad; rostrum elongate; adult male cheliped either longer than walking legs or very little shorter.
[Hyas] 2
2. Hepatic region behind postorbital spine not expanded (slightly so in large individuals); fixed basal antennal article elongate and subtriangular . . .
H. araneus

Hepatic region behind postorbital spine expanded laterally; fixed basal antennal article elongate with sides nearly parallel, granulate, outer side ending in blunt tooth
H. coarctatus

## Genus Chionoecetes Kröyer 1838

Garth 1958:148.

## Chionoecetes opilio opilio (O. Fabricius)

(Snow crab)
Figs. 242, 245a
Cancer phalangium O. Fabricius 1780:234 (not C. phalangium J. C. Fabricius 1775).
Cancer opilio O. Fabricius 1788:182, plate.
Chionoecetes opilio.—Kröyer 1838:249.—Rathbun 1925:233, text-figs. 88-89, pls. 84-85.—Garth 1958:150, pl. I, fig. 5; pl. 14.—Sakai 1976:185 (English text), pl. 64.

Recognition characters.-Carapace ovate in outline, length and width subequal; surface covered with very short pubescence and scattered unequal prominences, blunt, wartlike and granulate about middle but more acute anteriorly and at sides; gastric region depressed and well separated from branchial regions; paralleling channels above posterolateral margin nearly smooth but with double margins granulate; anterolateral row of marginal small teeth diminishing in size anteriorly. Rostrum short, divided into 2 flat, triangulate horns. Orbit large, shallow, open above leaving eyes visible when retracted; cornea large. Postocular tooth large, directed forward.

Chelipeds 1.5 times as long as carapace, twice as long in old individuals; fingers 1.5 times as long as palm. First 3 walking legs about twice as long as carapace, 3 times as long in old; last leg about as long as cheliped; legs slightly pubescent, meri scabrous or echinulate above; chelipeds somewhat scabrous above, muricate along angles.

Abdomen 7 segmented in both sexes, 3 proximal segments strongly granular; width in males $1 / 3$ width of sternal plastron at its penultimate segment; third and fourth segments widest. Male first pleopod with tip reflexed, almost ringed with subterminal filaments.

Measurements in mm.-Carapace: male, length
69.3, width 69.3 ; ovigerous female, length 53.8 , width 54.5 (Garth 1958). Male, length 125.5 , width 127.5 (Rathbun 1925); male, length 126 , width 128 (Sakai 1976).

Color.-Light brick red above, often iridescent, yellowish white below; sides of legs shining white (Stimpson in Garth 1958). Sakai (1976) gave the color as "light brownish or copper-colored," which is faithfully shown in his plate 64.

Habitat.-Green and black mud, fine gray sand and shell (Garth 1958; Rathbun 1925); mud (Brunel 1961; Prowles 1968); 12.8 to 640 m , rarely to 2222 m (Rathbun 1925; Squires 1966). Sakai (1976) gave the bathymetric range as 20 to 1200 m ; Motoh (1973) placed a lower limit for fishing at about 1500 m .

Type-locality.—Greenland.
Known range.-Western Atlantic Ocean from Greenland south to St. Lawrence estuary and Gulf of Maine; arctic Alaska (Pt. Barrow) and northeastern Siberia through Bering Strait to Alaskan Peninsula and Aleutian chain; Kamchatka; Okhotsk Sea and southward to Japan. Prowles (1968) characterized these waters as subarctic in the northeastern Atlantic and Bering Sea, and the northeast Pacific.

Remarks.—Rathbun (1925) and Garth (1958) both regarded a population from Japan as the subspecies, C. o. elongatus Rathbun. Sakai (1976) did not distinguish this population, but Watson (1970) in biological studies recognized its distinctness.

The species is a commercial fishery resource in the northern Pacific (Slizkin 1974). It had limited development in the northwestern Atlantic until 1966 (Brunel 1961; Wilder 1966); thereafter production increased markedly (Watson 1970). Brunel (1961) showed that catches were made off Gaspe Peninsula where the species seemed confined to water between $-1^{\circ}$ and $4^{\circ} \mathrm{C}$. Males in samples attained much larger weight (mean 628 g , rarely 1268 g ) than females ( 108 g , rarely 239 g ), hence by size alone were separated in the then limited fishery. Deveau and Aucoin (1966) found greatest abundance north of Cape Breton Island in depths of 90 to 137 m , and Prowles (1968) found it most com-


Fig. 242. Chionoecetes opilio opilio (O. Fabricius). Male in dorsal view, third left walking leg missing, 5 cm indicated (USNM 17075).
monly in trough areas 73 to 165 m deep on mud bottom in water $-1^{\circ}$ to $2^{\circ} \mathrm{C}$. Temperature tolerance experiments by McLeese (1968) and McLeese and Watson (1968) largely confirmed these early environmental observations on temperatures favored by the Canadian population.
Watson (1970) found that $50 \%$ maturity occurs in males at about 57 mm carapace width (minimum 51 mm ), and at 47 mm carapace width in females (minimum 51 mm ). After attainment of maturity, males show allometric growth, but females do not grow after a pubertal molt. He suggested that only hard-shelled males are capable of mating, and described the mating of a captive male and female. The female had just molted and was still in soft condition. The following day this female laid fertile eggs. Field observations indicate that new eggs are produced within a few days after a female has released a hatch of larvae, and that one mating fertilizes more than one spawning. Watson (1972) described mating behavior in which males hold females in precopulatory embrace for a period which ends when they assist females in molting, then mate. During postcopulatory embrace, both animals flex abdomens, spermatophores issue from the male's pleopods, and the female's waving pleopods draw spermatophores toward her abdomen. It is possible that emission of spermatophores by males and gathering of them by females may induce egg laying; many spermatophores were seen within egg masses soon after laying. Alternatively, the first batch of eggs may be
externally fertilized and subsequent batches may be fertilized from spermatophores stored in the spermathecae. Eggs are laid in late May to early June and hatch about 11 months later (Prowles 1968). Watson (1971) also described molting in captive crabs, showing that its duration increases with size, lasting two to nine hours. Newly molted crabs of commercial size take two to three months to harden sufficiently for commercial acceptability.

