

slender, third joint from proximal end of 7-segmented carpus longest. Third to fifth legs bearing curved spines on flexor margin of dactyls, penultimate spine strong, shorter than terminal spine but making tip biunguiculate; meri bearing small lateral spines, third with about 5–6, fourth with about 3–5, fifth with about 1–2, distalmost on each leg longest.

Abdomen with pleura of first 3 segments rounded; third with posterodorsal margin produced slightly posteriorly; fourth segment with small posteroventral spine; fifth similar though with spine directed more posteriorly; sixth with even less prominent posteroventral spine and above it an acute lateral spine with ventral shoulder overhanging base of telson. Telson with 3 pairs of terminal spines, outermost shortest, and 3–5 pairs of dorsolateral spines.

Measurements in mm.—Length of body: male 47; female 74; smallest ovigerous female (Norway) 39 (Greve 1963).

Variation.—Females are stouter than males; for a given carapace length, females have greater carapace height than males, a linear relationship probably reflecting differences in room needed for gonads (Allen 1962). The ventral part of the female rostrum is definitely convex, that of the male slightly so, but intermediates exist, and the dimorphism becomes more pronounced with age (Greve 1963). Dons (1915) showed variant rostral shapes of *S. securifrons* (= *liljeborgii*).

Color.—“Body bright red. Extremities with ribbons of red. Ends of claws and eyes brownish black” (Greve 1963). “Bright red with yellow and white spots” (Squires 1965a).

Habitat.—Mainly hard bottom, but sometimes on mud (Greve 1963; Allen 1966); 20 to 1200 m, mostly 35 to 90 m (Holthuis 1950).

Type-locality.—Lofoten, [Norway] on sandy bottom, 40 fm.

Known range.—Greenland; Nova Scotia to off Delaware Bay; arctic Alaska; Iceland; Spitzbergen and Murman coast to south coast of England and west and southwestern Ireland (Holthuis 1947, 1950; Smaldon 1979).

Remarks.—Ovigerous females in the USNM collection are from Hudson Canyon off New York in November and February, and the Gulf of Maine in September. Breeding indications in these spotty records are in agreement with times in published reports. From Foxe Basin, Frobisher and Ungava bays, Squires (1965a) found one ovigerous female in July, but 75% were ovigerous in December. They are known from November to May in southern and western Norway (Holthuis 1950; Greve 1963).

Pike (1954) showed from study of gonads and

other structures that *S. liljeborgii* is a dioecious species; no protandrous hermaphrodites have been seen. He found that most males in the Firth of Clyde, Scotland, become sexually mature by age 7–9 months; some of these may die after fertilizing females and the majority die after fertilizing females during a second year (age 18 months). His study suggested that only a small proportion of females breed in their first year, all breed during the second year, and a few appear to live for a third year. His count on egg production was 130–160 in the first year and 450–650 in the second year. Egg laying begins at the end of November and hatching is complete by the end of March. Off north-eastern England, females are ovigerous from December to April, bear 350 to 850 eggs once during the season for a period of 12–13 weeks, and a few spawn during a second year. Some individuals are thought to live up to 2½ years (Allen 1962, 1966).

The larval stages of *S. liljeborgii*, reviewed by Pike and Williamson (1961), are very similar to those of *S. spinus*, there being minor differences in spination.

Spirontocaris liljeborgii has a large mandible with flat crushing molar surface (Allen 1962, 1966). The species feeds primarily on foraminiferans and to some extent on gastropods, but also on crustaceans, hydroids, pelecypods, annelids, etc.

A bopyrid, *Hemiarthrus abdominalis*, is parasitic on this as well as other species of *Spirontocaris* (Allen 1962). No parasitized females bear eggs, and their size is generally smaller than that of unparasitized individuals.

Spirontocaris phipp sii (Krøyer)

Fig. 92

Hippolyte Phipp sii Krøyer 1841:575.

Spirontocaris phipp sii.—Holthuis 1947:8 (synonymy).

Spirontocaris phipp si.—Leim 1921:142, pl. 6, fig. 13.—

Greve 1963:33, fig. 2C, D.—Couture and Trudel 1968:867, fig. 8.

Recognition characters.—Rostrum deep, dorsal margin about horizontal, tip reaching to or beyond antennular peduncle in males and females respectively; upper margin with rather closely spaced large teeth becoming smaller near tip and continuous with more widely spaced teeth on middorsal carina not extending beyond posterior ⅓ of carapace; some sexual dimorphism in shape and tooth number, that of females deeper with 9–13 teeth in dorsal series and 3–6 ventrally, that of males less deep with 7–12 in dorsal series and 1–4 ventrally; lateral carina slanting obliquely upward to near tip. Carapace

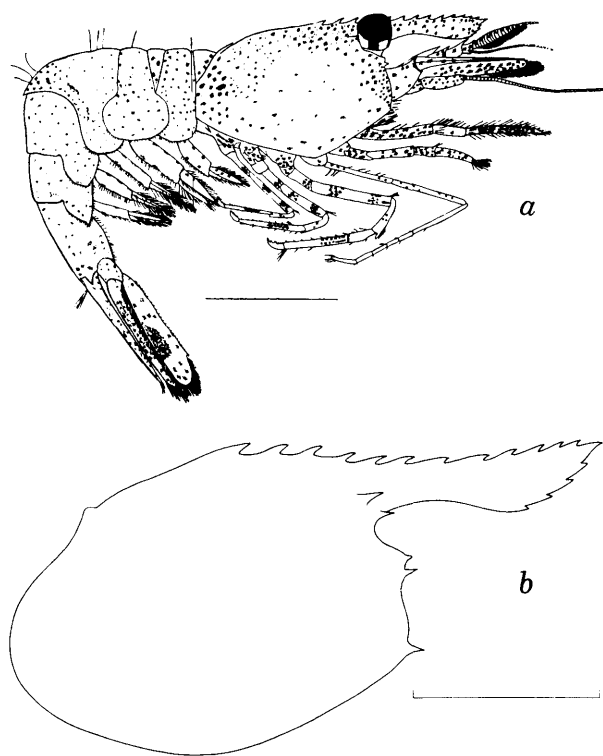


Fig. 92. *Spirontocaris phippisii* (Krøyer. *a*, Female in lateral view, approx. 3 mm indicated (from Leim 1921); *b*, carapace in lateral view, 5 mm indicated (from Williams 1974c).

bearing 2 supraorbital spines on each side, upper one definitely larger; suborbital lobe distantly flanked by antennal spine; anteroventral margin almost straight; pterygostomial spine small and acute. Antennular peduncle with basal article bearing rather broad distolateral spine and ventromesial spine; stylocerite strong, acute, mesial margin tapered somewhat obliquely to tip, reaching about to dorsal margin of second article bearing strong, slender distolateral spine; thick lateral ramus with short distal flagellum, slender mesial ramus longer. Antennal peduncle reaching about as far forward as stylocerite; basal article with ventrolateral spine and dorsolateral lobe; scale with lateral margin straight, lamella with rounded tip exceeding distolateral spine. Third maxillipeds reaching beyond antennal scale, exopod and epipod present.

First 3 legs with epipods. First leg moderately stout, reaching about half length of palm beyond antennal peduncle; fingers darkened at tips, that of dactyl cleft to accommodate tip of fixed finger; palm about length of merus; merus with small proximolateral spine. Second leg much longer and more slender, third joint from proximal end of 7-segmented carpus longest. Third to fifth legs bearing curved spines on flexor margin of dactyls, penultimate spine strong, shorter than terminal spine

but making tip biunguiculate; meri bearing small lateral spines, third with about 2–7, fourth with about 2–6, fifth with 1–3, distalmost on each leg longest.

Abdomen with pleura of first 3 segments rounded; third with posterodorsal margin produced slightly posteriorly; fourth segment with small posteroventral spine; fifth similar though with spine directed more posteriorly; sixth with even less prominent posteroventral spine and above it an acute lateral spine with ventral shoulder overhanging base of telson. Telson with 3 pairs of terminal spines, outermost shortest, and 2–5 pairs of dorsolateral spines.

Measurements in mm.—Length of body: male 28; female 45.

Variation.—Variation in number of rostral spines trends toward a smaller number in males (Greve 1963). Dons (1915) showed variations in tooth pattern on the rostrum as well as the sexual dimorphism in depth for *S. turgida* (= *phippisii*). The supraorbital spine closest to the orbital margin is variably smaller than the spine posterodorsal to it, and rarely is absent (Leim 1921).

Color.—Rather large brownish red spots over body and appendages; more closely spaced on upper half, anterior and posterior end of carapace than on its remainder; also grouped on posterodorsal margin of third abdominal segment and on uropods (Leim 1921). Reddish brown with small light spots (Squires 1965a).

Habitat.—Chiefly firm bottom among algae in usually low positive temperature (Heegaard 1941); 10 to 270 m (Holthuis 1947; Squires 1965a).

Type-locality.—Spitsbergen, Norway's west coast (and Greenland?).

Known range.—Circumarctic southward to near Martha's Vineyard; northern Norway; Shumagin Islands, Alaska; Plover Bay, Siberia (Holthuis 1947; Squires 1965a).

Remarks.—In the USNM collection, ovigerous females are present from Franz Joseph Land in June, northern and northeastern Greenland from June to August, Labrador in August and Nova Scotia in September, arctic Alaska in August and September, and Foxe Basin, Canada, and Plover Bay, Siberia, in September. Breeding indications in these spotty records are elaborated by accounts of several authors. Heegaard (1941) found ovigerous females in east Greenland during July and August (as *S. turgida* = *phippisii*); MacGinitie (1955) found them at Point Barrow, Alaska, in mid-October. Squires (1965a) indicated an annual autumn spawning period for the species in Foxe Basin and found ovigerous females from June to early August around the Queen Elizabeth Islands (1968).

Summarizing Norwegian breeding records, Greve (1963) reported ovigerous females in autumn and winter from the north, but none during May to September.

Larvae of this species have not been reared in the laboratory, but Pike and Williamson (1961) reviewed published records of identifications from plankton as stage II from off Portland, Maine, and stage III from Greenland, as well as assessing status of similar larvae belonging to *Spirontocaris* and closely related genera.

Stomach contents in Foxe Basin consisted largely of foraminiferans and phyto-benthos, ostracods and crustacean fragments including mysids and copepods, hydroids, small pelecypods, and rhodophytes in descending order of abundance (Squires 1965a). He (1967) thought that the species might feed selectively on ostracods in addition to detritus. He also listed cod as a predator on the Grand Banks and St. Pierre Bank.

MacGinitie (1955) reported a male parasitized by the isopod *Phryxus abdominalis*.

Spirontocaris spinus (Sowerby)

Fig. 93

Cancer Spinus Sowerby 1805:47, pl. 23.

Spirontocaris spinus.—Holthuis 1947:8 (synonymy).—Greve 1963:30, fig. 1A, C.—Couture and Trudel 1968:868, fig. 9.—Hayashi 1977:177, figs. 8–9.—Smaldon 1979:66, fig. 25A-C.

Recognition characters.—Body robust. Rostrum deep, upper margin with many small irregular teeth continuous with middorsal carina running nearly full length of carapace and armed with 4 or 5 large teeth, anterior 1 or 2 often bearing a few small secondary teeth; tip not extending beyond end of antennal scale, single but often almost equaled or surpassed by prominent ventral tooth, secondary teeth may lie in distal notch thus formed as well as behind prominent ventral tooth; lateral carina turned slightly upward near tip. Carapace bearing 2 supraorbital spines on each side; suborbital lobe distantly flanked by rather strong antennal spine; anteroventral margin almost straight; pterygostomian spine small and acute. Antennular peduncle with basal article bearing distolateral spine, acute in dorsal view but rather broad in lateral view, and slender ventromesial spine; stylocerite strong, acute, mesial margin tapered somewhat obliquely to tip, reaching distal margin of second article bearing slender distolateral spine; third article about half

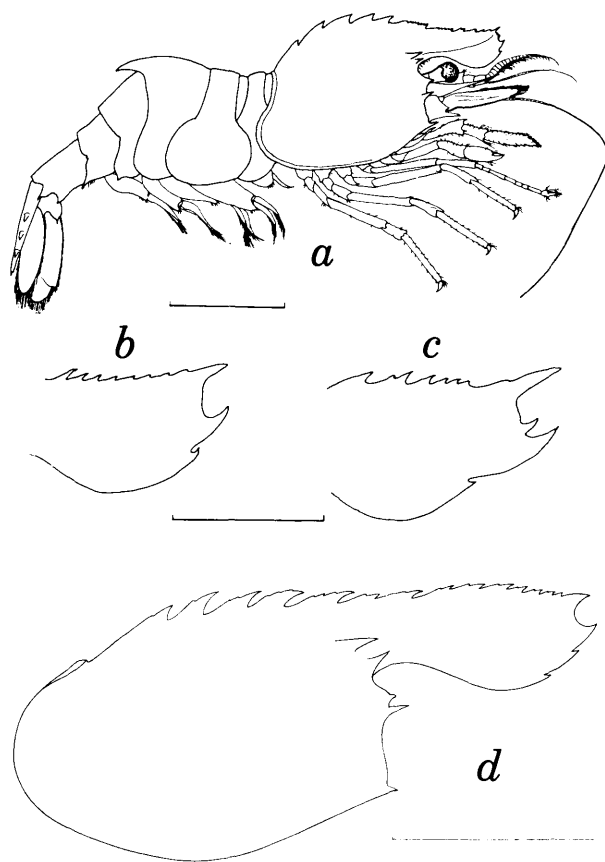


Fig. 93. *Spirontocaris spinus* (Sowerby). a, Female in lateral view; b-c, rostral variants; a, 10 mm, b-c, 5 mm indicated (from Smaldon 1979); d, carapace in lateral view, 5 mm indicated (from Williams 1974c).

length of second, with slender distodorsal spine; thick lateral ramus with short distal flagellum, slender mesial ramus longer. Antennal peduncle reaching about as far forward as basal antennular article; basal article with strong ventrolateral spine and dorsolateral lobe; scale with lateral margin about straight, lamella with somewhat rounded to subtruncate tip exceeded by distolateral spine. Third maxillipeds reaching to tip of antennal scale, exopod and epipod present.

First 3 legs with epipods. First leg moderately stout, reaching about to distal end of antennal peduncle; fingers darkened at tips, dactyl cleft at tip to accommodate tip of fixed finger; palm about length of carpus; merus with small proximolateral spine. Second leg much longer and more slender, third joint from proximal end of 7-segmented carpus longest. Third to fifth legs with dactyls bearing curved spines on flexor margin, penultimate spine strong, shorter than terminal spine but making tip biunguiculate; meri bearing lateral spines, third with

about 5–8, fourth with about 4–5, fifth with 1–3, distalmost on each leg longest.

Abdomen with pleura of first 3 segments rounded; third with posterodorsal margin produced posteriorly; fourth segment with small posteroventral spine; fifth similar though with spine directed more posteriorly; sixth with even less prominent posteroventral spine and above it an acute lateral spine with ventral shoulder overhanging base of telson. Telson with 3 pairs of terminal spines, outermost shortest, and 4–5 pairs of dorsolateral spines.

Measurements in mm.—Length of body: male 40; female 59.

Variation.—Leim (1921) found much variation in form and total number of teeth on the rostrum which may be pointed or concave anteriorly, depending on length of the ventral spine; 9–33 (\bar{x} = 18–20) dorsal spines and 2–5 ventral spines were observed. Moreover, the dorsal teeth of the carapace may number 5 or 6. Leim also noticed diversity in form of the dactyls on the third to fifth legs which may be longer and more slender than in other members of the genus. Dons (1915) illustrated several variant forms of the rostrum, and Hayashi (1977) commented on these and other variations, some of which have been the basis for nominal species or subspecies which he synonymized.

Color.—“Dull red with brown, bright red and green mottling and sometimes white marking on the legs” (Squires 1965a). Red and white with few olive-tan spots and a few chalky-white streaks (MacGinitie 1955). “Normally mottled dark red, brownish or light green. Sometimes bright red” (Smaldon 1979).

Habitat.—Hard bottom, stones, gravel, sand and algae, sometimes mud or clay (Christiansen and Christiansen 1962; Allen 1966); often associated with *Balanus* (Heegaard 1941; MacGinitie 1955); 5 to 465 m (Heegaard 1941; Holthuis 1947; Squires 1965a; Hayashi 1977).

Type-locality.—“Among oysters on the Scottish coast.”

Known range.—Circumarctic southward to near Martha's Vineyard, Mass.; northern Norway to northeastern England and Irish Sea; Shumagin Islands, Alaska; Puget Sound, Wash.; Plover Bay, Siberia; Bering Sea; Sea of Okhotsk; and Sea of Japan off Nigata Pref., Japan (Holthuis 1947; Squires 1965a; Hayashi 1977). Heegaard (1941) mapped the distribution in part.

Remarks.—Several authors have remarked that *S. spinus* is never found in large numbers (Allen

1962), although Greve (1963) considered it common off northern Norway.

Ovigerous females in the USNM collection are present from Hudson Canyon, USA, in February, Newfoundland in June and August, Gulf of Maine, northern and eastern Greenland in August, and Nova Scotia and Point Barrow, Alaska, in September. These spotty records are in conformity with more ordered findings of several authors. MacGinitie (1955) found new laid eggs at Point Barrow in early August. Greve (1963) reported ovigerous females in western Norway from February to April, northern Norway in March, and Ellesmere Land in July. Christiansen and Christiansen (1962) found them during July–August at Spitsbergen. Squires (1965a; 1967) found them off Newfoundland in June and October–November, and judged that 15% of females in Foxe Basin bore eggs that would probably hatch in autumn, thinking that if these individuals spawned twice in a lifetime, they would spawn annually. Off northeastern England, Allen (1962; 1966) found ovigerous females during December to April; the females bore one brood of 350–850 eggs per year that would be carried 12–13 weeks. He judged that the life span was up to 2½ years.

From hatching of eggs at Port Erin, Isle of Man, in April, Pike and Williamson (1961) reared larvae through early stages and studied latter stages from plankton. They described and illustrated five zoeal stages, a megalopa, and the first juvenile stage, and reviewed the work of Frost (1936), deciding that her “*Spirontocaris A*” should be referred to *S. spinus*.

Stomach contents of *S. spinus* in Squires's study (1965a) consisted of phytobenthos, foraminiferans, ostracods and infrequent other crustacean fragments, sponge spicules, small pelecypods, and hydroids. He commented especially on the massive molar process divided into two parts, describing its structure. Allen (1966) found predominantly small gastropods and bivalves with some admixture of foraminiferans and hydroids in stomachs. Cod is a frequent predator, and beluga whales occasionally eat this shrimp (Squires 1965a; 1967).

Off Northumberland, England, a good many individuals bear the isopod parasite *Hemiarthrus abdominalis* (see Allen 1962), as do individuals in Foxe Basin, Hudson Strait and northern Labrador (Squires 1965a).

Genus *Thor* Kingsley 1878

Kingsley 1878b:94.—Hemming 1958b:161.—Chace 1972:129.

Carapace with antennal spine; rostrum short, inclined ventrad, toothed above and below. Antennules with outer flagellum very stout; third article with broad movable plate at anterodistal margin.

Mandible without palp; with incisor process. (Holthuis 1955.)

Without ovigerous females, the following species are difficult to distinguish.

Key to Species

(Adapted from Chace 1972)

1. Merus of first leg armed with 1–2 spines (tiny) on distal half of flexor margin; eggs not very large, increasing from 0.36 to 0.74 mm in major diameter during development *T. dobkini*
Merus of first leg unarmed on distal half of flexor margin 2
2. Dactyls of fourth and fifth legs commonly armed with 4 or 5 (rarely 3 or 6) spinules on flexor margin proximal to distal pair of spines; eggs large and few, increasing from 0.66 to 1.40 mm in major diameter during development *T. floridanus*
Dactyls of fourth and fifth legs commonly armed with 3 (sometimes 2 or 4) spinules on flexor margin proximal to distal pair of spines; eggs not very large, increasing from 0.36 to 0.73 mm in major diameter during development *T. manningi*

Thor dobkini Chace

Fig. 94

Thor floridanus.—Dobkin 1968:1–7. (Not *T. floridanus* Kingsley 1878b.)

Thor dobkini Chace 1972:133, fig. 57a–y.

Recognition characters.—Rostrum inclined ventrad; tip not reaching distal margin of basal antennular article; dorsal margin usually armed with 4, sometimes 5 (rarely 3 or 6) teeth, posterior tooth in line with or slightly posterior to rear margin of orbit; ventral margin with single distal tooth, making tip bifid. Supraorbital tooth barely discernible, obtuse. Eyes well developed, cornea broader than and as long as eyestalk. Antennule with basal article large; stylocerite reaching beyond distal margin of second article and armed with small lateral tooth at base; second and third article short, second with curved lateral spine reaching $\frac{2}{3}$ length of distal article, latter with triangular dorsal scale. Antennal scale overreaching antennular peduncle by at least $\frac{1}{3}$ length; nearly straight lateral margin terminating in stout spine, lamella greatly exceeding spine; a ventrolateral spine on basal article of peduncle. Third maxilliped reaching a little beyond tip of antennal scale; last article bearing slender spine.

First legs reaching about as far as distolateral tooth of antennal scale; fingers slightly more than $\frac{1}{2}$ length of palm, carpus about as long as palm; merus nearly $\frac{1}{4}$ longer than carpus, armed with 1 or 2 movable spines distal to midlength of flexor

margin; ischium little more than $\frac{1}{3}$ length of merus. Second leg slightly overreaching antennal scale; fingers shorter than palm; carpus subdivided, joints decreasing from proximal end in order of 3, 6, 4, 1, 2, 5. Third leg of male prehensile, subchelate, overreaching antennal scale by length of dactyl and $\frac{3}{4}$ of propodus; dactyl with about 16 closely appressed spinules on flexor margin, propodus more than twice length of dactyl, distal $\frac{1}{3}$ of flexor margin oblique and densely spinose. Third leg of female not prehensile, similar to fourth but without microscopic comblike spines at distal end of propodus. Fourth leg not prehensile; dactyl usually bearing 5 (less commonly 3, 4, or 6) spines on flexor margin of propodus.

Abdomen smooth; pleura of segments 1–3 broadly rounded, those of 4–6 with posteroventral angles acute; sixth segment nearly twice as long as fifth but shorter than telson not including terminal spines. Telson elongate, triangular, with 3 or 4 pairs of prominent dorsal spines a little remote from edges and spaced equidistantly in posterior $\frac{3}{4}$ of length; tip with median point and usually 3 pairs of subequal spines, outer pair shortest. Uropodal exopods with outer edge ending in small spine flanked mesially by strong movable spine.

Measurements in mm.—Length of carapace: males 2.0; females 3.4.

Color.—Red eyestalks, red marks (USNM).

Habitat.—Grass flats and offshore reefs; to depth of 19 m (USNM).

Type-locality.—Punta Rassa (near mouth of Caloosahatchee River), Lee County, Fla.