The Japanese have studied the western Pacific populations in great detail, from both purely biological and economic standpoints. Motoh (1973), from an ovigerous female taken by fishermen in the Sea of Japan in February, reared, described and illustrated the two zoeal stages and megalopa. There is a transitory pre-zoeal stage. Comparisons were made with previous studies. Haynes (1973) described the pre-zoea and first zoea of C. opilio from Bristol Bay, Alaska, and compared them with similar stages of C. bairdi. Kon (1970) estimated planktonic larval stages to last only 63-66 days in Wasaka Bay water of $11^{\circ}-13^{\circ} \mathrm{C}$, based on laboratory experiment. Ito (1968) described the first crab stage as being near the surface until June, after which they move deeper, settling to the bottom as first crab stages the following fall and winter. Sinoda (1968) thought that females reach a terminal pubertal molt but that males keep on molting annually; females at a width of 75 mm were estimated to be six or seven years old; males as broad as 165 mm were recorded.

The above account makes no pretense of review-
ing the growing body of literature on this species, but such a review was provided by Adams (1979).

## Genus Hyas Leach 1814

Garth 1958: 142.

## Hyas araneus (Linnaeus)

## (Toad crab)

Figs. 243, $245 b$
Cancer araneus Linnaeus 1758:628.
Hyas araneus.-Leach 1814:431.-Rathbun 1925: 253, text-figs. 91-92, pls. 92-93.-Christiansen 1969:116, fig. 48.

Recognition characters.-Carapace longer than broad, more or less subtriangular, broadest posteriorly, convex anteroposteriorly, but deflexed in anterior part of gastric region; hepatic region not dilated laterally, lateral margins converging throughout length, tuberculate behind postorbital tooth; surface uneven, pustulate tubercles especially on median gastric area and in oblique row on each branchial region, 2 tubercles side by side on intestinal region (may be united in young). Rostrum triangular, flat, bifid, horns contiguous. Eyes not entirely concealed when retracted; fissures above and below orbit open; postorbital tooth large, acutely triangular, cupped. Basal antennal article longer than wide, subtriangular, narrowed anteriorly; first movable article curved laterally, last article of peduncle cylindrical.

Chelipeds compressed, stout, thick in large males with fingers narrowly gaping. First walking leg longer than cheliped, following legs progressively somewhat shorter.


Fig. 243. Hyas araneus (Linnaeus). Male in dorsal view, 2 cm indicated (from Christiansen 1969).

Abdomen 7-segmented in both sexes; that of male broadest at third and fourth segments, terminal segment transversely ovate; female abdomen broadly oval.
Measurements in mm.-Carapace: male, length 95, width 75 ; ovigerous female, length 81 , width 64 .

Color.-Reddish brown dorsally and dirty white ventrally (Christiansen 1969).

Habitat.-Hard, stony, sandy and soft bottom (Christiansen 1969); commoner on soft bottom where $H$. coarctatus is rarer, the two species being complementary (Hartnoll 1963); intertidal to 350360 m , usually less than 50 m .

Type-locality.-"Habitat in Oceano Europaeo."
Known range.-West Greenland; Labrador to Rhode Island; between Greenland and Iceland, through British Isles and northwest France to Spitsbergen and Kara Sea; intertidal to 360 m .

Remarks.-Hartnoll (1963) studied the biology of this species along with that of $H$. coarctatus (see below) at the Isle of Man, and Christiansen (1969) gave a general summary.

Christiansen (1973) reared larvae in the laboratory and compared results with earlier work. Incubation time and larval development are nearly identical with findings for $H$. coarctatus. Small differences between the larval morphology of the species were described. Temperature influenced rate of development and survival of the larvae, the megalopa being reached in $37.8(\overline{\mathrm{x}})$ days with $73 \%$ survival at $10^{\circ} \mathrm{C}$, first crab in $57(\overline{\mathrm{x}})$ days with $1 \%$ survival at $15^{\circ} \mathrm{C}$, and no development at $20^{\circ} \mathrm{C}$. Earlier (1971) she found that antibiotics aid growth and survival of this species in culture.

## Hyas coarctatus coarctatus Leach

## Hyas coarctatus alutaceus Brandt

(Toad crab)
Figs. 244, 245c
Hyas coarctatus Leach 1815b:329.-Rathbun 1925:258, text-fig. 93, pls. 94-97.—Christiansen 1969:118, fig. 49.

Recognition characters.-Carapace longer than broad, more or less shield shaped, broadest posteriorly; postorbital and hepatic regions dilated laterally into winglike expansion with rounded posterolateral angle, separated from branchial region by broad and deep sinus; ornamentation similar to $H$. araneus but tubercles of lateral margin extend only to posterior part of hepatic region, 1 tubercle


Fig. 244. Hyas coarctatus Leach. Male in dorsal view, 1.5 cm indicated (from Christiansen 1969).
on lateral margin just anterior to contraction, 2 large median tubercles on mesogastric region; carapace in old individuals rougher. Rostrum triangular, flat, bifid; horns contiguous, narrowly diverging or with buttonhole gape, meeting only at tips. Basal antennal article narrowing slightly forward, longitudinal margins granulated, outer side ending in blunt tooth; first movable article curved laterally, last article of peduncle cylindrical.

Chelipeds longer than in $H$. araneus, more roughly granulated in older individuals and sometimes exceeding second walking legs in length.

Abdomen as in $H$. araneus.
Measurements in mm.-Carapace: male, length 30.2 , width 19.7 (off Cape Cod); male, length 51.5, width 35 (Murman Sea) (both typical form, Rathbun 1925); male, length 8-62; female, length 9-45 (Squires 1967).

Variation.-Rathbun (1925) stated that H. coarctatus shows great geographic and individual variation manifesting these differences in three subspecies. Other authors (Christiansen 1969; Sakai 1976) have accepted her analysis. The typical form is relatively small and has a long rostrum. The essentially Arctic and Pacific form, H. c. alutaceus, with shorter, broader rostrum, is also broader across the anterior carapace embracing the hepatic region. The third hairier and proportionally different form, H. c. ursinus, is confined to the Pacific.

Color.-Similar to H. araneus, perhaps more reddish dorsally (Christiansen 1969).

Habitat.-Hard, stony, sandy and occasionally soft bottom; 1 to 1650 m , usually less than 50 m (Christiansen 1969; Squires 1966).

Type-locality.-Kent near Sandgate, England.
Known range.-Two subspecies occurring in the North Atlantic merge gradually into each other. Typical H. c. coarctatus ranges from off North Carolina northeasterly with the trend of the Gulf Stream to northwestern Europe, thence eastward in the Arctic to the Murman Sea. This form merges
into H. c. alutaceus around Cape Breton Island, Newfoundland, Greenland and Iceland, continuing as that form through Davis and Hudson straits and into Hudson Bay; westerly it is found along edges of the Beaufort, Chukchi and East Siberian seas, southward through the Bering Sea, on the east to Puget Sound, and on the west to the Sea of Japan and East China Sea. The third form, H. c. ursinus, is known only from the Sea of Japan and Singapore (Christiansen 1969; Rathbun 1925; Sakai 1976; Squires 1966, 1967).

Remarks.-Hartnoll (1963), studying the biology of $H$. coarctatus at the Isle of Man, outlined habitat preferences and noted omnivorous feeding habits (also Squires 1965a) with a preference for crustaceans. The growing crabs enter maturity in a terminal pubertal molt which may vary greatly in size; at Isle of Man mature males varied in length from 12 to 42 mm and females from 10 to 36 mm . At this molt the female abdomen changes from narrow to broad and fringed with hairs, the shallow sternal groove with locking buttons becomes a much broadened surface without buttons and the genital openings are converted from short diagonal slits to open slits, each around the inner edge of a small dome. In males, pleopods become much enlarged and hairy. Growth is allometric; there is greater increase in size at the pubertal molt than at any other, the male chelipeds showing marked increase in size but the female chelipeds only a slight increase. Male pubertal molts occurred from January to July, usually February to June, and females from May to September, usually May to July. Both season and size determine whether there will be further molts or the molt of puberty but the two conditions overlap. Immediately after this molt, gonads enlarge in the males.


Fig. 245. Subfamily Oregoniinae, tips of male first pleopods: $a$, Chionoecetes opilio (O. Fabricius); b, Hyas araneus (Linnaeus) USNM 122023; $c, H$. coarctatus Leach; $a, c, 1 \mathrm{~mm}$ (redrawn from Garth 1958); $b, 0.5 \mathrm{~mm}$ indicated.

Hartnoll (1974) pointed out that in this species as in others (among them Carcinus maenas, Ocypode quadrata, Macrocoeloma trispinosum, Microphrys bicornutus, and Stenorhynchus seticornis) the strong positive allometry of male chelipeds, low positive allometry of female chelipeds, strong positive allometry of female abdomen until the molt of puberty, and slight positive allometry of male gonopods until puberty, followed by a negative trend, are all adaptations to mechanical considerations and utilization of available resources. The male chelae continue to be implements of agression, defense and mating, the female abdomen is an incubatory chamber with no need to change once efficient size is reached, and male gonopods of intermediate size equip males with the capacity for mating with a range of sizes.

Post-pubertal females mate while soft and, having mature ovaries, spawn almost at once. By September females that had laid eggs in early summer again have full ovaries. Eggs laid from April to August are carried for 9-11 months until the following March or April. When larvae hatch, the females, already having full ovaries and spemathecae, lay eggs again almost immediately. Nearly $10 \%$ of mature females are in their second breeding season during April-June. Hartnoll (1963) could not determine whether any survived to lay more than two sets of eggs. A $19-\mathrm{mm}$ female can carry 1500 eggs; $32-\mathrm{mm}, 8000$.

Early in his studies Hartnoll (1960) described a hermaphrodite of the species, apparently unparasitized, that had male and female systems on both sides of the body. This was the only such crab among 250 examined and at that time was the fifth such occurrence recorded for decapod crustaceans.

Larval stages in this species were studied most recently by Christiansen (1973) who reared larvae in the laboratory and compared results with earlier work. She found this species to be ovigerous the year round in Oslo Fjord, Norway. From ovigerous females collected in May and maintained in laboratory running sea water of about the same tem-perature-salinity as outside $\left(6.5^{\circ} \mathrm{C}\right.$ at $32.9 \%$ and $7^{\circ} \mathrm{C}$ at $34.8 \%$ o), larvae hatched the following April. One female produced new eggs a few weeks later. Larvae were reared at $10^{\circ}, 15^{\circ}$, and $20^{\circ} \mathrm{C}$, some with water temperature abruptly raised, others gradually raised to the rearing temperature, but there were no observed differences between these two sets. Hatching was observed under the binocular microscope. There is a prezoeal stage which probably lasts a very short time and was never seen to swim. The two zoeal stages, megalopa and first crab stage, were described.

Temperature influenced rate of development and survival of the larvae, first crab being reached in $75.7(\overline{\mathrm{x}})$ days with $22 \%$ survival at $10^{\circ} \mathrm{C}, 57(\overline{\mathrm{x}})$ days with $11 \%$ survival at $15^{\circ} \mathrm{C}$, and attainment only of megalopa in 20.5 ( $\overline{\mathbf{x}}$ ) days with $21 \%$ survival at $20^{\circ} \mathrm{C}$. None survived to first crab at this last temperature.

## Subfamily Tychinae

Orbit consisting, if complete, of supraocular eave and postocular spine; intercalated spine lacking ... [but] . . . longer spinous outgrowths on supraocular eave and on postocular spine for most part present. Shape of body elongate, somewhat truncate in front, often provided behind with median spine or outgrowth (Balss 1929; Williams, et al. 1977).