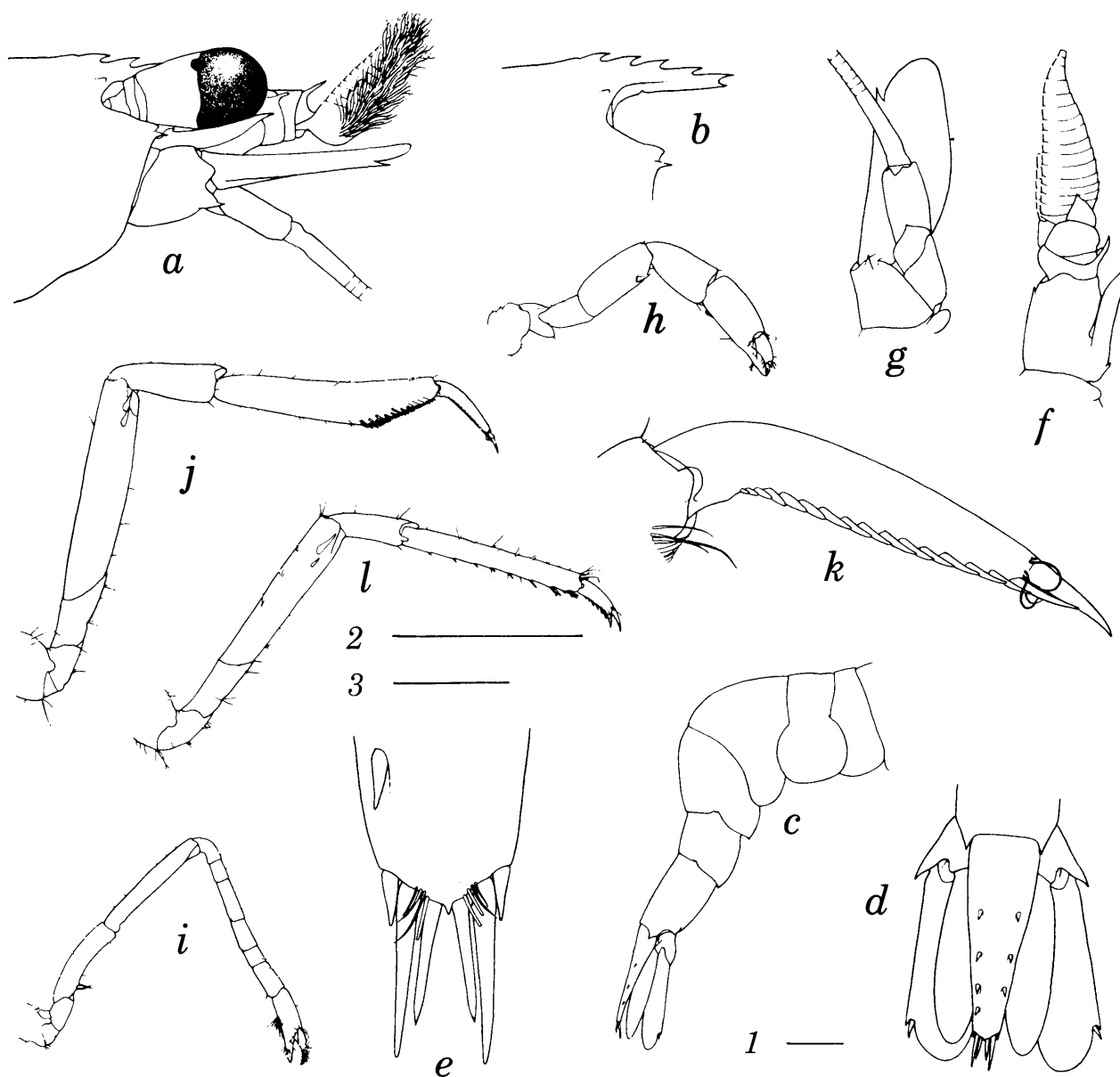


Fig. 94. *Thor dobkini* Chace. Male: a, anterior region; b, rostrum; c, abdomen; d, telson and uropods; e, end of telson; f, right antennule; g, right antenna; h, right first leg; i, right second leg; j, right third leg; k, same, dactyl; l, right fourth leg. Scales: 1(c)=1 mm; 2(e, k)=0.3 mm; 3(all others)=1 mm (from Chace 1972).

Known range.—Off Shackleford Bank, N. C., to Yucatan; Louisiana; north coast of Cuba.

Remarks.—Chace (1972) determined that *T. dobkini* is a protandrous hermaphrodite. Males are smaller than females.

Thor floridanus Kingsley

Fig. 95

Thor floridanus Kingsley 1878b:95.—Chace 1972: 136, fig. 58.

Thor species Dobkin 1968:1–18, figs. 1–9.

Recognition characters.—Rostrum inclined ventrad, tip not reaching distal margin of basal antennular article; dorsal margin usually armed with 4 or 5 teeth, posterior tooth in line with or slightly posterior to rear margin of orbit; ventral margin with single distal tooth, making tip bifid (sometimes unarmed). Supraorbital tooth barely discernible, obtuse. Eyes well developed, cornea broader than and about as long as eyestalk. Antennule with basal article large; stylocerite sharp, reaching slightly beyond distal margin of basal article and armed with small lateral tooth at base; second and third articles short, second with curved

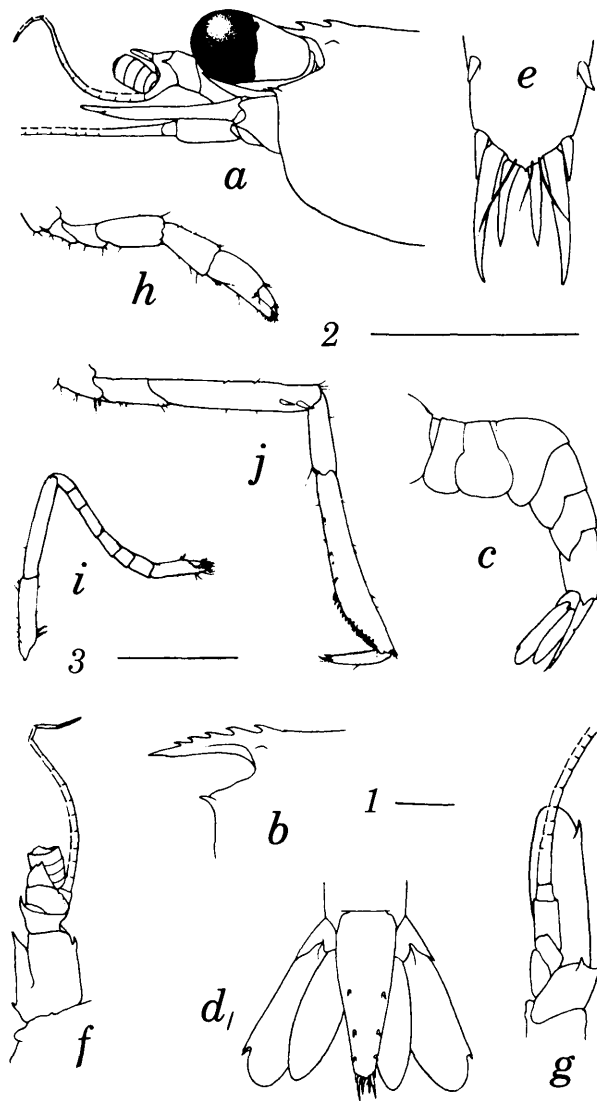


Fig. 95. *Thor floridanus* Kingsley. Male: a, anterior region; b, rostrum; c, abdomen; d, telson and uropods; e, end of telson; f, right antennule; g, right antenna; h, right first leg; i, right second leg; j, right third leg. Scales: 1(c)=1 mm; 2(e)=0.3 mm; 3(all others)=1 mm (from Chace 1972).

lateral spine reaching beyond midlength of distal article, latter with triangular dorsal scale. Antennal scale overreaching antennular peduncle by nearly $\frac{1}{2}$ length; nearly straight lateral margin terminating in stout spine, lamella greatly exceeding spine; a ventrolateral spine on basal article of peduncle. Third maxilliped reaching slightly beyond tip of antennal scale, last article bearing slender spines.

First legs reaching about to end of antennal peduncle, fingers slightly more than $\frac{1}{2}$ length of palm, carpus about as long as palm; merus somewhat longer than carpus, unarmed in distal half of flexor margin; ischium at least $\frac{1}{2}$ length of merus. Second leg overreaching antennal scale by about length of chela; fingers shorter than palm; carpus subdivided, joints decreasing from proximal end in order of 3, 6, 4, 1, 2, 5 (but at least one variant 4, 6,

3, 1, 5, 2). Third leg of male prehensile, subchelate, dactyl bearing about 13 closely appressed spines on flexor margin; propodus more than twice length of dactyl, distal $\frac{1}{3}$ of flexor margin oblique and densely spinose. Third leg of female not prehensile, similar to fourth but without microscopic comblike spines at distal end of propodus. Fourth leg not prehensile, dactyl usually with 4 or 5 (rarely 3 or 6) spines on flexor margin in addition to distal pair. Fifth leg similar but fringe of stout setae distally on flexor margin of propodus.

Abdomen smooth; pleura of segments 1–3 broadly rounded, those of 4–6 with posteroventral angles acute; sixth segment nearly twice as long as fifth but shorter than telson not including terminal spines. Telson elongate, triangular, with 3 pairs of prominent dorsal spines a little remote from edges and distributed in posterior $\frac{3}{4}$ of length; tip with median point and usually 3 pairs of subequal spines, outer pair shortest. Uropodal exopods with outer edge ending in small spine flanked mesially by strong movable spine.

Measurements in mm.—Length of carapace: males 1.3–1.6, females 1.5–2.3 (Chace 1972).

Habitat.—Grass flats; on *Halimeda*; to depth of 59 m.

Type-locality.—Key West, Fla.

Known range.—Black Rocks off New River, N. C. (?); to Yucatan.

Remarks.—Chace (1972) determined that this is the species of *Thor* whose larval development was discussed by Dobkin (1962; 1968). Ovigerous females are known in Florida throughout the year, although most abundantly so from May through July, and from Quintana Roo, Mexico, in April, North Carolina from June to September, South Carolina and Louisiana in August, and northern Gulf of Mexico in October. In southern Florida, Dobkin hatched eggs and reared larvae in temperatures of 11°–31°C. Larvae fed *Artemia* developed through two stages (described and figured) in 2–4 days, metamorphosing to postlarva after 48 h in temperatures of 25°C or higher. Dobkin attempted to cross mate this species with another having many small eggs. Although females of such matings produced eggs, none were viable. At the same time, within-species matings resulted in production of viable eggs. Three generations of *T. floridanus* were reared from the captive populations.

Imperfect protandry may be developed in this species (Chace 1972).

Both Broad (1957b) and Sandifer (1972) reared a species of *Thor* attributed to *T. floridanus* from ovigerous females collected at Beaufort, N. C., in August. In each case the larvae usually passed through 8 zoeal stages before metamorphosing to postlarvae (Sandifer's varied from 6 to 10 stages). On a diet of *Nitzschia closterium* or *Nannochloris* sp.,

larvae studied by Broad metamorphosed in 16 days. Sandifer's specimens, with experimental diets of starvation, algae, live *Artemia* nauplii, and mixed algae and *Artemia*, completed larval development in 14 to 29 days. Of non-starved groups, best survival to metamorphosis was among those fed the combination diet.

The true identity of these many-staged larvae is open to question since Dobkin reared few-staged larvae of true *T. floridanus*. Broad stated that his larvae differed from those reared at Bermuda by Lebour (1940a). Markham and McDermott (1981) recorded *T. amboinensis*, *T. floridanus*, and *T. man-*

ningi from Bermuda, thus it is not possible to single out which species from Beaufort was reared unless parent material from Broad and Sandifer's rearings is still available for study.

Thor manningi Chace

Fig. 96

Thor manningi Chace 1972:137, figs. 59–60.—Carrvacho 1979:464.

Recognition characters.—Rostrum inclined ventrad, variable in length, tip reaching from short of

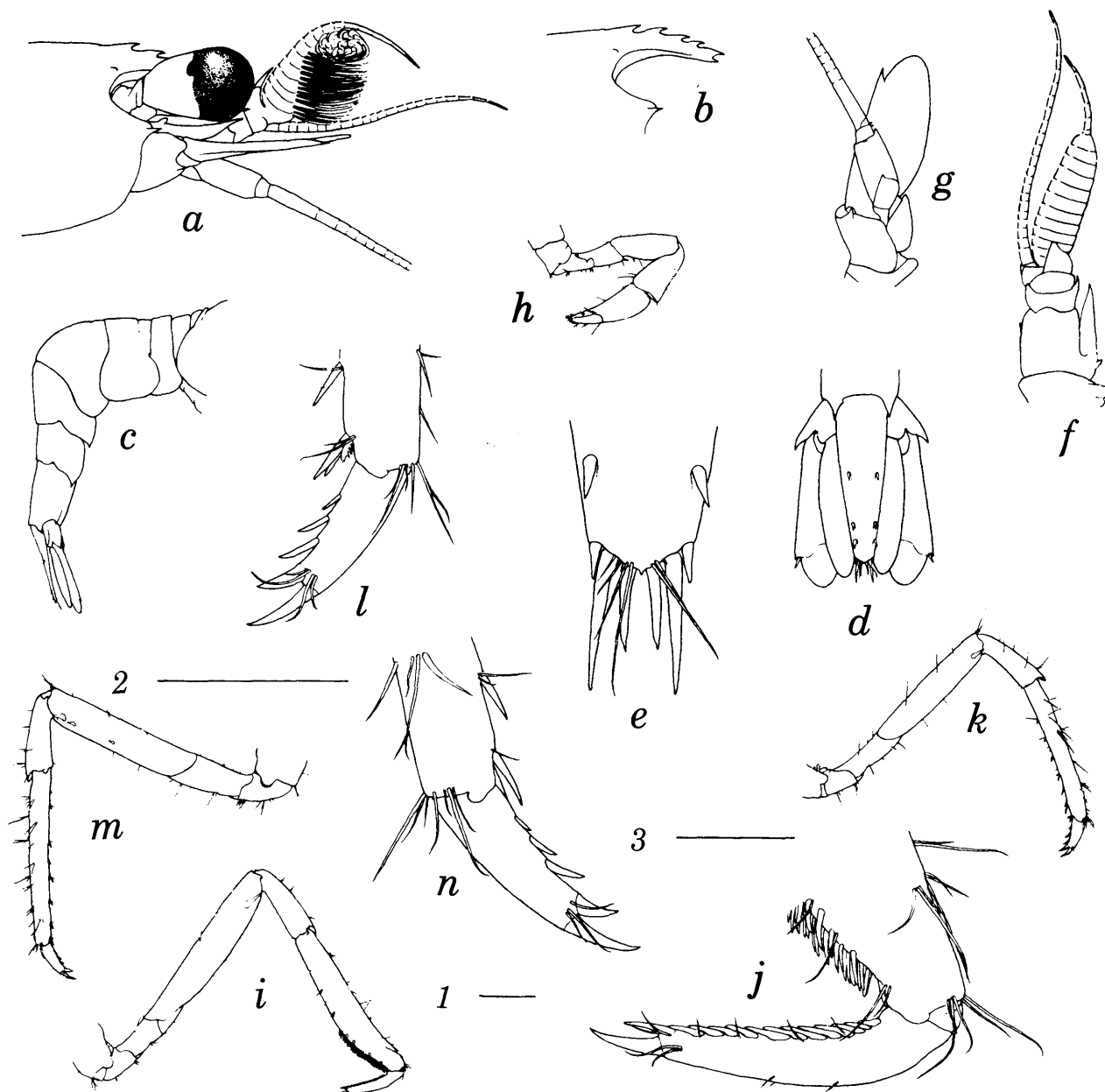


Fig. 96. *Thor manningi* Chace. Male: a, anterior region; b, rostrum; c, abdomen; d, telson and uropods; e, end of telson; f, right antennule; g, right antenna; h, right first leg; i, right third leg (prehensile); j, same, dactyl; k, right fourth leg; l, same, dactyl; m, right third leg (nonprehensile); n, same, dactyl. Scales: 1(c) = 1 mm; 2(e, j, l, n) = 0.3 mm; 3(all others) = 1 mm (from Chace 1972).

distal margin of basal antennular article to overreaching second article; dorsal margin usually armed with 4, sometimes 3 (rarely 5 or 2) teeth, posterior tooth usually in line with or slightly posterior to rear margin or orbit; ventral margin with single distal tooth, making tip bifid (rarely unarmed). Supraorbital tooth barely discernible, usually obtuse, rarely acute. Eyes well developed, cornea broader than and subequal in length to eyestalk. Antennule with basal article large; stylocerite sharp, usually reaching slightly beyond distal margin of second article and armed with small lateral tooth at base; second and third articles short, second with curved lateral spine reaching beyond midlength of distal article, latter with triangular dorsal scale. Antennal scale overreaching antennular peduncle by at least $\frac{1}{3}$ length, nearly straight lateral margin terminating in stout spine, lamella greatly exceeding spine; strong ventrolateral spine on basal article of peduncle. Third maxilliped reaching about as far as tip of antennal scale, last article bearing slender spines.

First legs reaching about midlength of antennal scale; fingers about $\frac{3}{4}$ length of palm, carpus about as long as palm; merus longer than carpus, unarmed on distal half of flexor (ventral) margin; ischium at least half length of merus. Second leg overreaching antennal scale by at least length of fingers; fingers shorter than palm; carpus subdivided, joints decreasing from proximal end in order of 3, 6, 4, 1, 2, 5. Third leg of functional males prehensile, subchelate, dactyl bearing 9–13 closely appressed spines on flexor margin; propodus more than twice length of dactyl, distal $\frac{1}{3}$ of flexor margin oblique and densely spinose. Third leg of fe-

males and nonfunctional males not prehensile, similar to fourth but without microscopic comblike distal spines on propodus. Fourth leg not prehensile; dactyl usually with 3 spines on flexor margin (rarely 2, 4 or 5) in addition to distal pair.

Abdomen smooth; pleura of segments 1–3 broadly rounded, those of 4–6 with posteroventral angles acute; sixth segment nearly twice as long as fifth but shorter than telson not including terminal spines. Telson elongate, triangular, with 3 or 4 pairs of prominent dorsal spines (occasionally 2 pairs, especially in juveniles, rarely 5 pairs) a little remote from edges and spaced equidistantly in posterior $\frac{3}{4}$ of length; tip with median point and usually 3 pairs of subequal spines, outer pair shortest. Uropodal exopods with outer edge ending in small spine flanked mesially by strong movable spine.

Measurements in mm.—Length of carapace: functional males 0.8–1.6; males with non-prehensile third leg 0.7–0.9; ovigerous females 1.4–2.5 (Chace 1972).

Habitat.—Common on grass flats from tide line to 11 m, living and dead coral, submerged timbers, among algae and hydroids; sometimes associated with sea anemones, *Bartholomea*; to depth of 44 m (Chace 1972).

Type-locality.—English Harbour, Antigua Island.

Known range.—Beaufort, N. C., to Yucatan and through West Indies to Curaçao; Islas Tres Marias, off west coast of Mexico (Chace 1972).

Genus *Tozeuma* Stimpson

Stimpson 1860:26.—Holthuis 1955:112.

Key to Species

(Adapted from Chace 1972)

1. Rostrum unarmed dorsally; third maxillipeds with rounded tip on terminal article *T. carolinense*
Rostrum armed with series of teeth both dorsally and ventrally; third maxillipeds with pointed tip on terminal article *T. serratum*

Tozeuma carolinense Kingsley

(Arrow shrimp)

Fig. 97

Tozeuma carolinensis Kingsley 1878b:90.—1880:413.—Schmitt 1935a:155.

Tozeuma carolinense.—Rathbun 1901:114.—Hay and Shore 1918:391, pl. 27, fig. 2.—Williams 1965:83, fig. 67.—Ewald 1969:510–514, figs. 1–20.—

Coelho and Ramos 1972:153.—Chace 1972:141.
Angasia carolinensis.—Holthuis 1947:17, 61.

Recognition characters.—Body elongate, compressed. Rostrum slender, almost twice as long as remainder of carapace, inclined slightly upward distally, its dorsally thickened, smooth and rounded part tapered gradually from broadened base to attenuated tip, abruptly narrowing throughout length to ventral lamellate part deepest anterior to orbit

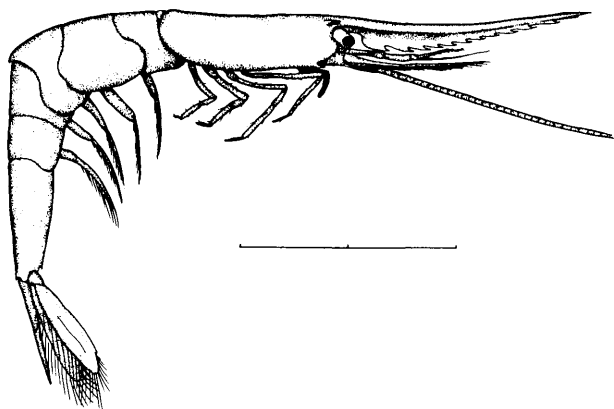


Fig. 97. *Tozeuma carolinense* Kingsley. Female in lateral view, 10 mm indicated (from Williams 1965).

and drawn to slender tip, ventral border with many (up to 19 or more) appressed teeth. Carapace smooth, polished; strong spine at either side of base of rostrum; anterior margin produced into triangular tooth below eye; anterolateral angle with spine. Eyes well developed. Antennular peduncle rather slender; first article longest, slender stylocerite reaching beyond distal margin of article up to $\frac{1}{2}$ length of second article; second and third articles progressively shorter; outer flagellum thick and much shorter than inner, outer ramus reaching tip of antennal scale. Antennae longer than rostrum; antennal scale lanceolate, less than half length of rostrum; basal antennal article with strong ventrolateral spine on anterior border. Third maxillipeds short, extending about to tip of pterygostomian spine; terminal article with tip rounded, about 2.5 times longer than broad and about 1.5 times length of penultimate article; both articles slightly spooned laterally, beset with stiff marginal setae and with smaller setae over mesial surface.

Legs relatively short; first pair very short, stout, hand inflated, fingers curved, closing completely, spines on fingers sometimes dark colored; second pair slender, longer, reaching about to base of spine on first antennal article; carpus with 3 joints, proximal joint nearly as long as merus; legs 3 to 5 with comblike spines on curved dactyls.

Abdomen smooth; strongly bent between third and fourth segments; third segment of male bearing low dorsal hump; fifth segment with spine at each side of posterior border; sixth with spine at posterolateral angle and broad spine at base of telson. Elements of tailfan long and narrow. Telson with 1 pair of dorsal spines at midlength, another at $\frac{3}{4}$ length; tip with strong pair of mesial spines flanked by weak lateral pair. Uropodal exopods with outer border terminating in small spine flanked mesially by movable spine.

Measurements in mm.—Length of body: male 40; ovigerous females 28 to 54 (Ewald 1969).

Variation.—The humped third abdominal segment is pronounced in young individuals of both sexes.

Color.—Apparently varying to some degree depending on background and feeding habits (Ewald 1969); shades of green from light yellowish green to rich deep green, or occasionally brownish or red in beds of *Diplanthera wrightii* and *Zostera marina* (see Bryce 1961); purple on alcyonarian corals *Antillogorgia* and *Pterogorgia* (see Voss 1956); nearly colorless (Verrill 1922; Ewald 1969, for juveniles).

Habitat.—Common in beds of vegetation or similar habitats in shallow water, this species often swims in a vertical position and rests in a clinging position on blades of grass. It blends well with the background because of shape and color and is aptly named “arrow shrimp.” Larvae are common in plankton of shallow coastal water around south Florida. Surface and intertidal to 75 m (Holthuis 1947; Ewald 1969; Rouse 1970).

Type-locality.—Fort Macon, N. C.

Known range.—Vineyard Sound, Mass., through Gulf of Mexico to Yucatan and southward to Colon, Panama; through West Indies to Curaçao; Pernambuco to Bahia, Brazil (Coelho and Ramos 1972).