## Key to Genera and Species

(Modified after Garth 1958)

1. Eyes furnished with projecting and tubular commencing orbits

Pitho lherminieri
Orbit completely unprotected below; eyes protected above by lamellate projection consisting of supraocular eave and outgrowth of hepatic region

Tyche emarginata

## Genus Pitho Bell 1835

Garth 1958:162.-Guinot 1964a:44.

## Pitho lherminieri (Schramm)

Figs. 246, 259a
Othonia lherminieri Schramm, in Desbonne and Schramm 1867:20.

Pitho lherminieri.-Hay and Shore 1918:459, pl. 38, fig. 8.-Rathbun 1925:362, text-fig. 117b, pl. 128, figs. 1-2; pl. 129, figs. 1-2; pl. 252, fig. 2.-Williams 1965:246, figs. 224, 233A.-Coelho and Ramos 1972:210.—Powers 1977:61.

Recognition characters.-Carapace as broad as long in adult males, longer than broad in other individuals, narrow behind in males, broader in females, roughened with tubercles of different sizes, and


Fig. 246. Pitho lherminieri (Schramm). Male in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).
adorned with scattered hooked hairs. Frontal teeth forming rostrum more advanced than orbital angles. Anterolateral margins armed with 5 strong teeth, exclusive of postorbital tooth; first tooth largest, second and third subequal, fourth and fifth much smaller, second occasionally bilobed. Orbits small, tubular, deep. Antennae short, with stiff hairs on borders; basal article lamellate, forming floor of orbit; second article flat, short, and broad; third article smaller, flattened.

Chelipeds of adult male from 1.5 times to nearly twice length of body; merus subcylindrical; carpus and hand more or less compressed and distinctly angled along margins; fingers of adult male spatulate, touching only at extremity. In female and young male, fingers short and weak, evenly dentate, with margins in contact.

Abdomen of both sexes with 7 free segments.
Measurements in mm.-Carapace: male, length 26, width 24 ; female, length 18 , width 17 .
Variation.-In females and young males the carapace is more tuberculate than in old males, the lateral teeth sharper, and the last two teeth more prominent.
Color.-Dirty brownish yellow (Schramm in Rathbun 1925).
Habitat.-This species has been found on a variety of bottoms including mud, sand, shell-sand, shell, rock and coral, and grass (Rathbun 1925); 1 to 51 m , rarely 220 m .

Type-locality.-Guadeloupe, in cavities of the keys.
Known range.-Off Beaufort Inlet, N. C., to west Florida; Veracruz, Mexico; West Indies to Islet of São Sebastião, São Paulo, Brazil.

Remarks.-Ovigerous females are known from May to November in the Bahamas and Florida, and in December from Brazil (Rathbun 1925 and USNM).

Hinsch (1973) described sperm structure of the male.

Randall (1967) reported P. lherminieri from stomach contents of the longspine squirrelfish, Holocentrus rufus.

## Genus Tyche Bell 1835

Garth 1958:172.-Guinot 1964a:44.

## Tyche emarginata White

Figs. 247-248, 259b
Tyche emarginata White 1847a:206.-Hay and Shore 1918:461, pl. 39, fig. 4.-Rathbun 1925:508, pl. 272; pl. 273, figs. 7-12.-Garth 1946:406-408, text-fig. 1.-Williams 1965:247, figs. 225, 226, 233B.-Williams, Shaw, and Hopkins 1977:890, figs. 4, 7, 10b.-Powers 1977:62.

Recognition characters.-Carapace oblong-oval, flattened, with lamellate expansions in front covering ocular peduncles, and another prolonged and bilobed behind, stout hooked hairs on rostrum and prominent elevations. Front wide, with 4 long horns, lateral horns forming anterior angles of orbit, divergent, longer and more elevated than submesial rostral horns. Ocular peduncles entirely uncovered below. Gastric region swollen, with 3 low tubercles, 2 anterior, and a third posterior and median; cardiac region depressed, with 3 small tubercles. Lateral borders straight and nearly parallel at hepatic regions, rounded at branchial regions. Dorsal surface of hepatic region concave; branchial region with large tubercle on anterior


Fig. 247. Tyche emarginata White. Male in dorsal view, legs of left side not shown, 5 mm indicated (from Williams 1965).


Fig. 248. Tyche emarginata White. Left outer maxilliped (redrawn from Garth 1946).
lobe, and prominent tuberculate crest above lateral margin. Exopod of third maxilliped with basal protuberance recurving to cover base of ischium, merus inserting deeply into outer distal portion of ischium by similar but less developed process, inner margin of ischium strongly dentate.
Chelipeds of male more than twice length of postorbital part of carapace; palms somewhat dilated and compressed; fingers gaping at base, dentate throughout length. Walking legs ornamented with stout hooked hairs; dactyls spinulous on middle third, spinules increasing in size distally.
Abdomen of both sexes with 7 free segments.
Measurements in mm.-Carapace: male, length to tip of submesial horns 19.1, width 10.8 ; female, length to tip of submesial horns 38 , width 23 .

Color.-Generally yellowish gray; carapace greenish above, with 2 triangular white spots; blackish above base of legs (various authors).
Habitat.-The species has been reported from rocky or coarse shell bottoms (Rathbün 1925); 1 or 2 to 36 m .
Type-locality.-West Indies.
Known range.-Off Beaufort Inlet, N. C.; through Bahamas to west coast of Florida.
Remarks.-Garth (1946) gave a detailed comparison of this species with its Pacific counterpart $T$. lamellifrons. He also (1952) named T. potiguara from northern Brazil, the type-locality of which Williams (1965) included in the distribution of T. emarginata. Williams, et al. (1977) gave detailed comparisons of selected mouthparts and male-female reproductive structures in the subfamily Tychinae.