Remarks.—Ewald (1969) gave a history of the specific name. Bryce (1961) gave general ecological observations on *T. carolinense* along with a detailed study of larval development. The adults apparently feed by grazing on faunal and floral growths on marine grasses and alcyonarians.

In North Carolina, ovigerous females are present from May to October, with one doubtful record in February. Elsewhere they have been taken year-round in Florida (Ewald 1969; Rouse 1970), their proportion to non-ovigerous but mature females always very high, and in a recorded period of December to August (USNM) in the West Indies and Gulf of Mexico.

Ewald collected ovigerous females from grass flats near Bear Cut and alcyonarians near Soldier Key off Miami, Fla., held them in the laboratory until eggs hatched, and reared the larvae through to metamorphosis on a diet of *Artemia* nauplii. Developing animals were held in water of 32–36‰ salinity at 15°, 20°, and 25°C in chambers alternating 12 h periods of light and dark. The developing larvae exhibited no distinct stages but passed through 5 to 13 intermolts ending in the postlarval stage, those from adults on alcyonarians passing through more stages than those from marine grasses. Provenzano and Dobkin (1962) found the same variability.

Bryce (1961) found that larvae hatched from

ovigerous females reared in culture dishes at fluctuating temperatures in an air conditioned room (during summer) usually passed through eight or nine larval stages before metamorphosing into postlarvae. However, the larvae did not always transform at these stages, and one group reared in early fall continued molting for an indefinite number of stages. One individual passed through 25 larval molts before the experiment was terminated. Variations in larval stages and examples of asymmetry were discussed, as were the effects of diet and temperature.

Ewald noted longer intermolt periods and a greater number of intermolts in lower temperatures, but mortalities were similar in the three levels tested.

***Tozeuma serratum* A. Milne Edwards**

Fig. 98

Tozeuma serratum A. Milne Edwards 1881:16.—1883, pl. 32.—Chace 1972:141.

Recognition characters.—More robust than *T. car-*

olinense. Body elongate, compressed. Rostrum slender, from about 1.4 to 2 times as long as remainder of carapace, inclined slightly upward distally, its dorsal part thickened and stiffened by dorsolateral carina, tapering from broadened base to attenuated tip and bearing 5 teeth on proximal $\frac{2}{3}$ of upper margin; abruptly narrowing throughout length to ventrally lamellate part deepest anterior to orbit and drawn to slender tip, ventral border with 10–14 teeth. Carapace smooth, polished; strong spine at either side of base of rostrum; anterior margin produced into triangular tooth below eye; anterolateral angle with spine. Eyes well developed. Antennular peduncle rather slender; first article longest, slender stylocerite reaching beyond distal margin of article and up to $\frac{1}{2}$ length of second article; second and third articles progressively shorter; outer flagellum thick and much shorter than inner, latter not reaching tip of antennal scale. Antennae longer than rostrum; antennal scale lanceolate, slightly over $\frac{1}{2}$ length of rostrum; basal article with strong ventrolateral spine on anterior border. Third maxillipeds long, extending to base of terminal article of antennal peduncle;

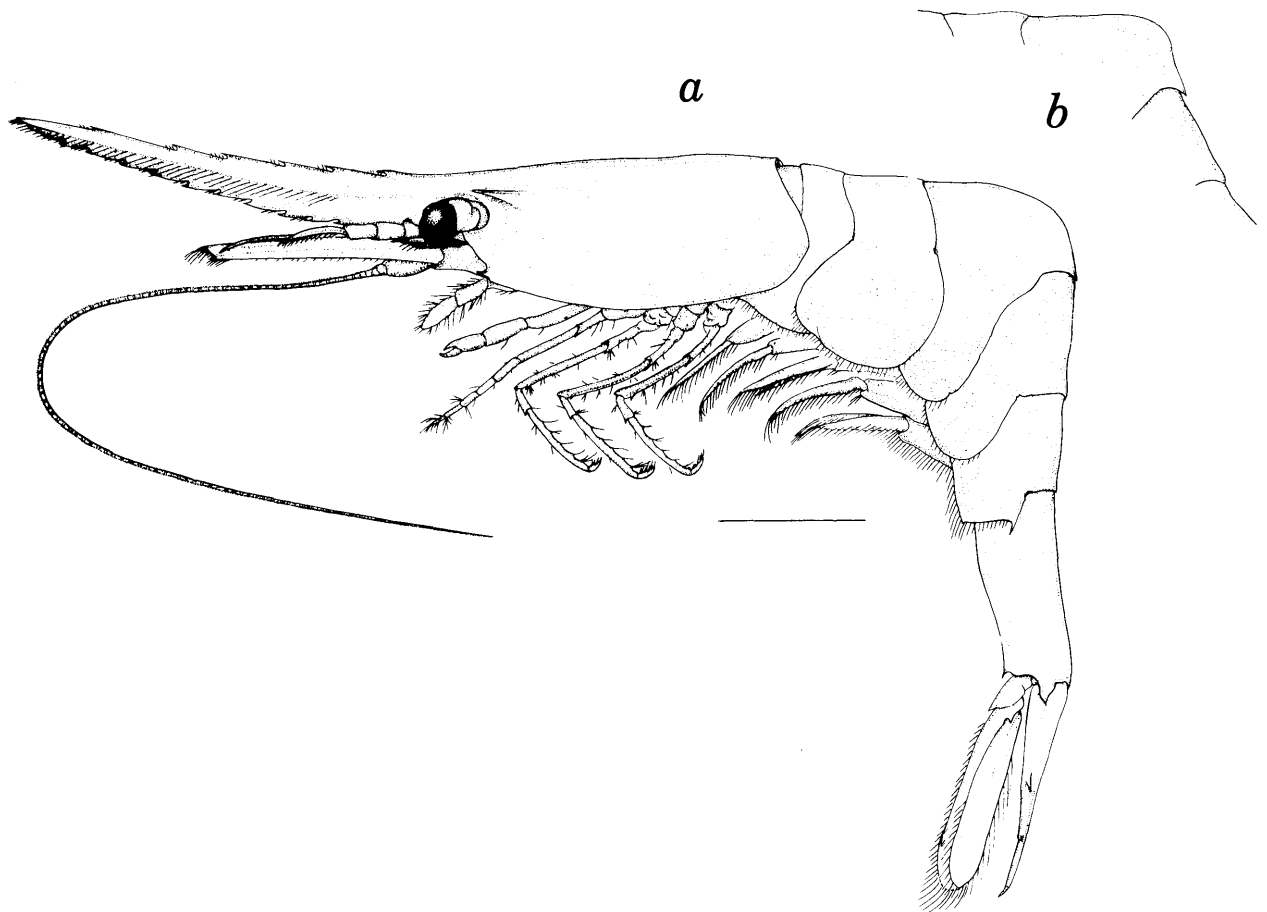


Fig. 98. *Tozeuma serratum* A. Milne Edwards. *a*, Female in lateral view; *b*, male abdomen, dorsal aspect of segments 2–5 in lateral view, 3 mm indicated (USNM 120102).

terminal article with pointed tip, about 2.9 times longer than broad and about 1.3 times length of penultimate article; both articles slightly spooned laterally, beset with stiff marginal setae and with smaller setae over mesial surface.

Legs relatively short; first pair very short and not much stouter than succeeding legs, palm and carpus of nearly equal length, fingers straight, tips corneous and crossed; second pair slender, longer, exceeding spine on first antennal article by length of chela, carpus with 3 joints, decreasing in length from proximal end in order 1, 3, 2; legs 3 to 5 with comblike spines on curved dactyls.

Abdomen smooth; strongly bent between third and fourth segments; third segment of male bearing low dorsal hump; fifth segment with spine at each side of posterior border; sixth with spine at posterolateral angle and broad spine at base of telson. Elements of tail fan long and narrow. Telson with 1 pair of dorsal spines at midlength, another at $\frac{3}{4}$ length; tip with strong pair of mesial spines flanked by weak lateral pair. Uropodal exopods with outer border terminating in small spine flanked by movable spine.

Measurements in mm.—Length of body: holotype 55; ovigerous females 40–50 (USNM).

Habitat.—4.6 to 102 m.

Type-locality.—Off Barbados.

Known range.—Nonamesset Island, Mass.; off Capes Hatteras and Lookout, N. C. (Herbst, et al. 1978; USNM), Cape Canaveral, extreme southern

and northwestern Florida, Colombia and Barbados (Chace 1972; USNM).

Remarks.—Ovigerous females are known in June from Massachusetts and eastern Florida, and at an unrecorded date from Colombia where they were associated with a hydroid.

Family Processidae

Body smooth; rostrum short, slender, apex bifid or simple, ventral border never armed. Carapace armed at most with antennal spines. Eyes relatively large, cornea well developed. Antennule with well developed stylocerite on peduncle, flagella simple, shorter ventromesial ramus thickened proximally. Antennal scale well developed. First leg with right side (usually) chelate, left with unopposed simple dactyl (except in symmetrically chelate *Ambidexter*). Second legs slender, carpus always, merus usually, and ischium occasionally subdivided; ischium with inner basal enlargement; right leg often longest. Third to fifth legs slender. (Abridged from Manning and Chace 1971.)

Manning and Chace's recent exhaustive account of processids from the northwestern Atlantic, followed by Hayashi's (1975) monograph, are so thorough that further elaboration is hardly necessary except for addition of geographic and depth records. For convenience, a key, short descriptions, and selected figures are given for species known to occur in the area covered here.

Key to Genera

1. First legs with exopod *Nikoides*
 First legs without exopod *Processa*

Genus *Nikoides* Paulson 1875

Manning and Chace 1971:7.

Nikoides schmitti Manning and Chace

Fig. 99

Nikoides schmitti Manning and Chace 1971:8, figs. 3–5.—Chace 1972:142.—Carvacho 1979:466.

Processa aff. *P. guyanae*.—Herbst, Williams and Boothe 1979:990, table 1.

Recognition characters.—Rostrum slightly deflexed, extending to cornea or slightly beyond anterior margin of eye; apex bifid, obscured by numerous long setae, lower tooth longer; lower margin sinuous, convex proximally, slightly concave distally. Antennal spine well developed. Eyes moderately large, corneal width twice or more greatest

width of antennal scale. Antennular peduncle with stylocerite broadly rounded, bearing small lateral tooth in largest specimens. Antennular peduncle extending to end of or beyond antennal peduncle by less than length of distal article; length of antennal scale about 4–6 times greatest width, distal spine overreaching blade in male, falling short of anterior margin in female.

First legs with exopods not extending beyond midlength of merus; right leg of pair chelate. Second legs decidedly unequal; right larger, overreaching antennal scale by chela, carpus, and half of merus, ischium with 3, merus with 23–24, and carpus with 43–49 joints, carpus about 13 times as long as chela in males, about 10 times in females; left overreaching antennal scale by chela and about $\frac{1}{3}$ of carpus; ischium not noticeably jointed, merus with 5, carpus with 17–18 joints, carpus more than 8 times length of chela, merus about 5 times. Third

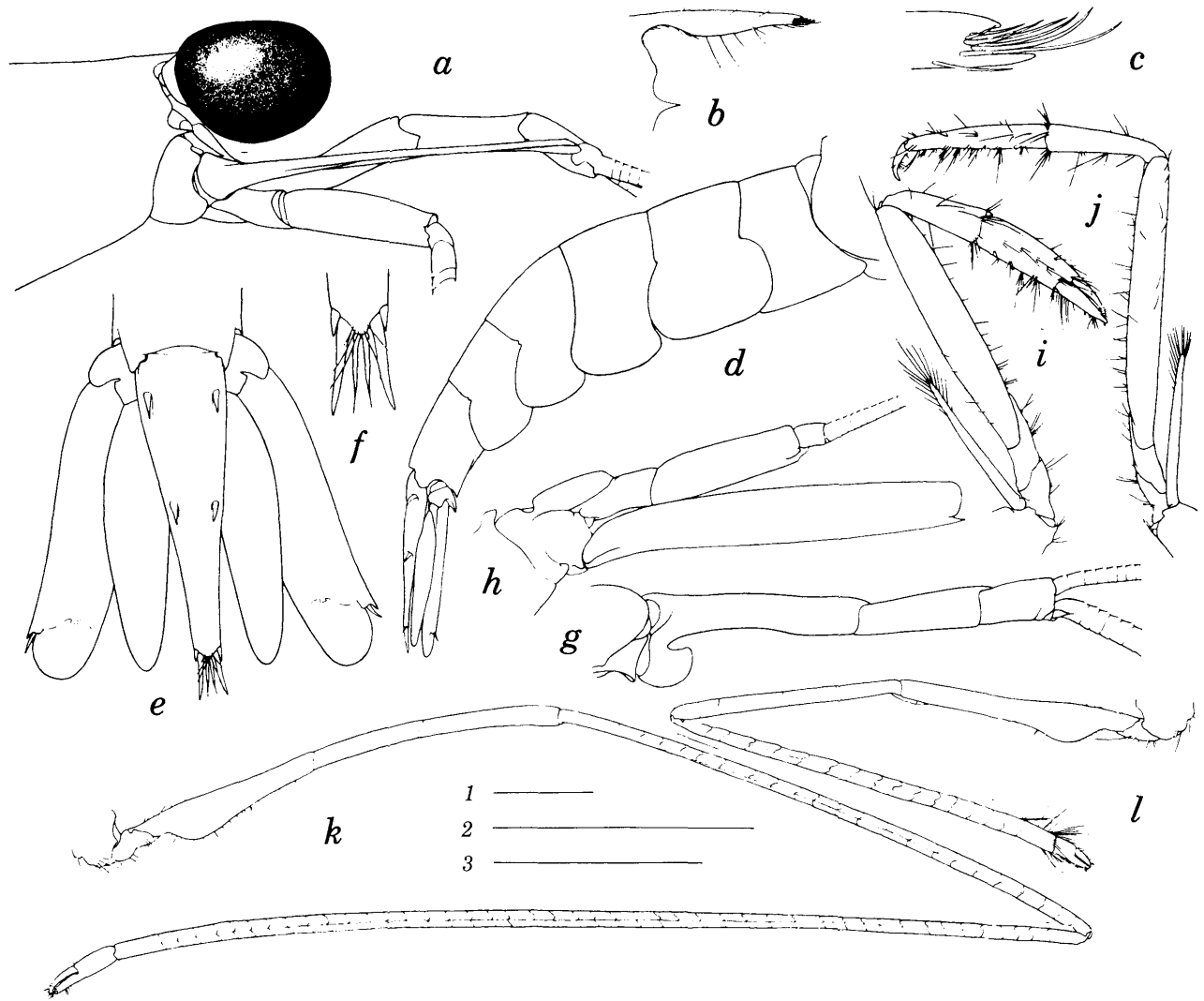


Fig. 99. *Nikoides schmitti* Manning and Chace. Male: *a*, anterior region, lateral view; *b*, rostrum; *c*, same, distal end; *d*, abdomen, lateral view; *e*, telson and uropods, dorsal view; *f*, tip of telson; *g*, right antennular peduncle, dorsal view; *h*, right antenna, dorsal; *i-j*, right and left first legs; *k-l*, first and left second legs. Scales: 1(*d*)=2 mm; 2(*c*)=0.5 mm; 3(all others)=2 mm (from Manning and Chace 1971).

to fifth legs slender; propodus-dactyl comparative lengths: third 3 times, fourth and fifth less than 3 times.

Fifth abdominal segment rounded posterolaterally; sixth abdominal segment less than twice as long as fifth, angled or bluntly spined posterolaterally; lobe above articulation of uropod usually unarmed. Telson about or slightly more than 1.5 times as long as sixth abdominal segment, length more than 3 times greatest width; 2 pairs of dorsal and 2 pairs of distal spines; anterior dorsal pair set in proximal $\frac{1}{4}$, posterior pair at midlength, distance between anterior margin and anterior pair less than half distance between pairs of dorsal spines; apex rounded.

Measurements in mm.—Carapace length: male 5.3; female 8.6; ovigerous females 7.0–8.8.

Habitat.—High salinity estuaries and shallow marine waters to 35 m.

Type-locality.—1.25 km south of Garden Key, Tortugas, Monroe County, Fla.

Known range.—E of Cape Lookout, N. C. (Herbst, et al. 1979; USNM), Biscayne Bay and Dry Tortugas; Guadeloupe and the Guianas.

Remarks.—Herbst, et al. (1979) mistakenly placed representatives of this species in *Processa*. Additional material from east of Cape Lookout, N. C., is now in the USNM collection. Ovigerous females are known from Florida in April and July, the Guianas in July, and North Carolina in August.

Genus *Processa* Leach 1815

Manning and Chace 1971:12.

Key to Species

(Adapted from Manning and Chace 1971)

1. Pleura of fifth abdominal segment with posterolateral spine; corneal width twice greatest width of antennal scale *P. fimbriata*
Pleura of fifth abdominal segment rounded or angled posterolaterally, lacking distinct posterolateral spine 2
2. Antennal spine absent 3
Antennal spine present 4
3. Second legs asymmetrical, right leg with 10–15 meral and 19–29 carpal joints, left leg with 3–4 meral and 13–15 carpal joints; rostrum not markedly deflexed anteriorly *P. bermudensis*
Second legs symmetrical, with 5 meral and 10–14 carpal joints; rostrum deflexed anteriorly *P. vicina*
4. Second legs symmetrical, with 4–6 (usually 6) meral and 10–15 (usually 11) carpal joints; rostrum anteriorly deflexed *P. hemphilli*
Second legs asymmetrical, more meral and carpal joints than above; rostrum not deflexed 5
5. Lobe on sixth abdominal segment above articulation of uropod produced into posterior spine; stylocerite with strong lateral spine, anterior margin evenly concave from inner angle to lateral spine *P. profunda*
Lobe on sixth abdominal segment above articulation of uropod unarmed; stylocerite with lateral tubercle *P. guyanae*

Processa bermudensis (Rankin)

Fig. 100

Nika bermudensis Rankin 1900:536, pl. 17, figs. 2, 2a, 2b.

Processa bermudensis.—Manning and Chace 1971:15, figs. 6a-o, 7a-o.—Hayashi 1975:78 (key).

Recognition characters.—Rostrum almost straight, not extending beyond eye; apex slightly deflexed, bifid tip obscured by long setae, lower tooth longer; lower margin convex proximally, concave distally. Antennal spine absent. Eyes moderately large, corneal width more than twice width of antennal scale. Antennular peduncle with stylocerite obtusely rounded laterally, inner margin projecting farther than outer, unarmed. Antennal peduncle extending about to midlength of second article of antennular peduncle, basal article lacking ventrolateral spine; length of antennal scale 5.6 times its greatest width, distal spine overreaching blade.

Second legs unequal; right longer, overreaching antennal scale by chela and nearly all of carpus, merocarpal articulation extending beyond eye, ischium with 5 indistinct, merus with 10–15, and carpus with 19–29 joints; left overreaching antennal scale by chela and slightly less than ½ of carpus, ischium undivided, merus with 3–4, and carpus with 13–15 joints. Third to fifth legs slender; propodus-dactyl comparative lengths: third about 3.6, fourth more than 4, fifth more than 3.5.

Fifth abdominal segment rounded posterolaterally; sixth abdominal segment less than twice as long as fifth, lobe above articulation of uropod rounded, unarmed. Telson about 1.5 times as long as sixth abdominal segment; 2 pairs of dorsal and 2 pairs of distal spines; anterior dorsal pair set in proximal ¼, posterior pair set at midlength, distance between anterior margin and anterior pair less than half distance between pairs of dorsal spines; apex produced into sharp median point. Abdominal sternites unarmed.

Measurements in mm.—Carapace length: male 3.4; female 5.8; ovigerous females 3.3–6.

Color.—"Background light with many small, red chromatophores and fewer, larger white ones scattered over body; eyes light green; distal segment of third maxilliped and bases of third, fourth and fifth pereopods and pleopods red; abdomen with transverse red bar across third somite; eggs yellowish" (Manning and Chace 1971).

Habitat.—Shallow marine waters including high salinity estuaries; grass flats, sand and shells; 1.8 to 45 m (Christoffersen 1979).

Type-locality.—Harrington Sound, Bermuda.

Known range.—Bermuda; North Carolina near Cape Hatteras to northwestern Florida; Veracruz, Mexico (Ray 1974); Cuba; Puerto Rico; Guadeloupe; Peninsula de Arago, Estado Sucre, Venezuela, in *Sargassum* (UNC-IMS 1854); Bahia and Rio de Janeiro, Brazil (Christoffersen 1979).

Remarks.—Manning and Chace (1971) discussed

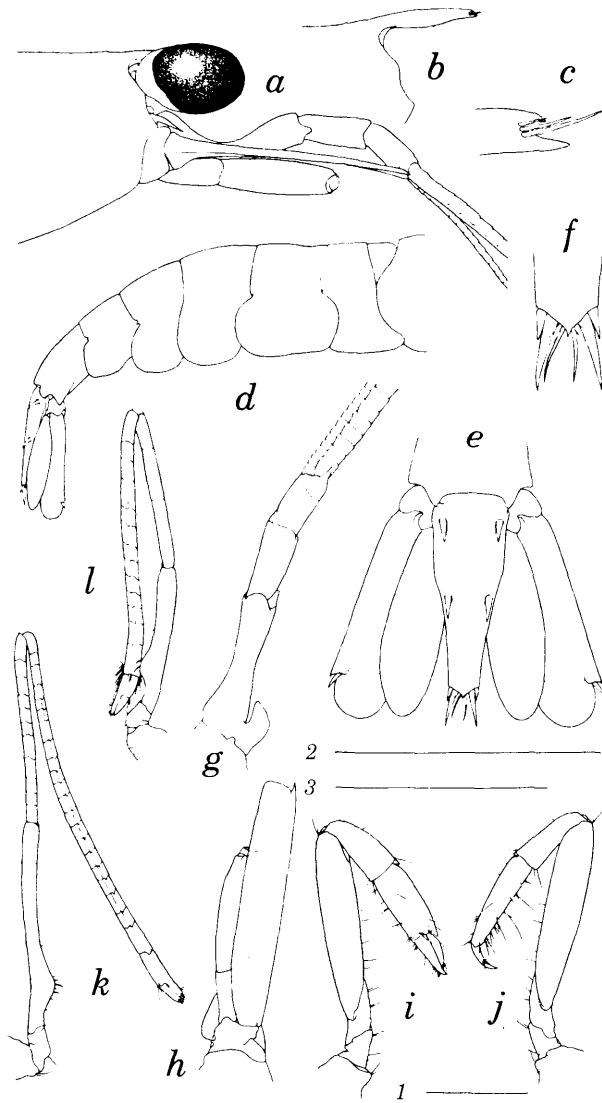


Fig. 100. *Processa bermudensis* (Rankin). Male: *a*, anterior region, lateral view; *b*, rostrum; *c*, same, distal end; *d*, abdomen, lateral view; *e*, telson and uropods, dorsal view; *f*, tip of telson; *g*, right antennular peduncle, dorsal view; *h*, right antenna, dorsal view; *i*-*j*, right and left first legs; *k*-*l*, right and left second legs. Scales: 1(*d*)=2 mm; 2(*c*)=0.5 mm; 3(*f*)=1 mm, all others=2 mm (from Manning and Chace 1971).

other processids occurring with this species in Puerto Rico. It also occurs with *P. hemphilli* in nocturnal surface plankton in Bogue Sound, Morehead City, N. C.

Ovigerous females are known virtually the year round in various parts of the range: March, July, August, December in Florida; April to October in Bermuda; June in Cuba and Puerto Rico; November in Bahia, and December in Rio de Janeiro, Brazil.

Lebour (1941) showed that *P. bermudensis* larvae are common in the plankton almost throughout the year in Bermuda, and adults were commonly found

in the dredge at night. Gurney (1936c) described eight larval stages.

Processa fimbriata Manning and Chace

Fig. 101

Processa fimbriata Manning and Chace 1971:19, figs. 8*a-p*, 9*a-o*, 10*a-c*.—Chace 1972:143.—Pequegnat and Ray 1974:254, fig. 67.—Hayashi 1975:76 (key).—Christoffersen 1979:367.

Recognition characters.—Rostrum straight, not extending to anterior margin of eye, lower margin evenly convex; apex bifid, obscured by few short setae, lower tooth longer. Antennal spine present. Eyes moderately large; corneal width about 1.6 times greatest width of antennal scale. Antennular peduncle with all of terminal article extending beyond antennal peduncle; stylocerite truncate anteriorly, with tiny outer spine. Length of antennal scale about 4 times greatest width, distal spine not overreaching blade; basal antennal article with outer spine.

Second legs asymmetrical; right stronger, overreaching antennal scale by chela and all but 1 or 2 proximal joints of carpus, merocarpal articulation extending to end of scale; ischium undivided, merus with 13–16, carpus with 31–40 joints, ischium longer than merus; left overreaching antennal scale by chela and less than $\frac{2}{3}$ of carpus, ischium undivided, merus with 4–6, and carpus with 15 joints, ischium slightly longer than merus. Third to fifth legs slender; propodus-dactyl comparative lengths: third 3.6, fourth more than 4, fifth more than 3; latter slightly less in males than in females, 4 or 5 spines on flexor margin, outer surface of propodus with scattered tufts of setae in females, completely obscured by short setae in males.

Fifth abdominal segment with small posterolateral spine; sixth abdominal segment with blunt posterolateral spine; lobe above articulation of uropod produced into blunt, triangular projection. Telson almost twice as long as fifth abdominal segment, length 3 times greatest width; with 2 pairs of dorsal and 2 pairs of distal spines, anterior dorsal pair set at end of proximal $\frac{1}{3}$, posterior pair beyond midlength; distal spines as in *P. bermudensis*; apex produced into sharp point. Abdominal sternites 1–5 with median ventral spine.

Measurements in mm.—Carapace length: male 4; ovigerous and non-ovigerous females 6.3.

Color.—Transparent, eyes black (Manning and Chace 1971).

Habitat.—Associated with sponges and on broken shell and coral bottom; intertidal to 50 m.

Processa guyanae Holthuis (1959)

Fig. 102

Processa guyanae Holthuis 1959:115, figs. 18, 19.—Manning and Chace 1971:22.—Christoffersen 1979:368.

Processa tenuipes Manning and Chace 1971:31, figs. 17a-v, 18a-c.—Hayashi 1975:80 (key).

Recognition characters.—Rostrum slender, convex dorsally, not exceeding eye; apex deflexed, bifid, obscured by long setae, lower tooth longer. Antennal spine small but distinct. Eyes of moderate size, corneal width more than twice greatest width of antennal scale. Antennular peduncle with stylocerite subtruncate anteriorly, anterior margin sinuous with blunt lateral angle or tubercle. Length antennal scale about 6.5 times greatest width, small distal spine not overreaching blade. Antennal peduncle reaching about to midlength of second article of antennular peduncle, basal antennal article with small but distinct outer spine.

Second legs strongly asymmetrical; right longer, overreaching antennal scale by chela, carpus, and slightly less than half of merus, merocarpal articulation extending well beyond eye, ischium divided into 4 (sometimes indistinct), merus into 18–28, and carpus into 48–69 joints; left overreaching antennal scale by chela and 4 distalmost joints of carpus, ischium not noticeably jointed, merus with 5–9, and carpus with 17–26 joints. Third to fifth legs slender; propodus-dactyl comparative lengths: third 4, fourth 4, fifth 6–7; latter with carpus longer than propodus, merus shorter than carpus.

Fifth abdominal segment bluntly angled posterolaterally; sixth abdominal segment less than twice as long as fifth, angled posterolaterally; lobe above articulation of telson unarmed. Telson slightly more than 1.5 times as long as sixth abdominal segment, length slightly more than 3 times greatest width, 2 pairs of dorsal and 3 pairs of distal spines; anterior pair of dorsal spines set near end of proximal ¼, posterior pair beyond midlength; distance between anterior margin and anterior spines more than distance between pairs of spines; apex produced into slender spine.

Measurements in mm.—Carapace length: male 10; ovigerous females 5.9–12.

Habitat.—Fine sediments through grades of sand, gravel and shells to coral and rocks; 31 to 331 m.

Type-locality.—NW of the Coppename River [Surinam] 6°54'N, 56°14'W, 49 m.

Known range.—Off Cape Hatteras, N. C., to eastern Gulf of Mexico, including northern coast of Cuba; Surinam, Ceará, Brazil, to Uruguay.

Remarks.—Christoffersen (1979) synonymized the southern *P. guyanae* and northern *P. tenuipes*.

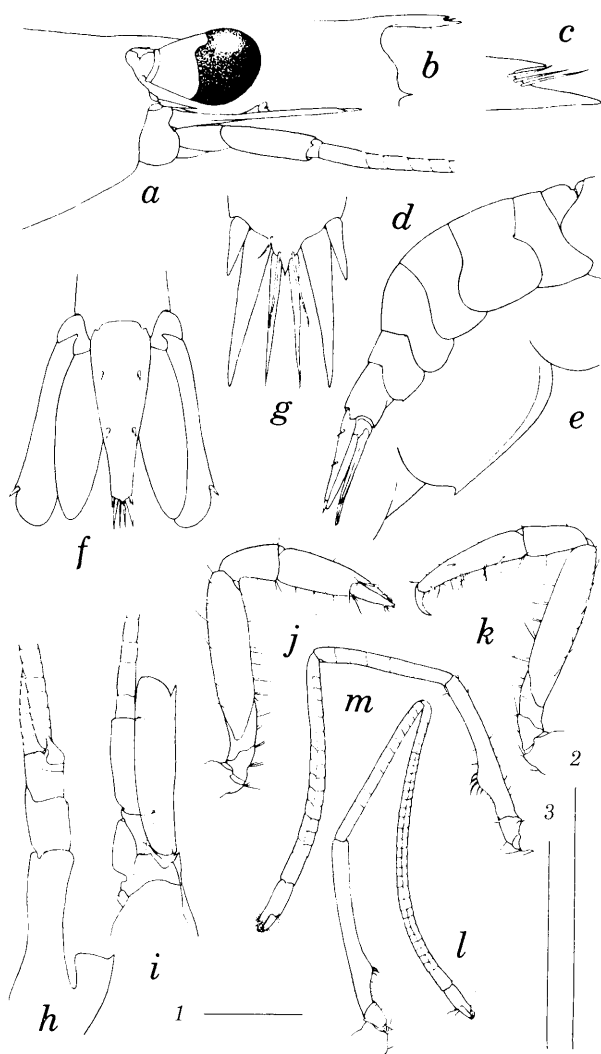


Fig. 101. *Processa fimbriata* Manning and Chace. Male: a, anterior region, lateral view; b, rostrum; c, same, distal end; d, abdomen, lateral view; e, margin of fifth abdominal pleuron; f, telson and uropods, dorsal view; g, tip of telson; h, right antennular peduncle, dorsal view (of female); i, right antenna, dorsal view; j-k, right and left first legs; l-m, right and left second legs. Scales: 1(d) = 2 mm; 2(c, g) = 0.5 mm; 3(e) = 1 mm, all others = 2 mm (from Manning and Chace 1971).

Type-locality.—Off East Key, Tortugas, Monroe County, Fla.

Known range.—Off New River, N. C., to Rio de Janeiro, Brazil (Christoffersen 1979).

Remarks.—A similar species, *P. riveroi*, is known from Puerto Rico. Manning and Chace (1971) suggested that there is a habitat difference, specimens of *P. fimbriata* being found in sponges, as noted also by Pearse (1932b, 1950) from *Sphaciospongia vespara*, *Hircinia strobilina*, and *Aulospongos schoemus*.

Ovigerous females are known from Florida in July-August, and the Bahamas in November-December (Manning and Chace 1971). Christoffersen (1979) reported them from Bahia, Brazil, in November, and Espírito Santo and Rio de Janeiro in January.

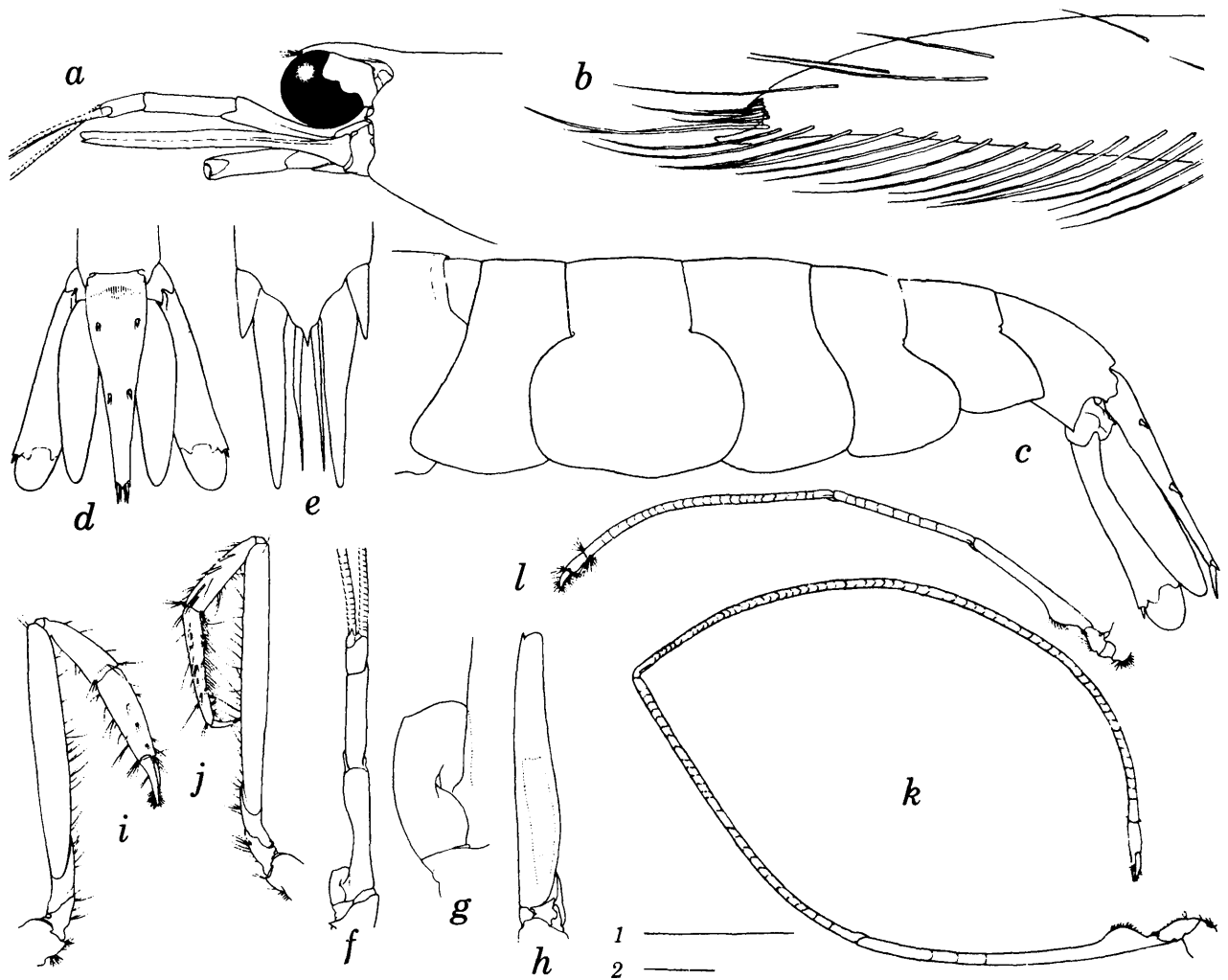


Fig. 102. *Processa guyanae* Holthuis. Ovigerous female: *a*, anterior region, lateral view; *b*, rostrum, distal portion; *c*, abdomen, lateral view; *d*, telson and uropods, dorsal view; *e*, tip of telson; *f*, right antennular peduncle, dorsal view; *g*, same, stylocerite; *h*, right antenna, dorsal view; *i*, *j*, right and left first legs; *k*, *l*, right and left second legs. Scales: 1 (*b*, *e*) = 0.5 mm, (*g*) = 1 mm; 2 (*i*–*j*) = 1 mm, all others = 2 mm (from Manning and Chace 1971).

Ovigerous females are known from Cuba in January, Florida in April, and North Carolina in April, May, and October. From south of the equator they are known from Uruguay in January and April, and from the Brazilian states of Rio Grande do Sul in January and May, São Paulo in May, August and December, and Rio de Janeiro in May and November (Christoffersen 1979).

Processa hemphilli Manning and Chace

Fig. 103

Processa hemphilli Manning and Chace 1971:23, figs. 11a–o, 12a–i.—Hayashi 1975:78 (key).—Carvalho 1979:466.—Christoffersen 1979:370.

Recognition characters.—Rostrum slightly deflexed, tapering distally, not exceeding eye; apex bifid, obscured by numerous setae, lower tooth longer. Antennal spine well developed. Eyes large, corneal width 1.6 times greatest width of antennal scale. Antennular peduncle with stylocerite subtruncate anteriorly, margin sinuous with small outer spine. Length antennal scale almost 6 times greatest width, distal spine exceeded by rounded terminal margin. Antennal peduncle slightly exceeding proximal article of antennular peduncle, basal antennal article unarmed.

Second legs symmetrical, overreaching antennal scale by slightly more than length of chela, ischium unsegmented, merus with 4, carpus with 10 joints. Third to fifth legs slender; propodus–dactyl comparative lengths: third 3, fourth 2.5, fifth less than 3.

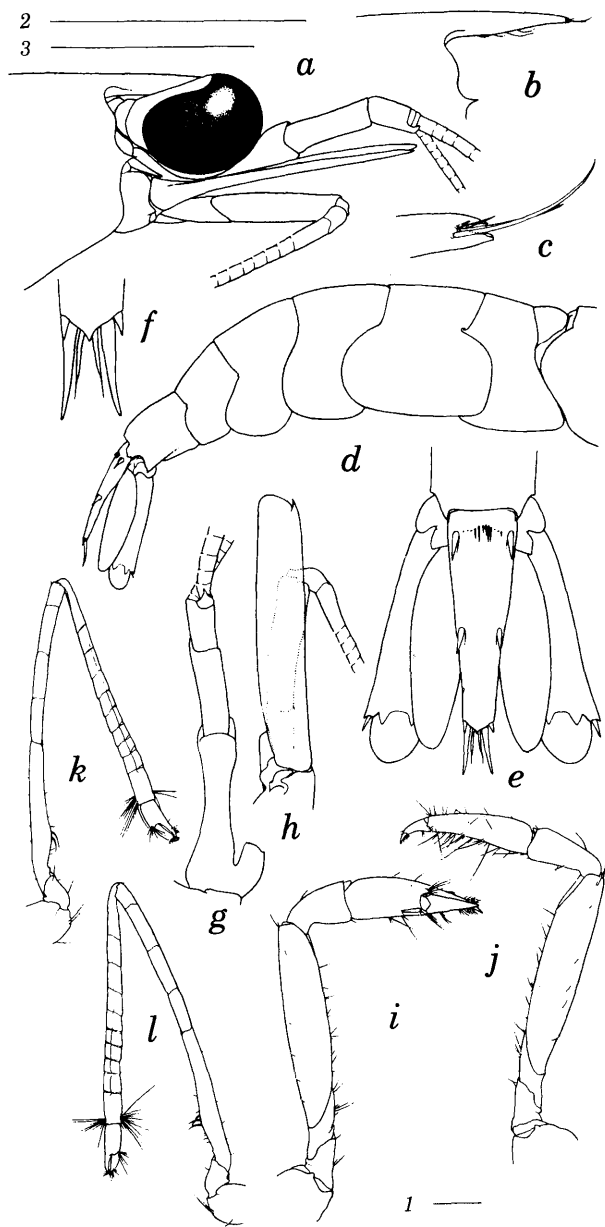


Fig. 103. *Processa hemphilli* Manning and Chace. Female: a, anterior region, lateral view; b, rostrum; c, same, distal end; d, abdomen, lateral view; e, telson and uropods, dorsal view; f, tip of telson; g, right antennular peduncle, dorsal view; h, right antenna, dorsal view; i-j, right and left first legs; k-l, right and left second legs. Scales: 1(d)=2 mm; 2(c)=0.5 mm; 3(f)=1 mm, all others=2 mm (from Manning and Chace 1971).

Fifth abdominal segment obtusely angled posterolaterally, unarmed; sixth abdominal segment subequal in length to fifth, with acute posterolateral angle, lobe above articulation of uropod angled but unarmed. Telson slightly more than 1.5 times as long as fifth abdominal segment, length slightly more than 3 times width; 2 pairs of dorsal and 2 pairs of distal spines, anterior dorsal pair set in proximal $\frac{1}{4}$, posterior pair set beyond midlength,

distance between anterior margin and anterior pair of spines about $\frac{1}{4}$ distance between pairs of dorsal spines; distal spines and apex as in *P. bermudensis*.

Measurements in mm.—Carapace length: female 3.9; ovigerous females 3.75.

Habitat.—Over mud, sand, shells, and algae; 1.8 to 154 m.

Type-locality.—Marco, Collier County, Fla.

Known range.—E Cape Lookout, and Bogue Sound, N. C.; E coast of Florida; NW Florida (Saloman 1979); Guadeloupe; Rio de Janeiro, Brazil, to Province of Buenos Aires, Argentina (Christoffersen 1979).

Remarks.—This is the species referred to by Williams (1965) as close to *P. wheeleri*. It occurs nocturnally with *P. bermudensis* in surface plankton in Bogue Sound, N. C., off the Institute of Marine Sciences, Morehead City. Specimens are in the UNC-IMS collection. Manning and Chace (1971) pointed out that similar species occur in the eastern Atlantic and Red Sea, and Carvacho thought his material from Guadeloupe might be intermediate.

Camp, et al. (1977) reported ovigerous females off central eastern Florida in May; Christoffersen (1979) reported them in December, April and August from São Paulo, January, April and August in Rio Grande do Sul, and December and August from Panama, Brazil.

Processa profunda Manning and Chace

Fig. 104

Processa profunda Manning and Chace 1971:25, figs. 13a-g, 14a-g, 15a-e.—Chace 1972:211.—Hayashi 1975:79 (key).

Recognition characters.—Rostrum almost straight, apex slightly deflexed, bifid, obscured by numerous long setae, lower tooth longer. Antennal spine present. Eyes moderately large; corneal width about twice greatest width of antennal scale. Antennular peduncle with terminal article and about half of second article extending beyond antennal peduncle; stylocerite with strong, acute lateral projection, anterior margin concave, sloping proximomesially. Length of antennal scale about 6.5 times greatest width, distal spine slightly overreaching rounded anterior edge of blade; basal antennal article with slender outer spine.

Second legs asymmetrical; right longer, overreaching antennal scale by chela, carpus and distal articles of merus; merocarpal articulation extending beyond eye; ischium with 3, merus with 21–22,

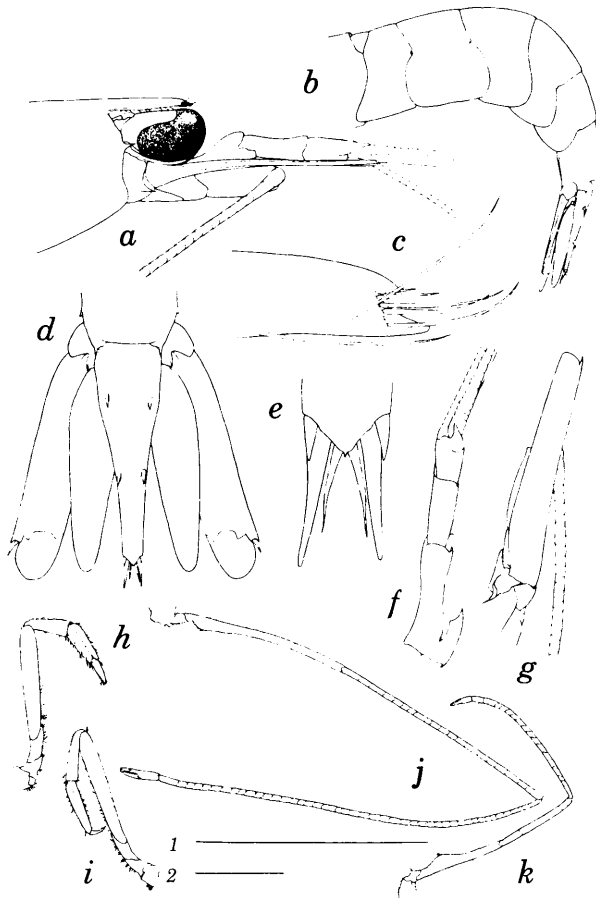


Fig. 104. *Processa profunda* Manning and Chace. Male: a, anterior region; b, abdomen; c, distal end of rostrum; d, telson and uropods, dorsal view; e, tip of telson; f, right antennule; g, right antenna; h, right first leg; i, left first leg; j, right second leg; k, left second leg. Scales: 1(b)=0.5 mm; 2 (e)=approx. 0.5 mm, (a, d, f, g)=2 mm, (c, h-k)=4 mm (from Manning and Chace 1971).

carpus with 45–56 joints, ischium shorter than merus; left overreaching antennal scale by chela and about $\frac{1}{3}$ of carpus, ischium undivided, merus with 5, and carpus with 18–21 joints, ischium slightly longer than merus. Third to fifth legs slender; propodus-dactyl comparative lengths: third 4, fourth slightly more than 3; fifth leg extending beyond antennal scale by $\frac{1}{2}$ of carpus and distal articles.

Fifth abdominal segment rounded posterolaterally; sixth abdominal segment with posterolateral spine; lobe above articulation of uropod produced into small, sharp spine. Telson slightly more than 1.5 times as long as sixth abdominal segment, length about 3.5 times greatest width; with 2 pairs of dorsal and 2 pairs of distal spines, anterior dorsal pair set at end of proximal $\frac{1}{4}$, distal pair beyond midlength; distal spines as in *P. bermudensis*; apex produced into sharp point.

Measurements in mm.—Carapace length: male 7.2; female 10.0; ovigerous females 9.3–10.8.

Habitat.—28 (USNM) to 346 m.

Type-locality.—Gulf of Mexico off the west coast of Florida, 202 m.

Known range.—Southeast of Cape Hatteras; off South Carolina; Gulf of Mexico off southern and western Florida; Surinam (USNM).

Remarks.—The shallowest record is that off Cape Hatteras.

Ovigerous females are known from the Gulf of Mexico in March and April, and from Surinam in July.

Processa vicina Manning and Chace

Fig. 105

Processa vicina Manning and Chace 1971:34, figs. 19a-x, 20a-m.—Hayashi 1975:78 (key).

Recognition characters.—Rostrum sinuous or convex dorsally, not exceeding eye; apex deflexed, bifid, obscured by long setae, lower tooth longer. Antennal spine absent, lower orbital angle an inconspicuous lobe. Eyes moderately large, corneal width 2.5 times greatest width of antennal scale. Antennular peduncle with stylocerite obtusely rounded laterally, mesiodistal apex armed with minute tubercle in some specimens. Length antennal scale about 6.5 times greatest width, distal spine overreaching blade. Antennal peduncle extending to about midlength of second article of antennular peduncle, basal antennal article unarmed.