## Subfamily Epialtinae

Manning and Holthuis 1981:255.
Eyes without true orbits; eyestalks very short or sometimes obsolescent, either concealed beneath anteriorly produced supraocular spine, or sunk in sides of huge beaklike rostrum; postocular spine or process sometimes present, but not excavated for reception of retracted eye. Basal antennal article elongate but truncate-triangular. External maxillipeds with merus as broad as ischium. Dactyls of walking legs prehensile or subchelate; last 3 pairs of legs often disproportionately short compared with first pair (Alcock 1895 [for Acanthonychinae]). Postocular spine not cupped (except in Sphenocarcinus); rostrum either simple or 2 -spined; palp on third maxilliped arising from anterointernal angle of merus (Rathbun 1925). First pleopod of male medium stout, apex most varying (ham-mer-shaped; divided into 3 or 4 lobes; etc.); second pleopod short (Stephensen 1945).

## Key to Genera and Species

1. Rostrum single or secondarily bifurcate at tip; 6 free abdominal segments in male, 5 in female

Epialtus dilatatus
Rostrum double, deeply forked; 7 free abdominal segments in both sexes
Sphenocarcinus corrosus

## Genus Epialtus H. Milne Edwards 1834

Garth 1958:227.

## Epialtus dilatatus A. Milne Edwards

Figs. 249, 259d
Epialtus dilatatus A. Milne Edwards 1878:140, pl.

27, figs. 4-4b.-Rathbun 1925:153, text-fig. 53j, pl. 45, fig. 2.-Williams 1965:249, figs. 228, 233D.-Powers 1977:42.
Recognition characters.-Small species. Carapace broad, subpentagonal, almost smooth, with hepatic and branchial projections more or less laminate. Rostrum broad, somewhat triangular, short, bilobed at tip, slightly depressed on median line


Fig. 249. Epialtus dilatatus A. Milne Edwards. Male in dorsal view, legs of left side not shown, 3 mm indicated (from Williams 1965).
dorsally with depression continued ventrally and limited by 2 crests uniting posteriorly in acute angle. Eyes small; preorbital angles scarcely marked; postorbital teeth minute. Basal article of antenna triangular, movable part concealed beneath rostrum.
Chelipeds moderate in size; carpus with 4 longitudinal crests; hand slightly enlarged distally, upper margin blunt, defined by depression on either side; fingers short and stout. Walking legs with slight tuft of hair on lower margin of propodi.
Abdomen of male with 6 , female with 5 free segments.
Measurements in mm.-Carapace: male, length 17, width 13 ; female, length 10 , width 8.
Variation.-Members of the genus Epialtus are variable in a number of respects. The hepatic expansion varies in shape and the rostrum varies from triangular to suboblong in shape. Williams and Pearse (1951) listed specimens that could not be placed with certainty in dilatatus.
Rathbun (1925) recognized from southwestern Florida an elongate form of E. dilatatus which has a longer rostrum and slightly different lateral expansions than the typical form. The complex should be reviewed as more material becomes available.
Habitat.-The species has been reported from shell reefs and coarse coral sand, and the elongate form has been found on sandy-grassy bottoms as well; 4.6 to 22 m .
Type-locality.-St. Thomas.
Known range.-Off Beaufort Inlet and New River, N. C.; southwest Florida; Yucatan; Bahamas to St. Thomas.

Remarks.-Ovigerous females are known from April through summer in Florida, June in North Carolina, September in Brazil, and November in Puerto Rico (Rathbun 1925; USNM). An ovigerous female collected in May from Biscayne Bay, Fla., produced 60 larvae whose development was followed in the laboratory (Yang 1968). Reared in bay water $33-36 \%$ at $25^{\circ} \mathrm{C}$, larvae fed Artemia nauplii passed through the standard stages for spider crabs. Zoea I lasted 2.5 ( $\overline{\mathrm{x}}$ ) days; zoea II, 3 ( $\overline{\mathrm{x}}$ ) days; megalopa, 6.5 ( $\overline{\mathrm{x}}$ ) days. Only 5 individuals reached first crab and none reached the second crab stage. Yang described the stages and compared them to other known developments of Epialtinae (eight species to that date) and to representatives of other subfamilies.

## Genus Sphenocarcinus A. Milne Edwards 1875

Garth 1958:217.

## Sphenocarcinus corrosus A. Milne Edwards

Figs. 250, 259c
Sphenocarcinus corrosus A. Milne Edwards 1875, pl. 17, figs. 5-5c.-1878:136.-Hay and Shore 1918:460, pl. 39, fig. 1.-Rathbun 1925:187, textfig. 73, pl. 62; pl. 223, figs. 3-5.-Williams 1965:248, figs. 227, 233C.
Recognition characters.-Carapace subpentagonal, broad behind, anterolateral margin concave, posterolateral margin convex. Dorsal surface deeply channeled, leaving symmetrical, coarsely punctate, or eroded elevations in regular pattern as follows: longitudinally placed, trefoil-shaped gastric, transversely placed cardiac with 2 deep posterior indentations, transversely elongate intestinal, paired laterals extending from near lateral angles to near eyes, and paired small postocular and larger supraocular elevations; margins of all elevations sharply defined with surface finely eroded. Rostrum usually longer than carapace, formed of 2 pointed horns contiguous to near tips, slightly divergent in old individuals. Eyes deeply sunk between 2 low smooth excrescences. Basal antennal article truncate, antennal flagellum hidden beneath rostrum. Epistome long, narrow.

Chelipeds weak; first pair of walking legs longer than others and exceeding length of chelipeds by more than length of dactyl.

Abdomen in both sexes with 7 distinct segments.
Measurements in mm.-Carapace: male, length 13 , width 7 ; ovigerous female, length 23 , width 11 .
Variation.-Divergence of the rostral horns varies individually. In some specimens the horns are contiguous nearly to the tip, in others the horns


Fig. 250. Sphenocarcinus corrosus A. Milne Edwards. Male in dorsal view, legs of left side not shown, 2 mm indicated (from Williams 1965)
may be divergent for half their length, and in still others there is no evidence at all of bifurcation.
Color.-Orange-red.
Habitat.-165 to 271 m , rarely 365 (?) m.
Known range.—Off Cape Lookout, N. C., Gulf of Mexico (Goeke and Shaw 1980) to Barbados.