Second legs symmetrical, overreaching antennal scale by chela and distal 3 articles of carpus, merocarpal articulation of second legs not extending beyond eye; ischium undivided, merus with 5, carpus with 10–14 joints. Third to fifth legs slender; propodus-dactyl comparative lengths: third 4, fourth 5, fifth almost 4.

Fifth abdominal segment rectangular posterolaterally; apex of pleuron rounded; sixth abdominal segment less than 1.5 times as long as fifth, bluntly angled posterolaterally, lobe above articulation of uropod irregular in outline, unarmed. Telson about 1.5 times as long as sixth abdominal segment, length slightly more than 3 times greatest width, 2 pairs of dorsal and 2 pairs of distal spines, anterior pair of dorsal spines set in proximal $\frac{1}{4}$, posterior spines beyond midlength, distance between anterior margin and anterior pair of dorsal spines less than $\frac{1}{3}$ distance between pairs of spines; distal spines and apex as in *P. bermudensis*.

Measurements in mm.—Carapace length: male 4; female 5.3; ovigerous females 4.3–5.3.

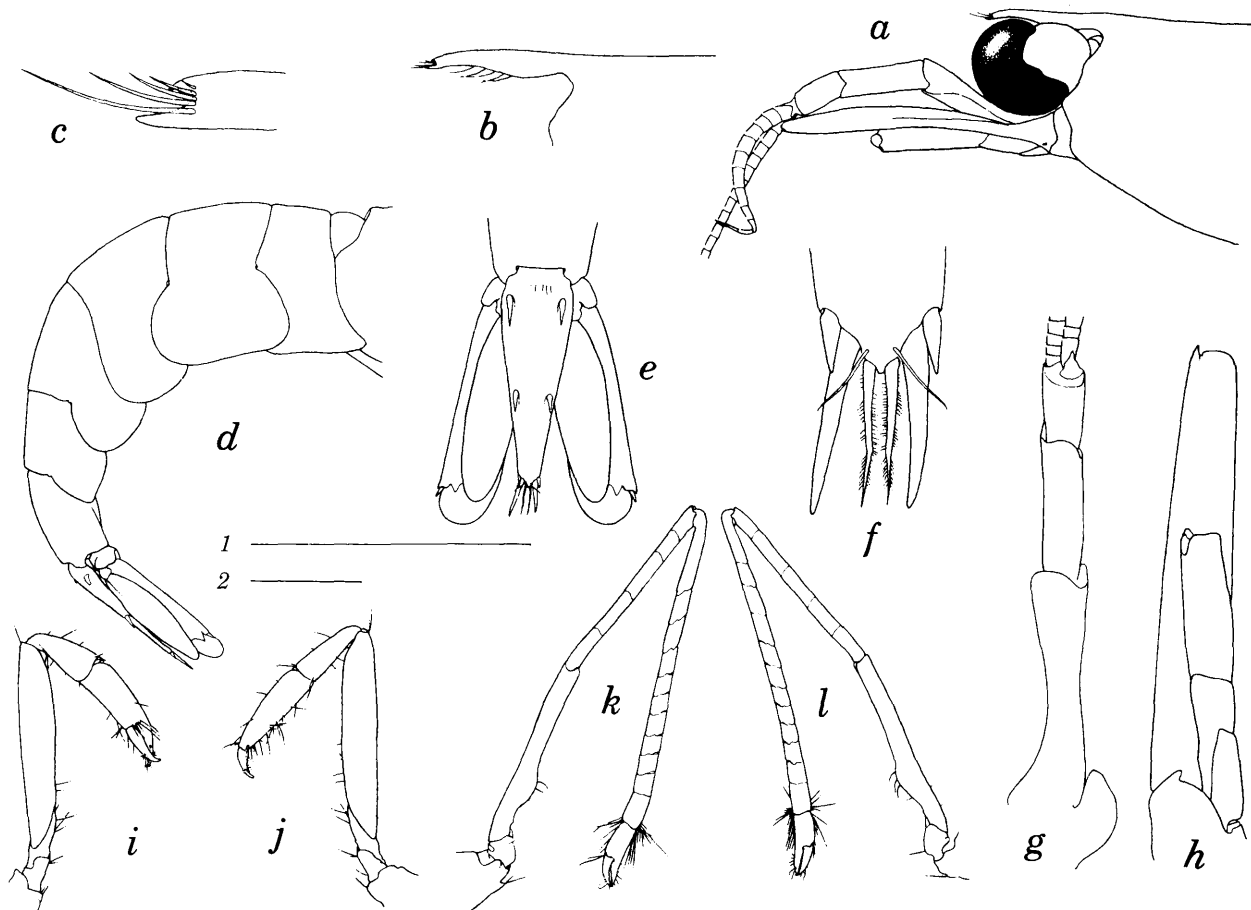


Fig. 105. *Processa vicina* Manning and Chace. Male: *a*, anterior region, lateral view; *b*, rostrum; *c*, same, distal end; *d*, abdomen, lateral view; *e*, telson and uropods, dorsal view; *f*, tip of telson; *g*, right antennular peduncle, dorsal view; *h*, right antenna, dorsal view; *i*, *j*, right and left first legs; *k*, *l*, right and left second legs. Scales: 1(*c*, *f*) = 0.5 mm; 2(*d*) = 4 mm, (*k*–*l*) = 0.5 mm, all others = 1 mm (from Manning and Chace 1971).

Habitat.—Over fine substrates, 2 to 223 m (Saloman 1979; Wenner and Read 1982).

Type-locality.—Off North Carolina, 34°35'30"N, 75°45'30"W, 59 m.

Known range.—SE Cape Lookout, N. C., northwest Florida, off Isla Margarita, Venezuela.

Remarks.—Ovigerous females are known from Florida in February, and North Carolina in October (Manning and Chace 1971).

Superfamily Pandalioidea

Family Pandalidae

Rostrum long and slender, laterally compressed, armed with teeth or spines. Eyes well developed. Mandibles with incisor process and a 2- or 3-jointed palp. First pair of legs simple or microscopically chelate; second pair long, slender, chelate, carpus subdivided.

Key to Genera and Species

1. Rostrum articulated with anterior margin of carapace *Pantomus parvulus*
 Rostrum fixed to carapace in normal way 2
2. Third maxillipeds with exopod *Dichelopandalus leptocerus*
 Third maxillipeds without exopod [*Pandalus*] 3
3. Rostrum dorsally toothed throughout length; abdomen with small median spine on posterior edge of third and fourth segments, median crest on third segment *Pandalus borealis*

- Rostrum with distal portion toothless dorsally; abdomen with no median spines or crest on segments. 4
4. Rostrum upturned at about 45° angle; distolateral spine of antennal scale exceeding extremely narrow lamella. *P. propinquus*
- Rostrum upturned at considerably less than 45° angle; distolateral spine of antennal scale not exceeding somewhat narrowed lamella
 *P. montagui*

Genus *Dichelopandalus* Caullery 1896

Caullery 1896:379.—Rathbun 1929:9.—Holthuis 1955:122 (synonymy).

Dichelopandalus leptocerus (Smith)

Fig. 106

Pandalus leptocerus Smith 1881:437.—1884:367, pl. 5, fig. 1.

Dichelopandalus leptocerus.—Rathbun 1929:10, fig. 7.—Couture and Trudel 1968:865, fig. 6.

Recognition characters.—Rostrum curved very slightly upward in distal 2/3 and tapering to slender tip, from 1.3 to 2 times as long as remainder of carapace; dorsally armed with 11–13 spines, movable except for distalmost remote from others and very near tip, usually only 2 spines (rarely 4) posterior to orbital margin; ventrally with 6–8 fixed teeth longest and most erect toward proximal end, proximal tooth curved. Surface of carapace and abdomen roughened with short, irregular, transverse, punctate ridges giving rise to bristlelike short hairs; antennal spine strong; anteroventral margin slightly convex; pterygostomial spine small. Eyes large, ocellus present dorsally. Antennular peduncle exceeding antennal peduncle by about length of distal article, basal article with conspicuous subdistal eye brush; stylocerite short, rounded distally. Basal antennal article with small ventrolateral spine; antennal scale long, narrow, subtrun-

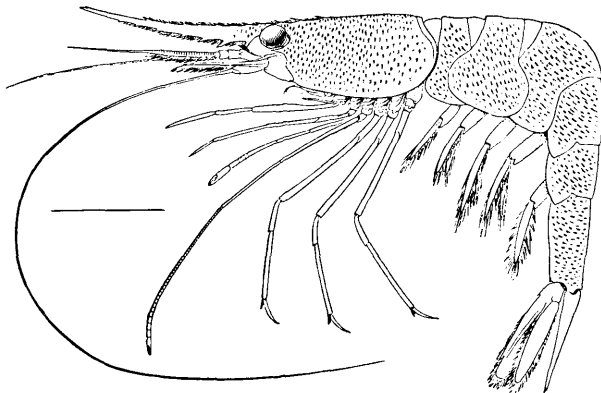


Fig. 106. *Dichelopandalus leptocerus* (Smith). Female in lateral view, 10 mm indicated (from Smith 1884).

cate blade slightly overreached by small distolateral spine. Third maxilliped with tip not reaching to end of antennal scale, slender exopod about 1/3 length of ischium, epipod present.

First 4 legs with epipods. First leg slender, with microscopic chela. Second legs unequal; right leg scarcely reaching tip of first leg, carpus usually divided into 5 unequal segments, chela about 1/2 length of carpus; left leg much longer with carpus divided into 52–64 segments. Third, fourth, and fifth legs slender; dactyls long, slender, curved, and armed only near base with few spinules on flexor margin.

Abdomen rounded dorsally; pleura of first segments rounded, small spine posterolaterally on fifth and sixth, and latter with broadly buttressed spine overlapping base of telson.

Measurements in mm.—Length of body (including rostrum): male 90 (USNM); female 98 (Smith 1881).

Variation.—A few specimens examined by Smith (1881) had 6 or 8 segments in the carpus of the left second leg, and one female had the right second carpus composed of about 18 segments. Smith felt that these variations might be attributable to injury and regeneration.

Habitat.—Common over sediments containing organic matter (Wigley 1960); surface to 790 m, –0.1° to 16.7°C (Williams and Wigley 1977, summary).

Type-localities.—Off Cape Cod, Mass., U. S. Fish Commission Stn. 372, [41°40'N, 69°28.5'W], 128 m; off Block Island, R. I., Stn. 870, [40°02'36"N, 70°22'58"W], 283.5 m; off Newport, R. I., Stn. 873, [40°02'N, 70°57'W], 183 m; off Block Island, R. I., Stn. 878 [39°55'N, 70°54'15"W], 260.6 m.

Known range.—Newfoundland Banks to off Oregon Inlet, N. C.; Shumagin Bank, Alaska (Rathbun 1929; Squires 1965).

Remarks.—Ovigerous females are recorded in the USNM collection from off the northeastern tip of Cape Cod to off the mouth of Chesapeake Bay during July to November, and from Hudson Canyon in February. A larva which Stephensen (1935) described as an early stage of *Pandalus propinquus* was regarded by Pike and Williamson (1964) as *D. leptocerus*. The latter authors described the larval development of *D. bonnieri* (northeastern Atlantic) from laboratory rearing through stage VI, and in-

licated that more stages were found in plankton. Haynes (1976) included comparative remarks on pandalid larvae.

Wigley (1960) stated that this species is most common in depths of 80–145 m off the northeastern United States and is the only pandalid common on Georges Bank and south of Cape Cod.

Uzmann and Haynes (1968) described a chytrid-like parasite from the gills of *D. leptocerus* and illustrated stages of its life cycle that could be deduced from available samples. In preserved trawl samples taken in June, January, and October, infection rates were 52%, 54% and 95% respectively. Diseased shrimp occurred at 79 of 126 sampling locations from southern Nova Scotia to off southeastern Long Island. Gross microscopic examination indicated that the parasite is confined to the branchial lamellae and suggested that the disease must have serious effects on respiratory efficiency of the host as it progresses. High incidence in all parts of the range suggests that the parasite may be an important cause of natural mortality in *D. leptocerus*, and undetected mature sporangia may indicate that terminal stages of parasite development are liberated from moribund shrimp not trawled from above the bottom.

Genus *Pandalus* Leach 1814

Holthuis 1950:28.—1955:123 (synonymy).—Hemming 1958:52.

Rostrum long, upper border with movable spines. Carapace smooth, without carinae, antennal and pterygostomian spines present. Eyes large, cornea broader than eyestalk. Antennule with elongate flagella, outermost with thickened basal joints; stylocerite broad and rounded.

Third maxilliped and all legs without exopods, all except first legs with epipods. First leg with microscopic chela; carpus and merus approximately equal in length, both longer than propodus; ischium about as long as propodus, thin but remarkably broad close to articulation with merus. Second legs unequal; left long and slender, right shorter and stouter; carpus of both subdivided into many segments. Last 3 legs long and approximately similar in structure, dactyl sickle-shaped with spinules on flexor margin, propodus approximately 3 times length of dactyl, carpus nearly half length of propodus, merus much longer than propodus; merus and carpus with longitudinal row of movable spines.

Pleura of first 3 abdominal segments rounded, that of fourth more narrowly so, fifth ending in posterolateral spine, sixth distinctly longer than fifth. Telson narrow, 2 longitudinal rows of movable spines, outermost very short.

Pandalus borealis Krøyer

(Northern shrimp, pink shrimp)

Fig. 107

Pandalus borealis Krøyer 1838a:254.—Rathbun 1929:8, fig. 4.—Holthuis 1950:31, fig. 9.—Coulture and Trudel 1968:863, fig. 3.—Smaldon 1979:92, figs. 35B, 38A, B.—Holthuis 1980:138.—Butler 1980:128.

Recognition characters.—Rostrum slightly up-curved, as long as or slightly longer than carapace; row of 12–16 movable dorsal spines extending into anterior $\frac{1}{3}$, normally 4 of these behind posterior orbital margin; 6–8 fixed ventral teeth, strongest proximally. Antennular peduncle exceeding antennal peduncle by length of distal article; basal article with conspicuous subdistal eye brush, distal 2 articles about equally short. Basal antennal article with small ventrolateral spine and distolateral lobe above it; antennal scale long, blade narrowed distally to rounded tip exceeding distolateral spine, slightly convex laterally. Third maxilliped with tip reaching about tip of antennal scale.

Legs as in generic diagnosis.

Abdomen with distinct, sharp dorsal crest on third segment, small median spine on posterior margin of third and fourth segments.

Measurements in mm.—Length of body including rostrum: male to 120; female to 170, but usually less. The slender rostrum is often broken. Rasmussen (1953) employed short carapace length (rear edge of orbit to rear edge of carapace) as a standard measure. He found the ratio of total length to this length to average 5.3 ($scl \times 5.3 = tl$).

Variation.—Makarov (1935) described a subspecies, *P. borealis eous*, from the northern Pacific on the basis of a longer rostrum and distally more rounded antennal scale on which the lamella exceeds the distal spine. Both Butler (1971) and Holthuis (1980) stated that while this subspecies is often recognized, its status remains doubtful; cursory examination of selected specimens indicates that these characters are variable. Butler (1980) did not mention the Pacific subspecies.

Color.—Thickly sprinkled with small red stellate spots, closer on tail; flagella of antennules banded with narrow white and broad red rings; antennae deep red (Rathbun 1929). Darker red due to concentration of red dots on dorsal surface, including other areas such as along ventral margin of carapace, distal part of rostrum, distally on abdomen and proximal part of telson, as well as fifth legs (Butler 1980).

Habitat.—Soft mud or sediment high in organic matter, but occasionally on sand and gravel to rocky

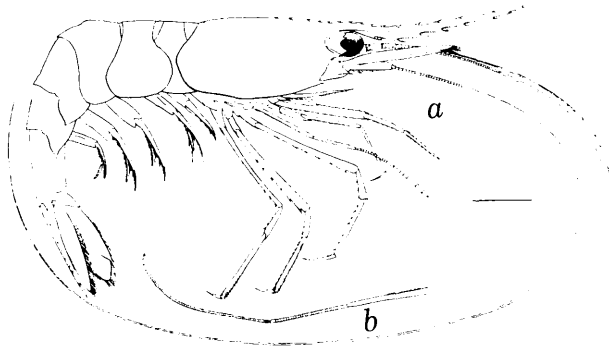


Fig. 107. *Pandalus borealis* Krøyer. a, Lateral view; b, second leg with subdivided merus, carpus, and tiny chela; 10 mm indicated (from Holthuis 1950).

substrate; -1.4° to 13.6°C , 30 to 1150 m (Makarov 1967; Williams and Wigley 1977, summary); going into deeper water with increasing age (Allen 1966; Warren and Sheldon 1966).

Type-locality.—Sydprøven, Julianehaab, and Fiskenaasset, Greenland.

Known range.—Discontinuously arctic boreal. Northern Atlantic: Greenland southward to Martha's Vineyard, Mass.; Iceland; Novaya Zemlya, Franz Josef Land and Spitsbergen, southward to northern Europe including Britain. Northern Pacific: Bering Sea (and part of Chukchi Sea) southward, stragglers to San Diego; Hokkaido and Honshu, Japan, and South Korea to about $35^{\circ}30'N$ (Ito 1976). Distribution depicted by Allen (1959).

Remarks.—Species of *Pandalus* are fished commercially and their biology has been the subject of active investigation during much of this century. The greatest concentrations of these species are centered along the southern and western coast of Scandinavia, western Greenland, the Gulf of Maine, and from the Gulf of Alaska along the northeastern Pacific coast to Washington and Oregon, with some outlying populations beyond these regions (Bae 1963; Butler 1964a, 1971, 1980; Gulland 1970; Hjort and Rudd 1938; Holthuis 1980; Horsted and Smidt 1956; Ivanov 1969; Rasmussen 1953; Ronholt 1963; Squires 1965a; Scrivener and Butler 1971). Landings of shrimp (mainly *P. borealis*) from New England, for example, were reported as over 6 million pounds per annum during the 1974–78 period (Pileggi and Thompson 1980), and this represents a great decline in recent years from landings that exceeded 10 million pounds annually in the early 1970's. Landings of shrimp from a far more extensive area in the eastern North Pacific (*Pandalus jordani*, *borealis* which dominates in Alaska, *hypsinotus*, *platyceros*, and *Pandalopsis dispar*) totaled nearly 160 million pounds per annum during the 1974–78 period (ibid 1980). Barr (1970)

stated that the domestic Alaskan catch had been as much as 40 million pounds, plus Japanese and Soviet catches of 70 million pounds per annum. Ito (1976) reported a catch of about 4,700 tons in Japan in 1972. The relative importance of pandalids in fisheries is similar in other parts of the range, and this has led to a call for thorough knowledge of the biological potential of the group. The tremendous amount of literature can be no more than briefly and selectively summarized here.

Pandalus borealis is a protandrous hermaphrodite, as are other species of the genus. During studies in British Columbia, Berkeley (1930) described six larval stages from laboratory rearing and plankton. She found that larvae of *P. borealis* hatch mainly in late March-early April, pass through early larval stages at a depth of $91 + m$, but then migrate to shallower water where they spend the summer transforming, and by winter join older shrimp in deeper water. By their second autumn (the following year) individuals of this group produce their first and only sperm, and at the end of that winter they change into females and live more than a year as females. To that basic life history outline a number of authors have added details. Larval stages reared in Alaska in flasks submerged at sea (Haynes 1979) confirmed the larval development as described by Berkeley. Kurata (1964) described seven larval stages from laboratory rearing of eggs hatched in Hokkaido, comparing these to the work of Berkeley and Lebour (1940). He felt that stage III larvae begin to move toward the coast. Makarov (1967) found five stages plus a last stage on the Kamchatkan shelf during May-July and compared this occurrence to that in the western Gulf of Alaska where larvae are released in April and May. The earliest account of larvae is that of Sars (1900) who described and illustrated eight larval stages plus the postlarva, and adult, including some data on other pandalids.

In *P. borealis* and some similar crustaceans, the factor responsible for sexual differentiation is the androgenic hormone (Berreur-Bonnenfant and Charniaux-Cotton 1966). In presence of an androgenic hormone, the germinative tissues of these animals give rise to secondary spermatogonia during development of the male phase. When level of the hormone diminishes, development of the female phase takes place with concurrent oogenesis. Histological studies confirm gonadal changes that accompany the secondary sexual changes (development of appendix masculina on second pleopods and spines on first three abdominal sternites during male phase and regression of these features at onset of female phase [see also Allen 1959; Carlisle 1959, a, b]). Parasitism by bopyrids pro-

duces effects that are distinguishable from the normal phases.

Both the life span and ages at which sexual maturity and sex reversals occur are greatly influenced by temperature (latitude) (Rasmussen 1953, 1967; Horsted and Smidt 1956). In high latitudes, the shrimp may not mature as males until their third year and change sex in the sixth year, whereas in areas such as the North Sea maturity is reached in 18 months, and more than 30% may never show male characters (Allen 1959); in deep fjords of Norway where conditions are more like the far north, the shrimp have the northern life pattern. Sex reversal in individuals showing male characters occurs before they are 27 months old in the south part of the range, and the shrimp as a whole do not live more than 38 months. In the Gulf of Maine, the average life span is 3.5 years, but may extend to 4.5 years for a few individuals (Haynes and Wigley 1969). These shrimps function first as males; most of the female phase spawn only once, 20% at 2.5 years, 70% at 3.5 years, and 10% at 4.5 years. In British Columbia the life history is similar. From a series of studies Butler (1980) amplified Berkeley's earlier work; almost as many females as males mature at 18 months, and males begin sexual change in spring when about 2 years old, passing through four or five transitional molts during summer to become functional females. By age 30 months all are females.

In summary, these populations are composed of three general sexual categories (Jagersten 1936): (1) primary females which mature early, their male characters being repressed; (2) secondary females in which male characters are repressed soon after they appear, becoming females in their second year; and (3) hermaphroditic females in which male potentialities are repressed after function as males (Allen 1959). Rasmussen (1953) was able to predict proportions of immature males and females from the size range of the age group at the beginning of the breeding season.

Haynes and Wigley (1969) and others found that clutch size increased with shrimp size. In the Gulf of Maine, females spawn 800–3,400 (\bar{x} = 2,400) eggs in August–September, and hatching occurs in March–April. The females migrate from deeper to shallow areas during the maturation period, hence it is ovigerous females in the nearshore and estuarine areas that make up the bulk of the commercial catch. Allen (1966) found that females off the Northumberland coast of England bear 300–1,500 eggs in one brood per year borne from November to May, and he judged these animals to live for 2.5 years. At the end of the first breeding period (1.5 years) approximately 35% are primary or second-

ary females, as opposed to the 5%–10% primary females predicted from Rasmussen's data. In southern Norway, the shrimp spawn during mid-October to early December (Rasmussen 1953) and eggs hatch during late February to April, the number of eggs varying from about 460 to 2,700, depending on size. In Greenland, Horsted and Smidt (1956) found a comparable range (180–3,800; \bar{x} = 1,300) depending on age and size. Ito (1976) found 579 to 4,904 (\bar{x} = 2,219) in Japan during October–December. In general, the colder the earlier the spawning, the longer the incubation period, and the later the hatch. Maximum size attained is the same regardless of latitude, but shrimp in colder waters take much longer to reach large sizes. For example, length-weight relations of shrimp from the Gulf of Maine are similar for males and non-ovigerous females (Haynes and Wigley 1969). Ovigerous females are about 1.4 g heavier for any given length than non-ovigerous ones, and the growth rate of the population is faster at ages of 2 years and older than that of any other population of *P. borealis* reported to that date.

These variations naturally influence the productivity and renewal of stocks, hence the commercial fishery. Jensen (1967) gave a short history of the *P. borealis* fishery which developed in this century in the North Sea and Skagerak. The fishing season in the Skagerak is mainly March to October by fishermen from Denmark, Norway, and Sweden, with maximum effort during summer. The Norwegian effort is to large part carried out in winter when shrimp carry roe, like that in Maine. Great diminution of relative abundance of larger shrimp was evident during the 1950's. In Greenland, Horsted and Smidt (1956) recorded generally increasing yield as the fishery developed, but concern was expressed that the stocks not be taxed too heavily. Fluctuations in that fishery are mainly due to uncontrollable natural variations in density presumably caused in most cases by water temperature (Smidt 1969). Squires (1968a) noted that some populations near Newfoundland live throughout the year in temperatures close to 5°C, apparently maturing into females in their fourth year and spawning annually in the next two or three years that they live. But some populations live in temperatures close to 0°C; the proportion of females in these is low and natural mortality may ensue before most males become females. Such cold water populations appear to be scarcely self propagating and not likely to withstand intensive fishing. Dow (1967) summarized the association of fishery yields with temperature in the Gulf of Maine in a set of tables, stating that high yields have consistently been associated with a set of temperatures that range

from 0° to 16°C in the October-July period, allowing a two-year lag for growth and development. Temperatures higher or lower than the optimum seem to result in diminished yield.

Temperatures of less than -1°C are deleterious (Horsted and Smidt 1956); indeed, Ekman (1953) questioned whether the species could reproduce in high arctic waters, but a number of authors (including Christiansen and Christiansen 1962) have shown that arctic populations such as those around Spitsbergen within the influence of the Gulf Stream do reproduce (ovigerous in July).

Stomach contents of *P. borealis* are very finely divided, but include copepods and larvae of other carideans (Allen 1966), benthic and planktonic microorganisms (Hjort and Rudd 1938; Horsted and Smidt 1953; Squires 1965a); the latter author showed that the incisor process of the mandible is sharp and the molar bears a shearing cusp at the edge of the grinding surface. The species often forms a large part of the diet of cod (Blacker 1957).

A number of parasites have been recorded from pandalids (bopyrid isopods, *Hemiarthrus* species; rhizocephalans, *Sylon hippolytes* and similar forms; and microsporidia); occurrences of these forms is summarized by Butler (1980). Margolis and Butler (1954) noted an unusual infection of *P. borealis* by a nematode, *Contaracaecum*, usually found in the digestive tract of fishes.

Pandalus montagui Leach

(Striped pink shrimp)

Fig. 108

Pandalus montagui Leach 1814:432.—Smith 1887:662[58], pl. 13, fig. 2.—1879:87.—Calman 1899:30, pls. 1-4, fig. 1.—Kemp 1910:86, pl. 10, fig. 8.—Rathbun 1929:8, fig. 5.—Holthuis 1950:28, fig. 8.—Couture and Trudel 1968:863, fig. 4.—Simpson, Howell, and Warren 1970:1230, fig. 1.—Smaldon 1979:94, fig. 39A-B.—Holthuis 1980:141.

Pandalus annulicornis Leach 1815a, pl. 40.

Pandalus levigatus Stimpson 1854:58 (sic *longivatus*, Couture and Trudel 1968).

Recognition characters.—Rostrum upcurved at considerably less than 45° angle, as long as or slightly longer than carapace; row of 10-12 movable dorsal spines extending about ½ its length and remote, tiny subdistal spine making tip bifid, normally 4 (rarely 3) of spines behind posterior orbital margin; 5-6 (rarely 7) fixed ventral teeth, strongest proximally. Antennular peduncle exceeding

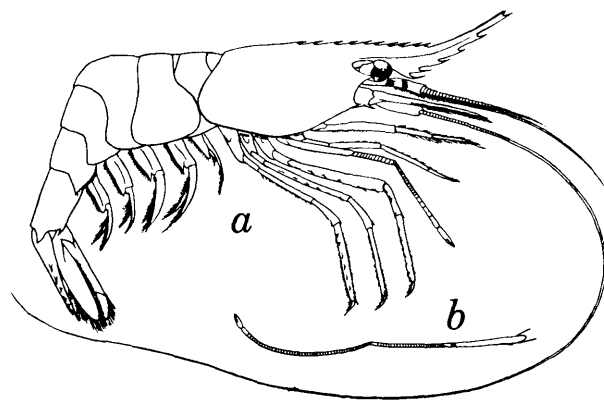


Fig. 108. *Pandalus montagui* Leach. *a*, Lateral view; *b*, second leg with subdivided merus, carpus, and tiny chela; 10 mm indicated (from Holthuis 1950).

antennal peduncle by about length of distal article; basal article with conspicuous subdistal eye brush, distal 2 articles equally short. Basal antennal article with acute ventrolateral spine and distolateral lobe above it; antennal scale long, blade narrowed distally to rounded tip not usually exceeded by distolateral spine, almost straight laterally. Third maxilliped reaching about to tip of antennal scale.

Legs as in generic diagnosis.

Abdomen with dorsal side rounded, no carina or knob present.

Measurements in mm.—Maximum length: Norwegian coast and North Sea 160, southeastern England 90, Ungava Bay 108, Labrador 130, Maine 110 (Simpson, et al. 1970, summary); total length = 4.5 × carapace length (Mistakidis 1957).

Color.—“Usually semi-translucent, with red chromatophores giving overall pink color,” often with oblique red lines on carapace, becoming more horizontal on abdomen (Smaldon 1979); “usually very pale yellow, with narrow blue lines on back” (Stimpson 1854). Kemp (1910) gave a detailed color description.

Habitat.—Prefers hard sandy bottom with variable amounts of gravel and shell where the polychaete, *Sabellaria spinulosa*, is present (southeastern England, Mistakidis 1957); gravel to mud (Allen 1966); sand and gravel, -1.0°C to 21°C, below 10°C in western Atlantic but in reduced numbers below 6°C (Couture and Trudel 1969); 5 to 790 m (Williams and Wigley 1977, summary).

Type-locality.—Zetland (= Shetland Islands).

Known range.—Boreo-arctic; Greenland to Rhode Island; Iceland; northern Europe including British Isles (Williams and Wigley 1977, summary). Heegaard (1941) mapped the distribution.

Remarks.—A northern and eastern Pacific form long known as *P. montagui tridens* Rathbun was af-

forded full species rank by Butler (1980) who compared adult morphology of rostrum, spines on dactyl of legs 3–5, relative lengths of dactyl/propodus, and morphology of larvae from the eastern Atlantic, Quebec, and the eastern Pacific. Although there is overlap in the features examined, the geographically separated Atlantic and Pacific populations seem distinct. Squires (1965a) thought that differences in color alone indicated specific separation. Butler also demonstrated minor differences in adults of the eastern and western Atlantic populations and thought that this should be studied further.

Much of the literature on *P. montagui* was cited by Scrivener and Butler (1971), and biological data were summarized by Simpson, et al. (1970). A fishery exists off southeastern England where annual yield has been estimated at about 800,000 lbs. (Mistakidis 1957).

Pandalus montagui like *P. borealis* (see above) is a protandrous hermaphrodite; transformation from male to female phases is broadly as that described for *P. borealis*, though some males may breed more than once, and proportion of primary females is higher (30%–35%) than in that species (Mistakidis 1957; Allen 1963).

Spawning at the mouth of the Thames River, England, begins in November (possibly October) approximately 10 to 12 weeks after the first sign of ovarian maturity, and continues through February, with stragglers ending in March (Mistakidis 1957). The larger females spawn first, followed by females which are spawning for the first time, some of which spawn before one year of age. It is probable that hatching there occurs in late February or early March to April (Mistakidis 1957; Allen 1966). The number of eggs is correlated with body size (136–3,796 observed), the mean for large shrimp (14–17 cl) running around 2,500. Following the hatch, females molt and lose the ovigerous setae. Older individuals tend to move offshore in winter toward higher salinities and temperatures but return in some instances to shallows in spring. Those males that do not transform in the first year move to deeper water and mature a second time (Allen 1963; 1966). Whereas the males move to deeper water in March, females do not do so until October.

Along the Gaspé, Quebec, coast spawning begins in July at the time offshore migrations are most evident, and during this time maturing males migrate more than immature males (Couture and Trudel 1969). The male phase there appears to last three years at most; after the second year most males transform to females which mostly live at least two years longer (Couture and Trudel 1969a). Eggs

hatch the following June, thus incubation lasts longer than in Europe because the temperature is lower.

From eggs hatched at Port Erin, Isle of Man, and Millport, Scotland, Pike and Williamson (1964) reared 9–11 larval stages at 10°C, with stage X and XI, when present, showing some megalopal characters. At 18°C no larvae developed beyond stage V, although this larva appeared identical to that reared at 10°C. Larvae from plankton were comparable except that those in stage VI molted directly to the megalopa. Earlier work on larvae was reviewed.

Growth is rapid during the first year but then tapers off; males attain a length of 44 mm by November of the first year in England, females approximately 50 mm, but increase stops during winter. The species lives to an age of 3–4 years in the Thames estuary, but this cannot be judged by size alone (Mistakidis 1957).

Food of *P. montagui* is mainly polychaetes (Mistakidis 1957; Allen 1963), but includes crustaceans, small lamellibranchs, hydroids and algae, depending on substrate. Squires (1965a) reported phyto-benthos, fragments of amphipods and calanoid copepods, occasionally polychaetes, pelecypod shells, ophiuroids and euphausiids. Warren and Sheldon (1967), by analysis of sand grains in stomachs and by timing rates of passage through the gut, were able to determine the main feeding ground for a population off England; sand is a natural tag.

Predators recorded are *Gadus merlangus* and *G. luscus*, *Pleuronectes* sp., *Raja* sp., and *Cottus* sp. in southeastern England (Mistakidis 1957), and cod, seals (Squires 1957) and guillemots (Tuck and Squires 1955) off eastern northern Canada.

An incidence of about 3% infestation by the bopyrid *Hemiarthrus abdominalis* is recorded (Mistakidis 1957; Allen 1963). Allen (1966a) found the parasite also on *Spirontocaris liljeborgii*, *S. spinus*, and *Eualus pusiolus*, but never on *P. borealis* even though it is abundant in samples taken off Northumberland, England, a fact noted by others off Norway. Moreover, the parasite has a clear preference for the hippolytid species. Hosts show a great difference in response to the parasite; there is no specific difference between parasites from different host species; egg size of the parasite does not vary with host nor with size of adult parasite, although size of parasite is related to size of host. No more than one *H. abdominalis* female is found on a host; only female hippolytids are parasitized, but *P. montagui* males, females and transitionals are all parasitized (in numbers 7, 93, and 14 respectively in samples examined). There, 85% of these belonged to host

year-class I which constitutes about 60% of the total population; 30% of this population were primary females, but there was no evidence to show that transition from male to female is accelerated by the parasite. The parasite breeds year-round. Presence on hippolytids prevents ova from becoming mature but seems only to retard growth of ova, reduce their size, and prolong incubation time during which they may regress in size on *P. montagui*.

Marr (1958) pointed out that *P. montagui* has no statocyst and does not respond to inertial stimulation, but possesses an additional sense which enables it to respond to water movement when it is rotated; this sense normally augments response to visual and tactile stimuli. Of four possible mechanisms to give information about displacement (image displacement on retina, inertial stimuli; tactile stimuli or passage of water over surface) no crustacean is known to use more than three to control direction of movement.

Pandalus propinquus G. O. Sars

Fig. 109

Pandalus propinquus G. O. Sars 1869:148.—Smith 1887, pl. 13, fig. 1.—Calman 1899:32, pls. 1–4, fig. 2.—Kemp 1910:89, pl. 11, figs. 1–4.—Couture and Trudel 1968:864, fig. 5.—Williams 1974c:13, fig. 33 (key).—Smaldon 1979:96, fig. 40.

Recognition characters.—Rostrum upcurved at about 45° angle, longer than carapace; row of 8–10 movable dorsal spines extending about to base of upturned part, and remote, tiny subdistal spine making tip bifid, normally 3 of spines behind posterior orbital margin; 5–7 fixed ventral teeth, strongest proximally. Antennular peduncle exceeding antennal peduncle by about length of distal article; basal article with conspicuous subdistal eye brush, distal 2 articles equally short. Basal an-



Fig. 109. *Pandalus propinquus* G. O. Sars. Carapace and antennal scale (arrow) in lateral view, 10 mm indicated (from Williams 1974c).

tennal article with acute ventrolateral spine and distolateral lobe above it; antennal scale long, blade exceedingly narrowed distally to truncate or slightly angled tip exceeded by distolateral spine, slightly concave laterally. Third maxilliped reaching about to tip of antennal scale.

Legs as in generic diagnosis.

Abdomen with dorsal side rounded, no carina or knob present.

Measurements in mm.—Length of body: 150 off Norway but usually 70–90 (Wollebaek 1908); 110 (Smith 1881).

Variation.—Right and left chelipeds may be reversed (Calman 1899).

Color.—Carapace often uniform red; transverse bands of red on first to fourth abdominal segments; fifth segment pale red with darker dots, sixth segment and tail fan darker red; shrimp from deep water with pale red legs except for colorless second pair, those from shallow water with carpus and propodus of last three pairs milk white (Kemp 1910). Rostrum yellowish toward tip (Rathbun 1929).

Habitat.—Over sediment of medium to high organic content (Wigley 1960); 2.6°–9.9°C; 20 to 2,000 m, mainly 165 to 350+ m (Williams and Wigley 1977, summary).

Type-localities.—Lofoten near Skråva, Guldbrandsøy, and Brettesnes, rare in depths of 200–300 fm.

Known range.—North Atlantic deep-sea species (Stephensen 1935); Davis Strait; Newfoundland Banks to Delaware; Iceland; NW Europe (distribution illustrated, Heegaard 1941).

Remarks.—Ovigerous females are known from the Hudson Canyon off New York in November and February (USNM). Squires (1965a) stated that *P. propinquus* is not hermaphroditic. Ovary development indicated that almost 80% of the females off eastern Canada would be ovigerous in autumn, and one female with eggs in an advanced state of development was taken in April. Indications were that the majority of the population spawns annually.

Pike and Williamson (1964) reared larvae of *P. propinquus* from eggs taken at Millport, Scotland, in April to stage VII. None were found in plankton. Parents of this group were of the type known from shallow water (see Kemp 1910). The authors pointed out that the first larvae ascribed to *P. propinquus* by Stephensen (1916) were later shown to be *P. borealis*, but his stages I and II that were subsequently described from Greenland appear to be correctly identified. Comments were given on other of Stephensen's larvae. Haynes (1976, 1978a) reviewed the literature on pandalid larvae, described his method for rearing larvae in flasks suspended

in the sea, reiterated the comment of Pike and Williamson (1964) that *P. montagui* and *propinquus* may develop through more larval stages when reared in the laboratory than in nature, and noted that *P. borealis* under laboratory conditions prolongs molt periods from 10–15 days to as much as 5 weeks and may have as many 11 zoeal stages before reaching postlarva.

Stomach contents consist of phyto-benthos, crustacean fragments (copepods, euphausiids, amphipods and isopods), and lesser amounts of polychaetes and small gastropod shells (Squires 1965a). Mandibles of the species resemble those of *P. borealis* and *montagui*.

Genus *Pantomus* A. Milne Edwards 1883

Rathbun 1901:117.—Hemming 1958b:159.

Pantomus parvulus A. Milne Edwards

Fig. 110

Pantomus parvulus A. Milne Edwards 1883, pl. 26, fig. 1, la.—Rathbun 1901:118.—Schmitt 1935a:138.—Williams 1965:88, fig. 71.

Recognition characters.—Rostrum longer than carapace, articulated with anterior margin of carapace; basal portion with 3 dorsal spines; lower margin with numerous slender overlapping spines; terminal half directed upward; tip bifid, lower prong longest. Carapace carinated on anterior half and armed with 3 spines, posterior 2 near together and movable, anterior spine adjoining articulation of rostrum; antennal and pterygostomian spines present. Eyes large. Antennular peduncle with basal article excavate above and longer than nearly equal second and third articles combined; stylocerite wide, broadly pointed, inner margin sinuous, tip reaching to midlength of cornea; upper flagellum about twice diameter of lower flagellum at base. Antennal scale, slender, reaching $\frac{2}{3}$ length of rostrum, broadest near base; distolateral spine exceeded by lamella.

Third maxilliped and first pair of legs reaching to tip of antennal scale. Second pair of legs longer than first; carpus subdivided; one leg with 15 to 17 carpal joints, other leg shorter, with 10 to 12 carpal joints. Third to fifth legs progressively longer than second pair.

Abdomen with third segment broadly carinate on posterior half; sixth segment elongate, 2.5 times length of fifth. Telson nearly as long as sixth segment, slender; sides concave, tapering to tip ending in small, median, bulblike enlargement; 2 pairs of spines at tip, outer pair longest and sinuous at

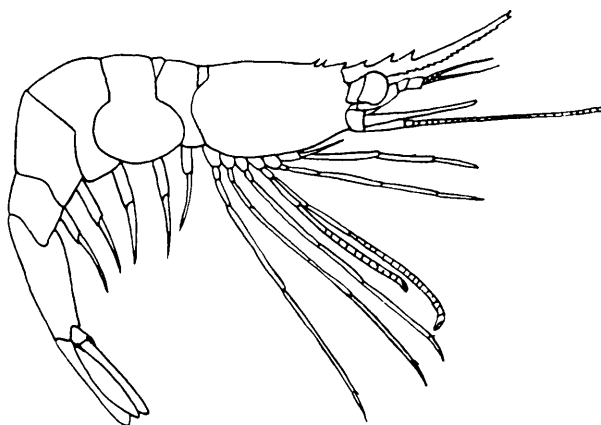


Fig. 110. *Pantomus parvulus* A. Milne Edwards. Animal in lateral view (from A. Milne Edwards 1883).

base, inner spines shorter, arising on terminal bulb; a row of 7 or 8 small dorsolateral spines on each side in distal $\frac{2}{3}$ of length. Uropods long, narrow; exopod with lateral border ending in slender movable spine.

Measurements in mm.—Length of body: ovigerous female, approximately 30.

Variation.—Among four of the syntypes, the rostrum varies somewhat in length and the number of carpal segments in the second legs is subject to variation.

Habitat.—137 to 454 m.

Type-locality.—Northern part of Yucatan Bank, 23°13'N, 89°16'W, 153.6 m.

Known range.—Cape Lookout, N. C., to Yucatan, Mexico; Puerto Rico; St. Croix, V. I.; Surinam (USNM).

Remarks.—The Catalogue of the Books, Manuscripts, Maps and Drawings in the British Museum (Natural History), vol. VI, Supplement, 1922, lists Milne Edwards' 1883 paper as follows: "The title-page (wanting to this copy), the 'Liste des Planches,' and many of the plates themselves are lithographed. Only fifty copies were issued and sent mostly to fellow workers, but few were sold, (See letter by the Author in 'Ann. and Mag. Nat. Hist.' Vol. vi, 1890:471)."

Ovigerous females in the USNM collection are from Mayaguez Harbor, P. R., in January, off west Florida in March, Surinam in July, and North Carolina in October.

Superfamily Crangonoidea

Family Crangonidae

First pair of legs subchelate, stouter than second. Second pair of legs slender, equal; carpus not subdivided; chelate (minutely) or simple. Rostrum small, usually dorsally flattened, not toothed.

Key to Genera and Some Species

(Modified from Couture and Trudel 1968)

1. Dactyls of fourth and fifth legs broadened, modified for swimming, unlike third *Argis dentata*
Dactyls of fourth and fifth legs not broadened, digitiform, like third. 2
2. Second legs chelate 3
Second legs reduced and simple, not chelate *Sabinea*
3. Second legs short, not extending beyond merus of third leg *Pontophilus*
Second legs long and slender, extending far beyond merus of third leg. 4
4. Integument smooth; antennal scale with blade narrowed distally
. *Crangon septemspinosus*
Integument sculptured, rugose and hairy; antennal scale with blade rounded and broad distally *Sclerocrangon boreas*

Genus *Argis* Krøyer 1842

Holthuis 1955:134.—Hemming 1958b:153.—
Squires 1964a:461–462.

***Argis dentata* (Rathbun)**

Fig. 111

Nectocrangon dentata Rathbun 1902:892.—1904:138,
figs. 76–77.

Argis dentata.—Rathbun 1929:21, fig. 27*a-d*.—
Squires 1964a:461–466 fig. 1B.—Couture and
Trudel 1968:880, fig. 20.

Recognition characters.—Integument smooth and
shining. Carapace somewhat sculptured, low me-

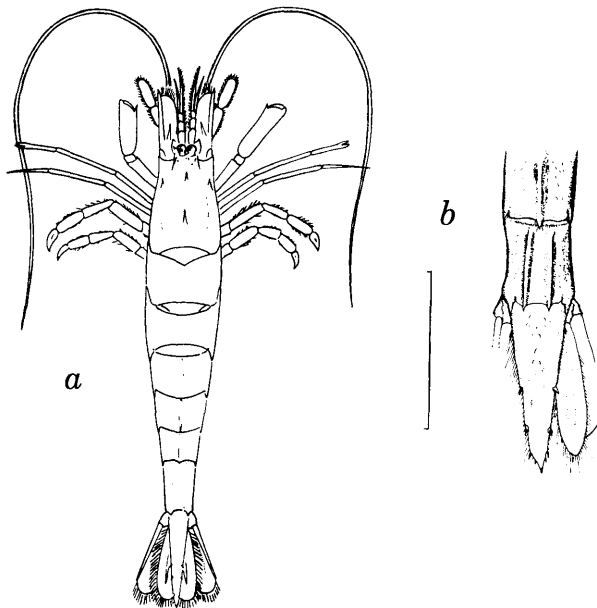


Fig. 111. *Argis dentata* (Rathbun). *a*, Animal in dorsal view (from Couture and Trudel 1968); *b*, posterior abdominal region in dorsal view, 10 mm indicated (from Squires 1964a).

dian dorsal carina running from rostrum nearly to posterior margin bearing 2 acute spines, distance between them greater than from anterior spine to anterior margin and about equal to or less than distance from posterior spine to posterior margin of carapace; hepatic and antennal spines present, hepatic spine on variably developed lateral carina. Orbits coalesced, raised and projecting anterodorsally; rostrum reduced to short, elevated spine. Eyes immediately below rostrum, very close together, their peduncles parallel in line with body, relatively larger in males than in females and bearing blunt distal tubercle. Antennule with first article of peduncle long; stylocerite broad, exceeding distal edge of cornea, sinuously truncate distally and bearing rather blunt anterolateral spine; second and third articles progressively shorter, flagella about as long as peduncle. Antennal scale extending to tip of antennal peduncle, broad, somewhat convex laterally, its broadly rounded to slightly truncate tip equaled or slightly exceeded by distolateral spine.

Subchela of first legs about 5 or more times as long as width across palm. Dactyls of fourth and fifth legs subspatulate.

Abdomen with median dorsal carina extending from first to fifth segment; sixth segment (42%–58% length of carapace) bearing 2 high carinae, each ending in small sharp tooth or spine on either side of posterior margin above base of telson; transverse proximal ridge not joining proximal ends of carinae but often bearing fringe of short setae. Telson with 2 blunt carinae armed with 3 pairs of spines on terminal half, middle pair of spines nearer to distal than proximal pair. Outer ramus of uropod distinctly shorter than inner.