Remarks.-Ovigerous females have been reported from North Carolina in April (Rathbun 1925).

## Subfamily Pisinae

Eyes with commencing orbits; each eye retractile into sometimes large, blunt, usually isolated, cupped postocular tooth or lobe, but never to such extent as completely to conceal cornea from dorsal view; usually prominent supraocular eave with anterior angle sometimes produced forward as a spine; eyestalks short. Basal antennal article broad, at least at base, anterior angle generally produced to form tooth or spine. Merus of external maxilliped broader than ischium owing to expansion of anteroexternal angle, and carrying palp at anterointernal angle. Rostrum [except in Neodoclea among New World forms] 2-spined; legs often very long (Alcock 1895). First pleopod medium stout to slender, usually apically somewhat tapering, but apex extremely varying (blunt, acute, filiform, straight, geniculate, etc.); second pleopod short (Stephensen 1945).

## Key to Genera and Some Species

(Adapted in part from Garth 1958)


Genus Coelocerus A. Milne Edwards 1875
Rathbun 1925:446.

## Coelocerus spinosus A. Milne Edwards

Figs. 251, $259 i$
Coelocerus spinosus A. Milne Edwards 1875:85, pl. 18, figs. 2-2b.-Rathbun 1925:446, text-fig. 130,
pl. 263; pl. 264, figs. 1, 2.-Felder 1973:49, pl. 7, fig. 6.—Powers 1977:50.
Libinia cavirostris Chace 1942a:86, pl. 27.

Recognition characters.-Covered almost everywhere except on fingers and greater part of dactyls on walking legs with short, close pile. Carapace swollen, spinose; 6 median spines ( 2 gastric, 1 urogastric, 2 cardiac, 1 intestinal), lateral gastric spine


Fig. 251. Coelocerus spinosus A. Milne Edwards. Female in dorsal view, 5 cm indicated (from Rathbun 1893).
anterolateral to each side of anteriormost median spine; 5 spines above lateral margin, first (hepatic) strongest, small dorsal hepatic mesial to it; 6 dorsal branchial spines, 4 arranged in 2 longitudinal rows of 2 each; 1 spine above posterolateral margin in line with intestinal spine. Rostrum short, ascending extremity slightly bifid; in form of gutter open below, lateral margins folding under; longitudinal depression at base between orbits. Orbit with narrow buttonhole fissure above and below, preocular angles spiniform, postocular cup produced laterally. Basal antennal article with strong anterior tooth pointing downward, proximolateral tooth smaller; small spine immediately behind article, another at buccal angle; 2 strong pterygostomian spines.

Legs stout. Chelipeds of female no longer, but those of male longer than next leg; merus with blunt spine near each end; palms of male elongate, granulate, those of female diminishing in width dis-
tally; fingers finely toothed on cutting edges, proximal gape in male. Walking legs with short, blunt, terminal spine on merus.

Abdomen of both sexes with median spine on first 2 segments, lateral lobes on second.

Measurements in mm.-Carapace: male, length 119 , width including spines 102 ; female, length 108 , width including spines 94 .

Variation.-Spines are proportionally longer and the extremity of the rostrum is more deeply bifid in the young. There is a tendency to doubling of the branchial spines.
Habitat. - 17 to 71 m .
Type-locality.—Off Florida, 34.75 m .
Known range.—Off Cape Fear, N. C., to near Cape Canaveral, Fla. (B. B. Boothe, Jr., personal communication); W Florida to E of Mississippi River delta.

Remarks.-Coelocerus spinosus was placed in the Mithracinae by Garth (1958) but allied to Stenocionops in the Majidae by Rathbun (1925). The general shape of the carapace, ventral aspect of the rostrum, and conformation of the orbital region resemble those features in Libinia (see also Chace 1942a), and the male pleopods resemble those of both L. dubia and emarginata as well as of Stenocionops furcata coelata and spinimana. There is little doubt that the species is close to the limits of both the Pisinae and Mithracinae, but in my opinion it is most closely allied to the former.

Recent records from the southeastern United States have extended the known range of this species outside the Gulf of Mexico. An ovigerous female is known from west Florida (no date).

## Genus Libinia Leach 1815

Garth 1958:322.

## Key to Species

1. Median line of carapace with about 6 spines; spine on anterolateral angle of buccal frame . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . L. dubia
Median line of carapace with about 9 spines; anterolateral angle of buccal frame without spine
L. emarginata

## Libinia dubia H. Milne Edwards

## (Spider crab)

Figs. 252, 259g
Libinia dubia H. Milne Edwards 1834:300, pl. 14bis, fig. 2.-Hay and Shore 1918:456, pl. 38, fig. 5.Rathbun 1925:313, text-figs. 105-106; pls. 114115; pl. 122, fig. 1.-Boone 1927:37.—Williams

1965:253. figs. 232, 233G.-Felder 1973:52, pl. 7, fig. 8.-Powers 1977:63.

Recognition characters.-Similar in general characters to L. emarginata but with more pyriform carapace and fewer spines; median row with but 6 spines, 2 gastric, 1 genital, 2 cardiac, and 1 intestinal; preorbital, subhepatic, and lateral spines stronger than in L. emarginata, but spiniform tu-
bercles few or wanting altogether. Rostrum slightly longer and more definitely bifid than in L. emarginata. Anterolateral angle of buccal frame armed with spine.

Measurements in mm.-Carapace: male, length 102, width including spines 82 ; ovigerous female, length 74 , width 64 ; mature female, length 38 , width 34 .

Variation.-Dorsal spines and tubercles variable in length.
Habitat.-Found on almost all types of bottom in the shallow ocean and saltier estuaries. Occasionally, large individuals are found in pools left by falling tide. Immature individuals are often completely overgrown with sponges, hydroids, ascidians, barnacles or worm tubes, but the larger ones are usually almost clean. Near shore to 46 m .

Type-locality.-"Cotes des Etats-Unis."
Known range.-Cape Cod, Mass., to southern Texas; Bahamas and Cuba.