Measurements in mm.—Length of carapace: males to 31 (Squires 1965a); females to 30 (USNM).

Color.—Brown (Squires 1965a).

Habitat.—Rock and sand, sand, mud with scat-

tered smaller stones (Frechette, et al. 1970); 0 to 320 m, -1.6° to 6.9°C (Williams and Wigley 1977, summary).

Type-locality.—Off Sitkalidak Island, Alaska, $57^{\circ}00'N$, $153^{\circ}18'W$, 126.6 m, *Albatross Stn.* 2855.

Known range.—Smith Sound, NW Greenland through arctic Canadian islands to Dease Strait and southward to SSW of Nova Scotia; Bering Sea to Sitka and SE coast of Kamchatka. Nesis (1963) summarized this range as arctic-boreal or lower arctic boreal.

Remarks.—There has been some confusion in generic placement of this species, but Squires (1964a) in establishing a neotype for *Argis lar* not only distinguished that species from *A. dentata* but reemphasized precedence of *Argis* over *Nectocrangon*.

From studies off Grand Rivière in the Gulf of St. Lawrence, Couture in a series of publications (especially 1968) showed that migrations of *A. dentata*, like those of *Pandalus montagui*, appear to be related to temperature. From samples taken in 18 to 110 m water, *A. dentata* was absent at 18 m where temperatures may reach 10°C . In spring at 55 m, the population is composed equally of juveniles and adults, but at the end of summer when temperatures at that depth reach 4.5°C only some young females remain. Frechette, et al. (1970) and Couture and Filteau (1971) showed that *A. dentata* is a protandrous hermaphrodite. Duration of the male phase is two years and span of the female phase is three years. Primary females may live five years or more. In young populations, males are more numerous than females, but older populations are composed of females only. Their samples showed that females had an average carapace length of 6.8 mm at six months, 11.1 at 1.5 yr, 14.3 at 2.5 yr, and 18.1 at 4.5 yr; males reached 6.4 at six months, and 9.1 at 1.5 yr. The length-frequency curves are typical of protandric species.

These results were confirmed by morphological and histological observations. Some females retain a remnant of the vas deferens. The androgenic gland degenerates in old males. In some transitory forms, the genital system is intermediate between male and female, i.e., the vas deferens and androgenic gland are atrophied and the gonad is full of young oocytes.

Ovigerous females from the southeast Canadian study area were first seen in mid-September with recently spawned eggs. Eggs in that locality mostly hatch in late spring, but a few females carry eggs in an advanced state of development as late as June (Squires 1965a). Ovigerous females from the Bering Sea are recorded in the USNM from June to early September. Squires (1965b) described two

zoal stages and the megalopa from plankton. Stage I was taken during the first plankton hauls of the season in Ungava Bay on June 24. Stage II appeared on July 3. Stage III and IV were never taken, although hauls continued until August 29. Megalopae were taken from August 11 to 20. Since considerable change occurs between stage II and stages III, IV or V, Squires considered that these were also present though never taken in plankton nets. Couture (1968) reported the first young females on the bottom in mid-August in the southeast Canadian area.

Makarov (1967) found larvae of *A.* (= *Nectocrangon*) *lar* to be very similar to those of *A. dentata*. He judged larval life to be less than one month and all larvae hatched from a local population to occur over a two-month period, May 1–July 1.

Squires (1965a) reported *A. dentata* from cod stomachs in the northwestern Atlantic. Its own stomachs contained phyto-benthos, occasionally a predominance of crustacean fragments, foraminiferans and small bivalves, and, infrequently, gastropods, ostracods and polychaetes.

Two ovigerous female shrimp from the Chukchi Sea identified as *Argis lar* bore egg capsules of a gastropod (*Buccinum* sp.?) attached among the eggs attached to their pleopods (McCauley 1964). Since attachment was by what appeared to be an expansion of the egg capsule and there was more than a single age group present, it was assumed that such attachment by the snail is not accidental and may even be a normal pattern.

Genus *Crangon* Fabricius 1798

Holthuis 1955:134.—Hemming 1958b:108.—Williams 1965:88.

Crangon septemspinosus Say

Fig. 112

Crangon septemspinosus Say 1818:246.—Williams 1965:89, fig. 72.—Squires 1965a:78.—Couture and Trudel 1968:879, fig. 18.—Haefner 1979:2. *Crango septemspinosus*.—Hay and Shore 1918:396, pl. 27, fig. 9.—Rathbun 1929:20.

Recognition characters.—Rostrum shorter than eyestalks, unarmed, tip obtuse. Carapace somewhat depressed, subcylindrical; dorsal surface with small appressed spine back of rostrum; anterior margin with suborbital spine obtuse; antennal spine strongly produced, equaling or slightly exceeding eyes and with minute spine below; hepatic spine well developed; anterior portion of carapace with

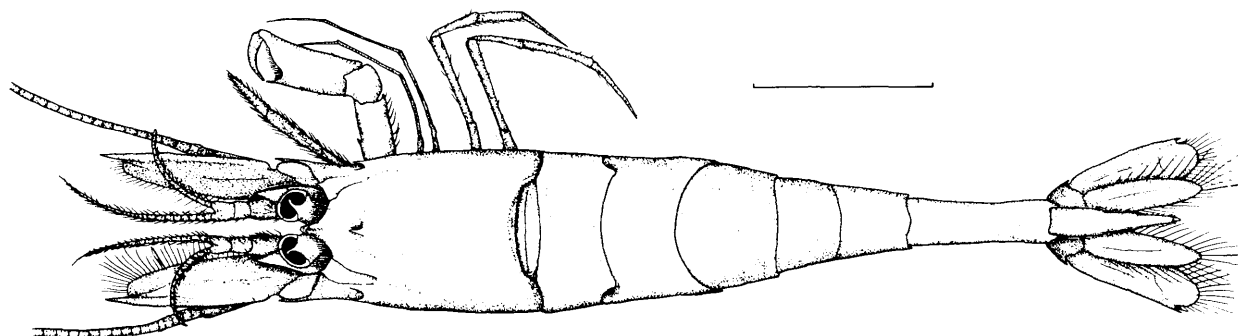


Fig. 112. *Crangon septemspinosa* Say. Ovigerous female in dorsal view, legs of left side not shown, 10 mm indicated (from Williams 1965).

2 impressed lines, 1 originating in fissure in superior margin of orbit, another originating lateral to suborbital spine, both uniting above hepatic spine and disappearing posteriorly; broad groove below and anterior to hepatic spine. Eyes moderately developed. Antennular peduncle with basal article hollowed out above, stylocerite broad, cupped longitudinally forming portion of socket for reception of eye, tip reaching nearly to end of article; second article of peduncle slightly shorter than third; inner flagellum hairy below, a little longer than antennal scale, broadest in posterior half, lamella tapering to narrow rounded tip; lateral border slightly convex; well-developed lateral spine exceeding lamella and as long as distal width of blade. Third maxilliped reaching nearly to tip of antennule, hairy.

First legs strong, subchelate; hand less than 3.5 times as long as wide, palm with strong spine at distal end of finger; merus with small spine on lower margin. Second legs almost filiform; chela minute, hairy. Third legs stronger; fourth and fifth normal.

Abdomen, viewed dorsally, tapering from broad first and second segments to narrow sixth segment. Telson slender, tapering; with 4 small spines above on lateral border, first pair at $\frac{2}{3}$ length, second midway between these and acute tip; tip flanked by 3 pairs of movable spines, median pair longest and stoutest. Uropodal exopods with lateral border ending in spine flanked mesially by longer movable spine.

Measurements in mm.—Length of body: ovigerous females from North Carolina, 25 to 60; from Delaware: males 47; females 70 (Price 1962).

Color.—Ash-gray with numerous irregular, stel-

late, blackish-brown spots or speckled with gray, imitating the color of sand; color subject to considerable variation in shade, tail often darker (various authors).

Habitat.—Usually near bottom over sand: low-water mark to 90 m, rarely to 450 m.

Type-locality.—“Bay shores and inlets of the sea” [east coast of United States].

Known range.—Primarily subarctic-boreal (Haefner 1979) although extending beyond these limits; northern part of Gulf of St. Lawrence, doubtfully Baffin Bay (Squires 1965a) to east Florida; Arctic Alaska southward to Shumagin Islands, Alaska; Sea of Okhotsk; and Ranshima, Hokkaido, Japan.

Remarks.—A recent publication (Haefner 1979) so completely summarizes the extensive literature dealing with distribution, environmental tolerance, osmoregulation, pigmentation, reproduction, larval development, age and growth, habitat, distribution, parasites and disease, and commercial fishery for this species that an abridged review here is superfluous.

Genus *Pontophilus* Leach 1817

Kemp 1910:159.—Rathbun 1929:21.—Holthuis 1955:136.—China 1966:204.—L. H. Pequegnat 1970:112.—Couture and Trudel 1968:881.

Carapace usually with longitudinal dentate carinae; rostrum depressed. Second pair of legs chelate and very short, rarely reaching distal extremity of merus of first pair; dactyls of last 2 pairs flattened but not spatulate.

Key to Species

1. Carapace with dorsolateral suture extending from notched orbital margin to dorsal branchial region 2
Carapace lacking dorsolateral suture *P. gorei*
2. Tip of rostrum falling far short of distal edge of eyes *P. brevirostris*
Tip of rostrum reaching about to distal edge of eyes *P. norvegicus*

***Pontophilus brevirostris* Smith**

Fig. 113

Pontophilus brevirostris Smith 1881:435.—1882:35, pl. 7, figs. 1, 1b.—L. H. Pequegnat 1970:113.—Williams 1974c:14, fig. 37 (key).

Recognition characters.—A rather small species. Carapace with 3 spines on middorsal carina and frequently a smaller fourth one in front of anteriormost spine just behind base of rostrum; first lateral carina bearing 2 spines and often a rudimentary spine behind these; second lateral carina armed with single spine and not extending beyond midlength of carapace. Suborbital spine short and acute, antennal spine stronger and acute. Rostrum short, tridentate, median tooth slightly longer than laterals, falling far short of distal edge of cornea and not extending beyond suborbital spine. Antennular peduncle with basal article longer than second and third combined, second longer than broad; stylocerite acute, tip reaching nearly to distal margin of basal article. Antennal peduncle extending nearly to tip of antennal scale; latter concave laterally, distolateral spine equal to or slightly overreaching broad lamella.

First legs lacking spine on flexor margin of merus.

Abdomen with first 4 segments rounded dorsally; fifth somewhat flattened, with subdorsal carinae diverging slightly and below on each side another nearly parallel carina; sixth segment also flattened, subdorsally carinate. Telson usually sulcate, shorter than inner ramus of uropods.

Measurements in mm.—Length of body: male 37 (USNM), female 36 (Smith 1881).

Variation.—Occasionally there are only two spines on the middorsal carina.

Habitat.—13 to 426 m (L. H. Pequegnat 1970).

Type-localities.—Material described from a series of U. S. Fish Commission Stations (*Fish Hawk*) 865–867, 870–874, 877 and 878, 119 to 283 m, off Martha's Vineyard, Mass., constitutes the type-series (Smith 1881). In 1882, Smith essentially repeated the original description, gave locality data for specimens studied from Stations 314–315, 321, 327, 333, 344–345, and illustrated a mature female from Station 873, one of the stations listed in the original description. Two females from this lot, 40°02'N, 70°57'W, 183 m, are in the type collection of the USNM as are many syntypes from Stations 865–67, 871, and 872.

Known range.—Gulf of Maine to Gulf of Mexico off Dry Tortugas and Cuba (Williams and Wigley 1977; L. H. Pequegnat 1970).

Remarks.—There are ovigerous females in the USNM collection from off Chesapeake Bay in March, North Carolina and Florida in April and

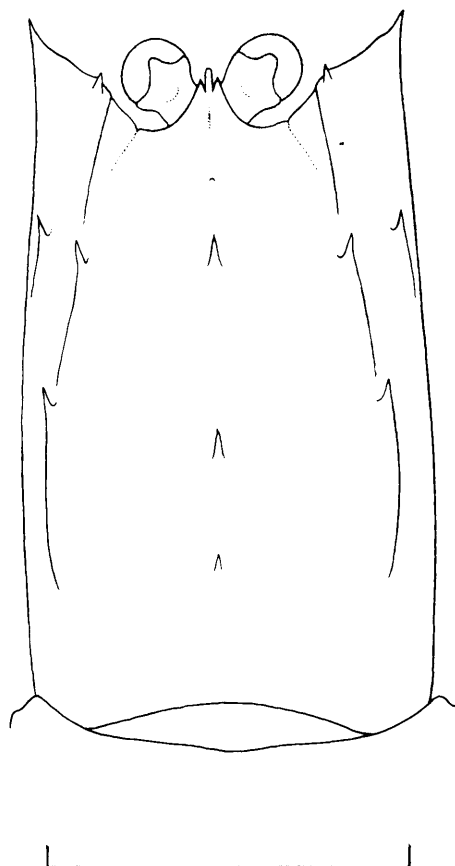


Fig. 113. *Pontophilus brevirostris* Smith. Carapace and eyes in dorsal view, 5 mm indicated (from Williams 1974c).

June, and off Martha's Vineyard and Long Island from June to September.

***Pontophilus gorei* Dardeau**

Fig. 114

Pontophilus gorei Dardeau 1980:563, figs. 1–4.

Recognition characters.—A tiny species. Carapace broad and slightly depressed, smooth; single strong, dorsomedial spine behind rostrum; suborbital spine dorsal and posterior to antennal spine from which faint longitudinal lateral carina extends posteriorly; pterygostomian spine strong and equal to or slightly exceeding distal edge of eye, minute spine posteroventral to it directed somewhat mesad. Rostrum extending slightly beyond distal edge of cornea, depressed, tip spatulate and laterally expanded, 2 blunt lateral spines. Eyes well developed, minute notch present on posterior orbital margin. Antennular peduncle shorter than flagella; stylocerite broad at base, anterior margin concave, distolateral acute tip reaching nearly to end of basal article; second article with minute distolateral spine, third article shorter than second.

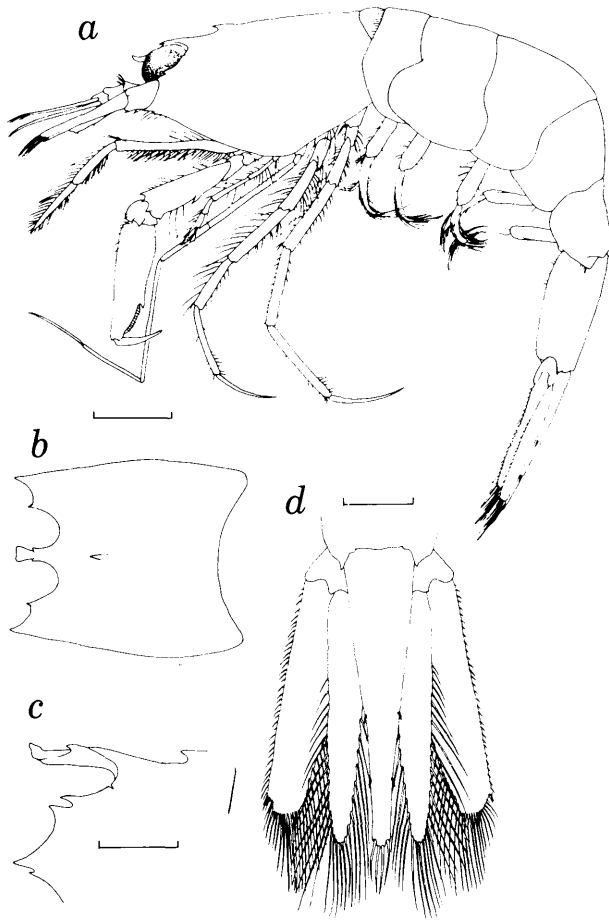


Fig. 114. *Pontophilus gorei* Dardeau. *a*, Female in lateral view; *b*, carapace in dorsal view; *c*, same, anterior in lateral view; *d*, telson and uropods; *a-b*, 1 mm, *c-d*, 0.5 mm indicated (from Dardeau 1980).

Antennal scale exceeding antennal peduncle, rather broad proximally, slightly concave laterally, lamella with somewhat rounded to slightly angled tip, reaching about same level as distolateral spine.

First leg with subchela $\frac{1}{3}$ as wide as long; strong spine on flexor margin of merus.

Abdomen smooth, tapered to narrow, elongate sixth segment; fifth segment with blunt posterolateral tooth. Telson narrow, longer than sixth segment; truncate tip bearing 3 pairs of spines, lateral pair minute; 2 pairs of lateral spines on distal half. Uropods long and narrow, inner slightly exceeding telson, outer shorter.

Measurements in mm.—Length of carapace: male 1.9, female 2.5 (Dardeau 1980).

Habitat.—Rarely 9, 37 to 182 m (Dardeau 1980).

Type-locality.—135 km due W Sanibel Island Light, [Fla.], 26°24'N, 83°22'W, 55 m.

Known range.—Off Georgia; off SW Florida, Cape San Blas and Padre Island, Tex.

Remarks.—Dardeau (1980) summarized all known

information on this species and compared it with other members of the genus.

Ovigerous females were reported from southwestern Florida in April, June, August, and October.

One specimen from off Padre Island, Tex., was taken from the stomach of a sea robin, *Prionotus rubio*.

Pontophilus norvegicus (M. Sars)

Fig. 115

Crangon norvegicus M. Sars 1861:248.

Pontophilus norvegicus.—M. Sars 1862:183.—1868: 242, pl. 1, figs. 1–25, pl. 2, figs. 17–37.—Kemp 1910:162, pl. 21, fig. 9*a-b*.—Rathbun 1929:21, fig. 26.—Squires 1965*a*:86.—Couture and Trudel 1968:881, fig. 21.—Williams 1974*c*, fig. 36 (key).—Smaldon 1979:109, figs. 41A, 48.

Recognition characters.—Carapace somewhat depressed, with 3 anteriorly directed spines on median dorsal carina, occasionally a small tubercle in front of first; 2 spines on anterior part of first lateral carina and 1 spine on second lateral carina in front of median anterior tooth; suborbital spine acute, antennal spine acute and strong. Rostrum extending to anterior margin of eyes, narrow and triangular with small anteriorly directed basal tooth at each side, slightly hollowed dorsally. Antennular peduncle with basal article longer than second and third combined, second longer than broad; stylocerite acute, tip reaching nearly to distal margin of basal article. Antennal peduncle extending beyond that of antennule but exceeded by antennal scale; latter concave laterally, distolateral spine not exceeding broad lamella.

First legs lacking spine on flexor margin of merus.

Abdomen with first 4 segments smooth, fifth with faint traces of posteriorly divergent carinae, sixth with 2 submedian carinae. Telson usually sulcate, shorter than inner ramus of uropods.

Measurements in mm.—Length of body: 80 (Rathbun 1929); male 55, female 76 (Wollebaek 1908). Squires (1965*a*) gave carapace length as: male 12, female 19.

Variation.—Small individuals have a relatively longer rostrum than adults and in some juveniles the posterior spine of the median and first lateral carina may be absent (Kemp 1910).

Color.—Carapace and abdomen pale dull reddish brown dorsally, often mottled and darkened on last three abdominal segments; carapace with two conspicuous oblique bands of white, traces of white on first two abdominal segments (Kemp 1910). Brown (Squires 1965*a*).

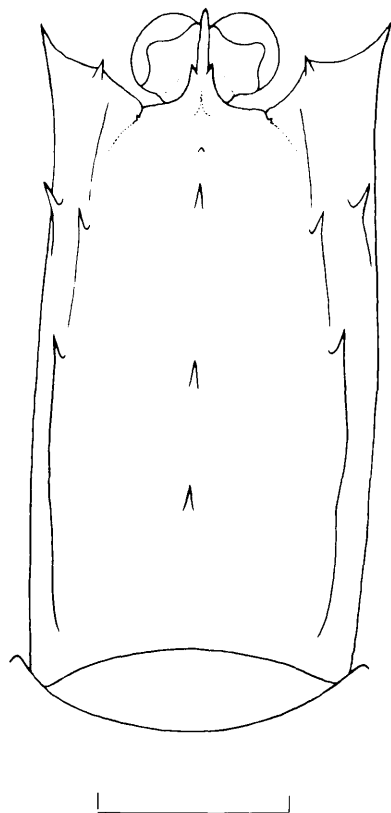


Fig. 115. *Pontophilus norvegicus* (M. Sars). Carapace and eyes in dorsal view, 5 mm indicated (from Williams 1974c).

Habitat.—Mud, sand, gravel and stones (Smith 1879), 50 to 1450 m (Sivertsen and Holthuis 1956) but usually 200 to 500 m (Smaldon 1979); never temperatures below 0°C (Heegaard 1941).

Type-locality.—Florøen (= Flora), Manger, and in Bundefjorden at Christiania [Oslo, Norway], 55 to 91 m.

Known range.—Greenland to Maryland and points southeast (38°41'N, 73°06'W) (Williams and Wigley

1977); Iceland; Spitsbergen; Murman coast and northwestern Europe including British Isles to Bay of Biscay; Balearic Islands (Forest 1965). The distribution was partly mapped by Heegaard (1941).

Remarks.—Wollebaek (1908) recorded ovigerous females off Norway from October to April, all females in spring having well-developed eggs. Larvae were found in surface layers from April on into summer. Sars (1890) described and illustrated the second larval stage, and Stephenson (1916, 1935) reported larvae from Greenland.

In the USNM crustacean collection, ovigerous females are known from southeast of Nantucket in July and off Martha's Vineyard and New York from August to November, and New York in February. Squires (1965a) remarked that about 90% of the females taken off Newfoundland and Labrador are ovigerous in autumn, first reaching maturity at about 10 mm carapace length, but that no ovigerous females were seen by him in June and July. Frost (1936) recorded larvae there in spring and fall.

Squires (1965a) found stomach contents to include phyto-benthos, crustaceans, polychaetes and foraminiferans. The mandible was described.

Dahl (1944) reported an unusual occurrence of the rhizocephalan parasite *Sylon hippolytides* on *P. norvegicus* where it was attached to the mouth opening rather than as usual on the under surface of the abdomen.

Genus *Sabinea* Ross 1835

Rathbun 1929:22.—Holthuis 1955:133.—Hemming 1958b:160.—Couture and Trudel 1968:882.

Second legs short, simple, not chelate.

Key to Species

1. Rostrum with acute tip reaching beyond eyes; telson ending in acute tip flanked by 1 or 2 spines *S. sarsii*
- Rostrum with rounded tip scarcely exceeding eyes; telson with narrow but truncate tip bearing 8 or more spines or stout setae *S. septemcarinata*

Sabinea sarsii Smith

Fig. 116

Sabinea Sarsii Smith 1879:59, pl. 11, figs. 6–8.—1886:655 [51], pl. 10, figs. 3, 3a, 4.

Sabinea sarsii.—Rathbun 1929:22, fig. 29.—Couture and Trudel 1968:883, fig. 22b-c.—Williams 1974c:13, figs. 5A-B (key).