Remarks.-Some authors attribute a geologic record to this species extending from the Upper Miocene of Virginia (Rathbun 1935) through the Pleistocene of New Jersey (Rathbun 1935) and Maryland (Easton 1940). Glaessner (1969) more conservatively limited North American records for Libinia to closely related L. emarginata, only from the Pleistocene.
Tabb and Manning (1961) found this species common in Florida Bay, and Dragovich and Kelly (1964) reported it as the most common spider crab in Tampa Bay; Wilson (1969) found young L. dubia in canal-lake waters of low salinity ( $0-10 \%$ ) in southwestern Louisiana.

An association of this species with the jellyfish Stomolophus meleagris has been reported. The crabs


Fig. 252. Libinia dubia H. Milne Edwards. Male in dorsal view, legs of left side not shown, 10 mm indicated (from Williams 1965).
have been found in the subumbrellar space, and on occasion small specimens have been taken from the genital pits. Corrington (1927) found medusae with crabs between Sullivan Island and Isle of Palms, S. C., in May, and Gutsell (1928) found the association in the vicinity of Cape Lookout, N. C., in summer and fall. The crabs, found in adult jellyfishes, varied in length from 3 to 37 mm . Near the mouth of the Patuxent River, Md., in late August and early September, 1963, at depths to 3 m in water 30 m deep, Jackowski (1963) found small L. dubia living on and within many medusae of Aurelia aurita. Concurrently, numerous young harvestfish were observed feeding upon the medusae. Eleven $L . d u$ bia collected from 10 jellyfish had carapace lengths of $10-25 \mathrm{~mm}$. Seven of these were clinging to the ventral surface of the subumbrella, two to the manubrium between oral arms, and two were in mesoglea of the umbrella. Several crabs appeared to be feeding upon a living medusa later in the laboratory. Crabs pulled fragments of tissue from the exumbrella with their chelipeds and ate them. None showed ill effect from eating or living in medusae. Incidence of crabs associated with swarms of jellyfishes (Chrysaora quinquecirrha, Stomolophus meleagris, and Chiropsalmus quadrumanus) in Mississippi Sound, Miss., varied from 0 to $100 \%$, being highest in populations trawled from the bottom (Phillips, et al. 1969); moreover, any scyphomedusae introduced into aquaria containing $L$. dubia harbored some crabs within a few hours. The crabs actively fed on medusae.
Ovigerous females are recorded from January to June in Florida, May in Connecticut, August in New Jersey, and April to August in North Carolina (various authors, museum records, and H. J. Porter, personal communication).

From laboratory cultures, Sandifer and Van Engel (1971) described two zoeal stages and a megalopa, the usual developmental sequence for spider crabs. Complete larval development required about nine days in water of $22 \%$ salinity at $25.5^{\circ}-28.5^{\circ} \mathrm{C}$. Zoeal molting behavior was observed on several occasions in which zoea I molting to zoea II apparently uses its old abdominal skin as a brace against which to exert pressure while withdrawing its carapace and appendages from the old skin. This "bracing" behavior was not seen in the molt from zoea II to megalopa. Only uninjured larvae were able to "brace" and molt successfully.

Planktonic larvae of Libinia spp. were found in samples taken from the mouth of Chesapeake Bay to lower York River from June to October, most common in July and September, in water of 15.74 to $32.34 \%$ salinity and $20^{\circ}$ to $28.1^{\circ} \mathrm{C}$ respectively (Sandifer, 1973d). Most of the larvae (zoea I and
II) occurred in bottom samples. Fish (1925) found planktonic larvae of Libinia spp. at Woods Hole from June to October, Hillman (1964) found them from early July to mid-September in Narragansett Bay, R. I., and Deevey (1964) found them from July to October in Delaware Bay. Larvae of Libinia spp. were found rarely at a station 1.6 km off Beaufort, N . C., in May, July and August at $8-\mathrm{m}$ depth; at stations 6.5 km offshore they occurred rarely in July at this depth (Dudley and Judy 1971).

Pearse (1929), studying the survival rates of various estuarine crabs in dilutions of sea water and in air, found $L$. dubia least able to survive desiccation and dilutions of sea water. Ayers (1938), in a study of the relationship of habitat to oxygen consumption among certain estuarine crabs, found that L. dubia lives much of the year in relatively deep [estuarine] water where there is low oxygen content, sometimes very little. The species is correspondingly sluggish and slow. Gray (1957) showed that gill area per gram of weight in this species is small.

Pearse (1952b) reported Octolasmis lowei (=mulleri) on the gills and mouth parts, and Chelonibia patula on the carapace of $L$. dubia in Texas.

## Libinia emarginata Leach

(Spider crab)
Figs. 253, 259h
Libinia emarginata Leach 1815:130, pl. 108.-Hay and Shore 1918:456, pl. 38. fig. 6.-Rathbun 1925:311, text-figs. $103-104$; pls. 110-113.Williams 1965:252, figs. 231, 233H.—Felder 1973:52, pl. 1, fig. 7.-Powers 1977:64.

Recognition characters.-Carapace orbicular, about 1.16 times longer than wide, spinose and tuberculate, with dense covering of short hairs. Larger spines arranged as follows: median row of about 9 extending from near base of rostrum to posterior border consisting of 4 gastric, 1 genital, 2 cardiac, and 2 intestinal; lateral marginal spines 5 on each side; 2 subhepatic spines; 2 or 4 spines above posterior margin, aside from median spine, and about 4 dorsal branchial spines; spiniform tubercles scattered about among larger spines. Gastric region marked off by deep groove. Rostrum slightly depressed, emarginate or bifid at tip; median groove between eyes. Orbits with prominent preorbital spine, 2 spines beneath on basal article of antenna; 1 fissure above and 1 beneath. Anterolateral angle of buccal frame spineless.

Chelipeds equal, larger in male; hands granulate; fingers smooth, evenly denticulate, and about
half as long as hand. Walking legs long, hairy, unarmed, often unequal and asymmetrical (result, perhaps, of injury and subsequent regeneration).

Measurements in mm.-Carapace: male length 124, width 124 ; ovigerous female, length 69 , width 66 .

Variation.-The number of median spines in the gastric region is subject to variation in size and number.

Color.-A brownish or dirty yellow.
Habitat.-Found on almost any kind of bottom; shore to 49 m , occasionally to 124 m .

Type-locality.—Unknown.
Known range.-Windsor, Nova Scotia, to western Gulf of Mexico.

Remarks.-The young of L. emarginata and L. dubia are difficult to distinguish. Wass (1955) pointed out useful distinguishing marks. "The rostrum of L. dubia is much longer, forming a $V$; the carapace is not so wide, and there is but one spine on the intestinal region . . . . whereas L. emarginata has two." Andrews (1883) gave a complete anatomical study of L. emarginata, and Meiss and Norman (1977a, b) almost a century later compared the stomatogastric ossicles and musculature to that in penaeideans, astacideans and anomurans, finding the structure to reflect generally accepted concepts of the phylogenetic position of brachyurans.

Hildebrand (1954) reported this species as the most common larger spider crab on the western Gulf of Mexico shrimping grounds. It was most common in July, at which time ovigerous females were observed. Juveniles were observed riding the bell of the scyphozoan Stomolophus meleagris, a habit noted by others for the young of $L$. dubia. Winget, et al. (1974) found L. emarginata seasonally commonest along, a breakwater in Delaware Bay in


Fig. 253. Libinia emarginata Leach. Male in dorsal view, legs of left side not shown, 20 mm indicated (from Williams 1965).
spring and summer, and also common in mud of sloughs where no other species of crab occurred in a salinity range of 15 to $32 \%$. They found a malefemale ratio of $3: 1$ in winter when the animals were less abundant.

In addition to the Texas records, ovigerous females are recorded from February to May in Connecticut, May to early September at Woods Hole, Mass. (Hinsch 1968), August in New Jersey, and March-April (H. J. Porter, personal communication) and June-August (Dudley and Judy 1971) in North Carolina. Eggs at oviposition are a bright orange-red color but change to brown as development progresses (Hinsch 1968). Ovigerous females taken in fall and spring in South Carolina and from Narragansett Bay, R. I., during summer, isolated in chambers under controlled conditions, produced broods of larvae which were reared in an array of salinities ( $15-45 \%$ ) and temperatures $\left(15^{\circ}-30^{\circ} \mathrm{C}\right)$ on a diet of Artemia nauplii, and were described and illustrated by Johns and Lang (1977). There are two zoeal stages and a megalopa. Optimal conditions for development differed for larvae from the two localities, probably showing latitudinal adaptations. At $30 \%$ salinity and $20^{\circ} \mathrm{C}$ Rhode Island larvae attained second zoea in five days, megalopa in eight and first crab in 14; South Carolina material reached the same stages in 3,6 and 14 days at $25^{\circ} \mathrm{C}$. The larvae showed no significant differences from those in plankton, but first stage larvae from South Carolina were smaller than those from Rhode Island. The zoeae cannot be differentiated from those of L. dubia, but megalopae of L. dubia have one cardiac protuberance on the carapace, $L$. emarginata two.

Bigford (1978) showed that survival is greater and development time shorter for larvae fed diets including Artemia salina nauplii either alone or in combination with other foods. Survival is also correlated with amount of Artemia nauplii fed and can probably be attributed to the high fat content in these nauplii (Sulkin 1975).
Hinsch (1969) stated that factors governing sexual maturation and onset of spermatogenesis in this species are unknown. Spermatogenesis occurs in testes of males having a carapace length as short as 19 mm ; the vas deferens from these animals contained spermatophores filled with spermatozoa that appeared to be structurally identical to those of larger males at light-microscope and ultrastructural magnifications. Spermatophores are found within the vas deferens at all times of year. Hinsch (1969, 1973) described ultrastructure of sperm. More detail on structure of the vas deferens and comparison with the virtually identical structure in L. dubia were given by Hinsch and Walker (1974);
in fact, the same structure and function were also found for Heterocrypta and Stenorhynchus. The male reproductive tract produces sperm long before the crab has attained full size and, presumably, ability to mate. The authors observed a male L. emarginata mating with a female for short periods (5-7 minutes) and mating frequently with several different females over a period of several days.

In an aquarium, females produced a new brood in less than 12 hours after releasing zoeae (Hinsch 1968). When females were about to release zoeae, males in the same aquarium could be seen walking on tips of their dactyls, apparently searching, and often fighting with each other. Under these conditions, two definite behaviors were associated with release of zoeae.

First, encounters with non-gravid females or females which had either released larvae or were about to do so generally resulted in the females mating in the "hard" condition (see also Hartnoll 1969). Whether the female first mates at times of final molt to adulthood is not known. Ovigerous females with eggs in early stages of development were never observed to mate. The male first grasped legs of the female and positioned her beneath him with the sterna face to face, then with his chelae grasped the female by the hepato-pterygostomian region. The abdomen of the female was pulled down and bent back at the same time the male's abdomen was lowered. Copulation then began and the male frequently rotated over onto his carapace holding the female above him. When copulation was completed, the male resumed a walking position, released his hold on the anterior part (head) of the female, once again grasped her by the legs and then released her.

Second, in a number of cases a female about to release zoeae would be captured by a male or fought over by two males only to be lost to a third. Eventually, a male grasped the female by the legs with his chelae, moved her behind him, their carapaces touching and the axis of their bodies at right angles to each other. The tips of his fifth legs were inserted beneath the abdominal flap to hold her in this position after which he often retreated to a protected area and stood with chelae outstretched, fending off other males. Held in this position the female released the zoeae, then cleaned remaining eggs cases from her pleopods, following which the male released her. Juvenile males or females and females with broods in early stages were never objects of this "obstetrical" behavior. Hinsch thought that predictability and specificity of these patterns suggested their possible initiation by pheromone(s).

Kalber and Costlow (1968) and Kalber (1970)