Recognition characters.—This species is generally similar to *S. septemcarinata* except in a few characters as follows: Carapace with dorsal carina sharper and its teeth somewhat more prominent and usually more numerous; lateral carinae distinct and rather regularly dentate. Rostrum with acute tip reaching beyond distal edge of eyes, its middorsal carina sharper and higher. Abdomen with pattern

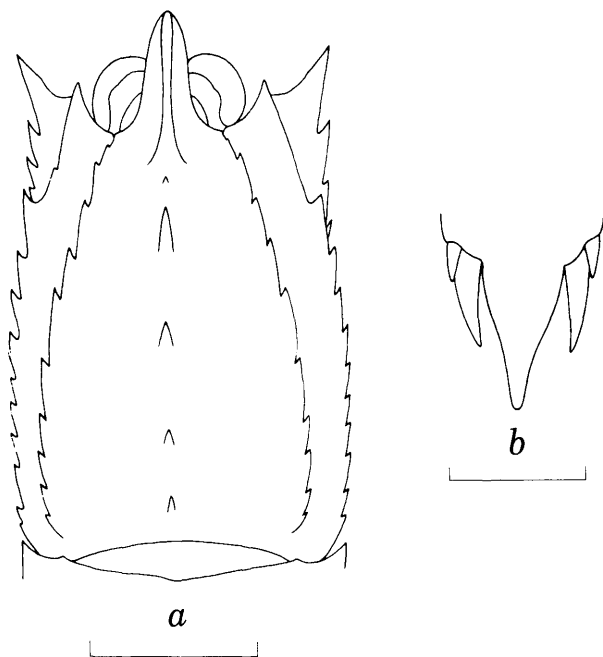


Fig. 116. *Sabinea sarsii* Smith. *a*, Carapace and eyes in dorsal view; *b*, tip of telson; *a*, 5 mm; *b*, 0.5 mm indicated (from Williams 1974c).

of sculpture more distinct. Telson ending in strong, acute tip flanked by 1 or 2 smaller spines; tip reaching to or slightly beyond inner ramus of uropods.

Measurements in mm.—Length of body: male 62 (Smith 1879), female 72 (Wollebaek 1908).

Variation.—In adults the telson terminates in an acute tip longer than its breadth at the base (separated from body of telson by an emargination at each side and from which an inner larger and outer smaller spine arise); in juveniles the tip may be triangular and flanked by three spines of nearly equal length on each side (Smith 1879).

Color.—Grayish brown (Squires 1965a).

Habitat.—Shells and sand, gravel, coarse gravel, stones and sponge (Smith 1879); -0.6° to 4.1°C (Squires 1965a), usually above 1.75°C (Blacker 1957); 48 to 710 m (Williams and Wigley 1977).

Type-localities.—Smith described a syntypic series from: Georges Bank, 110 m; Gulf of Maine, about ESE from Cape Sable, Nova Scotia, $42^{\circ}40'\text{N}$, $66^{\circ}58'\text{W}$, 205 m; Le Have Bank, $42^{\circ}44'\text{N}$, $64^{\circ}36'\text{W}$, 110 m (female USNM 39950); and Lofoten Islands, coast of Norway.

Known range.—Davis Strait to ESE Nantucket ($40^{\circ}01'\text{N}$, $65^{\circ}53'\text{W}$); Iceland; N Europe. The distribution was mapped by Stephensen (1935).

Remarks.—Squires (1965a) observed egg laying in late summer and fall in the western North Atlantic, with hatching in spring. Ovigerous females in the USNM collection are from Georges Bank in

autumn. Wollebaek (1908) reported females from the Barents Sea with partly filled ovaries in July and ovigerous females in the first half of September; Dons (1915) reported the latter from Norway in April, July and August. G. O. Sars (1890) described a very young stage in development.

Stephensen (1935) found *S. sarsii* north to about 60° latitude in Greenland but stated that it is a boreal species and is rare under arctic conditions. Christiansen and Christiansen (1962) found it rare in Isfjorden, Spitsbergen, but Blacker (1957) stated that it was numerous.

Stomach contents have included amphipod and copepod fragments, polychaetes and phyto-benthos (Squires 1965a).

Fontaine (1977a) described a relationship in the northwestern Atlantic between the prosobranch gastropod, *Lora cancellata cancellata*, and female *Sabinea sarsii* (27.3% of those ovigerous examined) and *S. septemcarinata* (4.8%, same) which bear ootheca of the snail on the second sternite of the abdomen under the egg mass. Eggs of the shrimp and mollusc have synchronous growth; at hatching time young molluscs are fully developed in the ootheca. This relationship is judged to be a non-parasitic association for transportation, but presence of the egg capsules reduces egg number in the shrimp. The association was not observed on *Pontophilus norvegicus*, *Sclerocrangon boreas* or *ferox*, *Sabinea hystrix*, or *Argis dentata*, although an analogous association involving *Argis lar* was reported from the Chukchi Sea (McCauley 1964).

Sabinea septemcarinata (Sabine)

Fig. 117

Crangon Septemcarinatus Sabine 1824:ccxxxvi, pl. 2, figs. 11–13.—Hemming 1958c:141.

Sabinea septemcarinata.—Ross 1835:1xxxii.—Smith 1879:57, pl. 11, figs. 5, 9–13.—Rathbun 1929:22, fig. 28a-c.—Couture and Trudel 1968:882, fig. 22a.—Williams 1974c:13, figs. 34A-B (key).

Recognition characters.—Carapace with median carina and 3 lateral carinae on each side, all variously toothed; median carina with up to 5 moderate teeth, anteriormost minute, second to fourth about equal, fifth smaller and near posterior margin, sometimes missing in smaller individuals; first lateral carina distinct and irregularly dentate posteriorly, but obscurely toothed on anterior $\frac{1}{3}$; second laterals terminating in short tooth at outer angle of orbit, but not distinctly dentate near anterior margin of carapace; third laterals strongly dentate anteriorly but armature becoming small or obso-

lete posteriorly. Rostrum tongue shaped, nearly horizontal, and bearing median dorsal carina most prominent near rounded tip; scarcely exceeding distal edge of eyes. Antennules and antennae with flagella relatively longer in males than in females; stylocerite broad and ending in strong, acute tip.

Abdomen with middorsal carina doubled on first segment and with 2 laterals on each side, second lateral ending in small, acute tooth on anterior margin; fifth segment similarly ridged but with second lateral carina obsolescent. Telson subtruncate, tip narrower in male than in female, armed with even number of spines or stout setae, 8 to about 14 (subject to wear); tip usually falling short of inner ramus of uropods.

Measurements in mm.—Length of body: male 45 (Smith 1879), ovigerous female 37–90 (Wollebaek 1908). “Length four inches” (Sabine 1824).

Color.—Varied red and white above, white beneath (Sabine 1824). Light brown, slightly darker or more reddish brown than *S. sarsii* (Squires 1965a). Dorsally with fuzzy edged brown spots resembling tufts of moss and a few yellowish green spots; under surface light with few red and reddish-orange spots, especially on legs; eyes green (MacGinitie 1955).

Habitat.—An arctic species (Stephensen 1935), usually in water below 1.5°C (Blacker 1957); occurs on a variety of substrates but most common on mud or mud mixed with small stones, shells, gravel and sand; 0–10 to 406 m, but most frequent from 80 to 200 m (Heegaard 1941; Christiansen and Christiansen 1962).

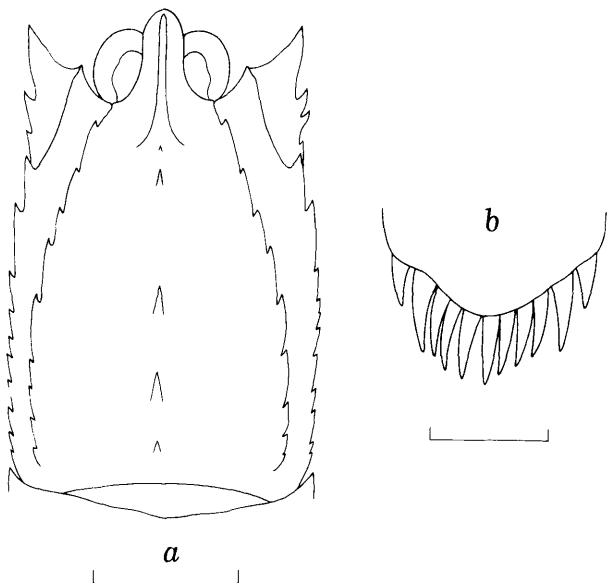


Fig. 117. *Sabinea septemcarinata* Sabine. a, Carapace and eyes in dorsal view; b, tip of telson; a, 5 mm; b, 0.5 mm indicated (from Williams 1974c).

Type-locality.—West coast of Davis Strait.

Known range.—Arctic Canada and Alaska to Point Barrow and Chukchi Sea (Makarov 1941); Greenland southward along eastern Canada to Massachusetts Bay; Iceland (except south coast); north of Faroes; Norway from 67°N through Barents Sea, White Sea, Kara Sea, and eastward to Wrangel Island (summary in Christiansen and Christiansen 1962, and mapped by Heegaard 1941).

Remarks.—Christiansen and Christiansen (1962) remarked that *S. septemcarinata* and *Sclerocrangon boreas* are the only decapods able to live on the soft mud near glaciers in the Arctic. They found ovigerous females at Isfjorden, Spitsbergen, from early July to early August. Heegaard (1941) stated that the females are ovigerous throughout the year, although he discussed differences of opinion regarding the spawning season. In the USNM collection they are present from Franz Joseph Land in June, and off Massachusetts and Nova Scotia from July to September. MacGinitie (1955) reported them from Point Barrow in September. Squires (1965a) found the breeding cycle to vary among populations, some larvae hatching in May-June, others in October, but he regarded egg laying as annual. In Hudson Bay (1967) he thought only 46% of females were potentially ovigerous each year, although numbers in the samples were small. Around the Queen Elizabeth Islands he (1968) found ovigerous females in July and August where 72% were thought to be potentially ovigerous annually. Maturity of gonads was considered to be an indication of cold adaptation. In his view, percent of females potentially ovigerous annually will indicate whether or not individuals of a population are under stress because of prevailing low temperatures. Of shrimp species taken in arctic waters, only five (*Eualus gaimardii*, *Spirontocaris phippisii*, *Lebbeus groenlandicus*, *Sabinea septemcarinata*, and *Sclerocrangon boreas*) provided numbers sufficient (but low) for assessment. These appeared to have good adaptation to low temperature and long arctic winters since most mature individuals appeared to spawn annually for the two or three times they probably spawn in a lifetime.

Sars (1890) described and illustrated the first and last larval stages of *S. septemcarinata*, and Stephenson (1916) described and illustrated an early juvenile stage which may be ascribed to this species (Stephenson 1935). Frost (1936) reported larvae in spring around Newfoundland and off Labrador.

Stomach contents consist of phytobenthos and detritus, polychaetes, crustaceans including euphausiids and amphipods, foraminiferans and hydroids, with some change in proportion in different areas. The shrimp was taken from stomachs of

beluga whales in southeastern Hudson Bay (Squires 1967).

Genus *Sclerocrangon* Sars 1883

Sars 1885:14.—Kemp 1910:139.—Rathbun 1929:20.—Holthuis 1955:136.—Hemming 1958b:161.

Zarenkov (1965), in restricting *Sclerocrangon*, erected three new genera to receive certain species of the genus that were included up to that time, the new treatment reflecting adaptations to burrowing, increase in body size, change in fecundity, egg size, and mode of larval development. Makarov (1968) amplified some of these conclusions with special reference to larval development, and Butler (1980) discussed other characters of the new genera.

Sclerocrangon boreas (Phipps)

Fig. 118

Cancer boreas Phipps 1774:190, pl. 12, fig. 1.

Crangon Boreas.—Sabine 1824:ccxxxv.

Sclerocrangon boreas Sars 1885:15.—Rathbun 1904:133.—1939:20.—Squires 1957:477, figs. 1A, B.—Couture and Trudel 1968:880, fig. 19.

Recognition characters.—Occurring in 2 forms in western Atlantic, a shallow water and a deep water-arctic form differing somewhat in sculpture and armature, see "Variation." Integument sculptured, rugose and hairy. Rostrum rather broad, exceed-

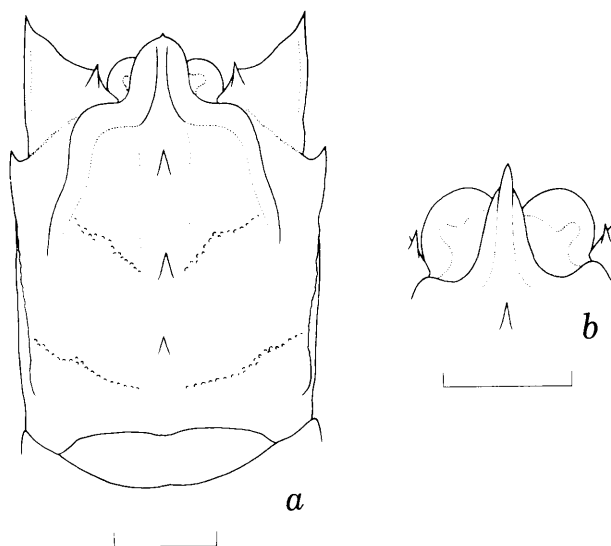


Fig. 118. *Sclerocrangon boreas* (Phipps). *a*, Carapace and eyes of adult in dorsal view; *b*, rostrum and eyes of juvenile; *a*, 5 mm; *b*, 2.5 mm indicated (from Williams 1974c).

ing eyes; tip acute to acuminate and with subterminal, median ventral projection; low median dorsal carina nearly continuous with middorsal carina of carapace bearing usually 3 teeth, middle one sometimes doubled, higher and thinner in juveniles; thickened edges of rostrum continuous with orbital margin and raised posterior margin of cephalic groove, and in turn with prominent lateral carina on each side; obsolescent longitudinal ridges above and below lateral carina. Hepatic spine present. Anterior margin with small, acute suborbital spine; prominent antennal spine long, wide-spread, bent somewhat mesially and barely exceeding rostrum; small pterygostomial spine hidden beneath. Stylocerite broad, truncate anteriorly but with distolateral spine. Antennal scale about twice as long as wide, convex laterally, rounded lamella exceeding distolateral spine.

Subchela more than twice as long as wide, distal margin obliquely transverse, spine obliquely longitudinal; merus with upper distal spine, carpus with lower distal spine.

Abdomen with median carina on first 5 segments, that on sixth doubled; dorsal tubercle on first segment variably produced forward; pleura each with 1 or more spines. Telson sulcate; 2 pairs of lateral spinules on terminal half, acuminate tip exceeding movable spine at each distolateral corner.

Measurements in mm.—Length of body: male 78; female 114 (USNM); that given by Rathbun (1929) as 120 is probably a female.

Variation.—Squires (1957) remarked that specimens from Ungava Bay differed considerably from the description given by Rathbun (1929) and from specimens found by him in shallow waters around Newfoundland, although those from deeper water there correspond with the Ungava material. In the form with a double middle dorsal tooth, the posterior member of the pair is reduced. The two forms were considered to be variants of the same species and were compared in illustrations and a table. His specimens (1965a) from deep water were larger than those from shallower depths.

Color.—Bright red marked with spots of reddish brown (Rathbun 1929). Brown (Squires 1965a). Brown and tan with few flecks of chalky white, green and yellow; eggs orange (MacGinitie 1955).

Habitat.—Arctic-boreal (various authors) on a variety of bottoms from fine mud to rock (Heegaard 1941; Blacker 1957; Christiansen and Christiansen 1962), often among *Balanus*; shore to 280 m (Wollebaek 1908).

Type-locality.—Near coast of Spitsbergen (in stomach of seal).

Known range.—East and west Greenland south to Cape Cod and SE of Nantucket (40°16'N,

67°26'W, Williams and Wigley 1977); arctic Canada and N coast of Alaska, Chukchi Sea (Makarov 1941) south to British Columbia (Butler 1956); Iceland excluding south coast; Faroes; Norway N of approximately 67°N and northward and eastward to Spitsbergen, Franz Joseph Land, Novaya Zemlya, White and Kara seas. The distribution is well mapped by Heegaard (1941).

Remarks.—MacGinitie (1955) regarded *S. boreas* as the most abundant large shrimp at Point Barrow, Alaska. He found ovigerous females there in September, sometimes washed ashore, bearing eyed embryos. Christiansen and Christiansen (1962) found ovigerous females in July at Isfjorden, Spitsbergen, among fairly abundant catches of the species and Blacker (1957) reported them in that area from May to October. Ovigerous females in the USNM collection are from from the Bering Sea in June, northwestern Greenland (see also Stephensen 1935), Alaskan panhandle and, Prince Edward Island, Canada, in August, and off Cape Cod in September. Squires (1965a) found about 65% of females from Foxe Basin and Labrador to be potentially ovigerous in late autumn, and they appeared to mature late at a carapace length of about 23 mm (~75 mm tl). In the Queen Elizabeth Islands (1968) 85% were potentially ovigerous in July and August. He considered that females spawn annually in these areas during their reproductive period, evidence that they are well adapted to reproduce in cold water.

The eggs are large (2.6–2.85 mm dia.), rather few in number, having been counted as up to 488 per female, and from all published accounts undergo an almost direct development (Heegaard 1941; Makarov 1967, 1968). In the latter paper, Makarov reviewed older work on the larval development obtained from embryos and added new data on development from work carried out in the Sea of Okhotsk. He described and illustrated two larval stages, both advanced, concluding that the younger is brief, representing the first stage after hatching, and that the second is a longer-lived postlarval stage. Neither stage is pelagic or free living, being passed under the abdomen of the female. The larvae are tightly covered by the pleopods of the female and cling with hooked dactyls on their fourth and fifth legs to one another, the egg shells and strings during the first stage, and with their chelae during the second stage. Seldom are they found dislodged in plankton.

Squires (1957, 1965a, 1967) reported *S. boreas* to be preyed upon by cod (*Gadus morhua*), the longhorn sculpin (*Myoxocephalus octodecimspinosus*), ringed, bearded and harbor seals, and the beluga whale. Food in stomachs of the shrimps was phy-

tobenthos, polychaetes, crustacean fragments (gammarid amphipods, ostracods, isopods and copepods), small pelecypod shells, ophiuroids, sponge spicules and foraminiferans. The mandibles were described.

The species at Point Barrow occasionally harbors a small clam, *Hiatella arctica*, under spines of the carapace, and bears egg capsules of the leech, *Crangonobdella murmanica*, on the pleopods (MacGinitie 1955).

Infraorder Astacidea

Superfamily Nephropoidea

Family Nephropidae

Eyes well developed or reduced, always present as movable appendages. Telson with lateral and/or posterolateral spines. Chelipeds equal or unequal, but fingers always considerably less than twice as long as palm; teeth on cutting edges placed in one plane. Fifth leg without true chela. Abdominal pleura large, triangular or ovate, usually ending in a point. Antennal scale, if present, with inner margin evenly curved, unarmed.

Holthuis (1974) amplified this general definition, that essentially covers the key characters, with great detail concerning the pattern of grooves, ridges, spines and teeth on the carapace, structure of the eyes, mouthparts, sternal armature, abdomen, pleopods, uropods, telson, and branchial formula.

Subfamily Nephropinae

Rostrum dorsoventrally depressed, with lateral and sometimes ventral (but no dorsal) teeth. Carapace without branchiostegal spine, but distinct postorbital spine, other spinules may be present. Body may be granulate. Lateral margin of telson with at most 3 small spines. Antennal scale present. Sternites of second to fifth abdominal segments each with sharp median spine in male. (From Holthuis 1974.)

Genus *Homarus* Weber 1795

Holthuis 1974:815.

Paraphrasing Holthuis (1974:815, including fig. 24): Essentially smooth, chelate lobster. Rostrum bearing lateral and sometimes ventral teeth. Carapace with postorbital and antennal spines present; distinct median dorsal groove extending from rostrum to posterior margin, subdorsal carinae low. A

set of other connecting grooves as follows: post-cervical distinct in upper part, lower part faint and almost entirely replaced there by intercervical connecting with cervical; urogastric, cervical and antennal distinct; gastroorbital and hepatic obscure. Thoracic sternum narrow; sternites between first to third legs with narrow single or double median or submedian ridges; that between fourth legs with 2 posteriorly divergent ridges in male, bearing sperm receptacle in female.

Chelipeds prominent, rather smooth and asymmetrical; major crusher with gaping fingers and molariform teeth in addition to smaller teeth; minor cutter without gape, cutting edges straight and armed with numerous nearly uniform small denticles, larger teeth if present neither molariform nor on cutting edge.

Abdomen smooth, no carina separating tergites from pleura. Telson narrowing posteriorly to convex terminal margin, short transverse proximal ridge and pair of posterolateral spines present. Exopods of uropods with transverse suture. Sternites of second to fifth segments with median spine in male, spines usually absent or greatly reduced in female. Male with first pleopods modified into rigid copulatory stylets.

The fossil record for the Nephropidae ranges back to the mid-Jurassic, and that of *Homarus* to the Cretaceous of North America and Europe (Glaessner 1969).

Homarus americanus H. Milne Edwards

(American lobster)

Fig. 119

Homarus americanus H. Milne Edwards 1837:334.—
Holthuis 1974:818.

Recognition characters.—This species is distinguished by generic characters.

Measurements in cm.—Total length, rostrum to end of telson: large male 64.3, female 61, but both usually much smaller (Wolff 1978).

Habitat.—Cool to cold temperate waters, shore to 480 m, usually found between 4 and 50 m (Holthuis 1974).

Type-locality.—Long Branch, New Jersey.

Known range.—Strait of Belle Isle, Newfoundland, to Cape Hatteras, N. C., and occasionally southward as far as off Rich Inlet, ENE Wilmington, N. C. (Holthuis 1974; Williams and Williams, 1981).

Remarks.—The American lobster has been the subject of such extensive study and reportage in the literature that attempt to summarize this information here seems an inadequate endeavor. The classic monographs of Herrick (1896, 1911) gave an exhaustive treatment of reproduction, embryology, larval and postlarval development, molting and growth, autotomy and regeneration, size, integumental glands and sense organs, variation in color and structure, structure of reproductive organs, predators, parasites and disease, ecology, and an extensive list of references.

Other bibliographies have been prepared by Everett (1972) who summarized fishing methods along with cited references, Lewis (1970) who compiled references on the genus *Homarus*, and Logan (1975) who reviewed literature concerning energy and physiology.

Holthuis (1974) provided a compendium of taxonomic and descriptive information on members of the superfamily Nephropoidea in the Atlantic Ocean. Phillips and Cobb (1977), and Cobb and Phillips (1980) edited a set of papers on lobsters, including *H. americanus*, that are not singled out here but which summarize much that is known of the group on molting and growth, sensory physiology, habitat and behavior, comparative studies on larvae, and comparative ecology among genera of nephropids.

Excellent general accounts of life history, ecology, fisheries and culture were provided by Cobb (1976), Dexter (1952), Scott (1973), Taylor (1975, general reading), Templeman (1966), and Wilder (1954); most of these papers provide further references.

Selected recent papers have treated: economic analysis of the lobster fishery and its response to environmental and other pressures (Bell and Fullenbaum 1975; Dow 1977); movements, migration and growth (Cooper and Uzmann 1971; Hughes and Mathiessen 1962; Uzmann, et al. 1977); mating (Templeman 1934; Bliss 1968); fecundity (Saila, et al. 1969); incubation (Branford 1978); larval and juvenile survival in culture (Sastry and Zeitlin-Hale 1977); comparative studies on growth and temperature tolerance (Gruffydd, et al. 1975); morphogenesis of larval mouthparts (Factor 1978); control of crusher-cutter development in juveniles (Lang, et al. 1978); genetic similarity of eastern and western Atlantic species of *Homarus*, with evidence for geologic age of divergence (Hedgecock, et al. 1977); and trophic relationships of *H. americanus* (Evans and Mann 1976; Breen and Mann 1976; Mann 1973).

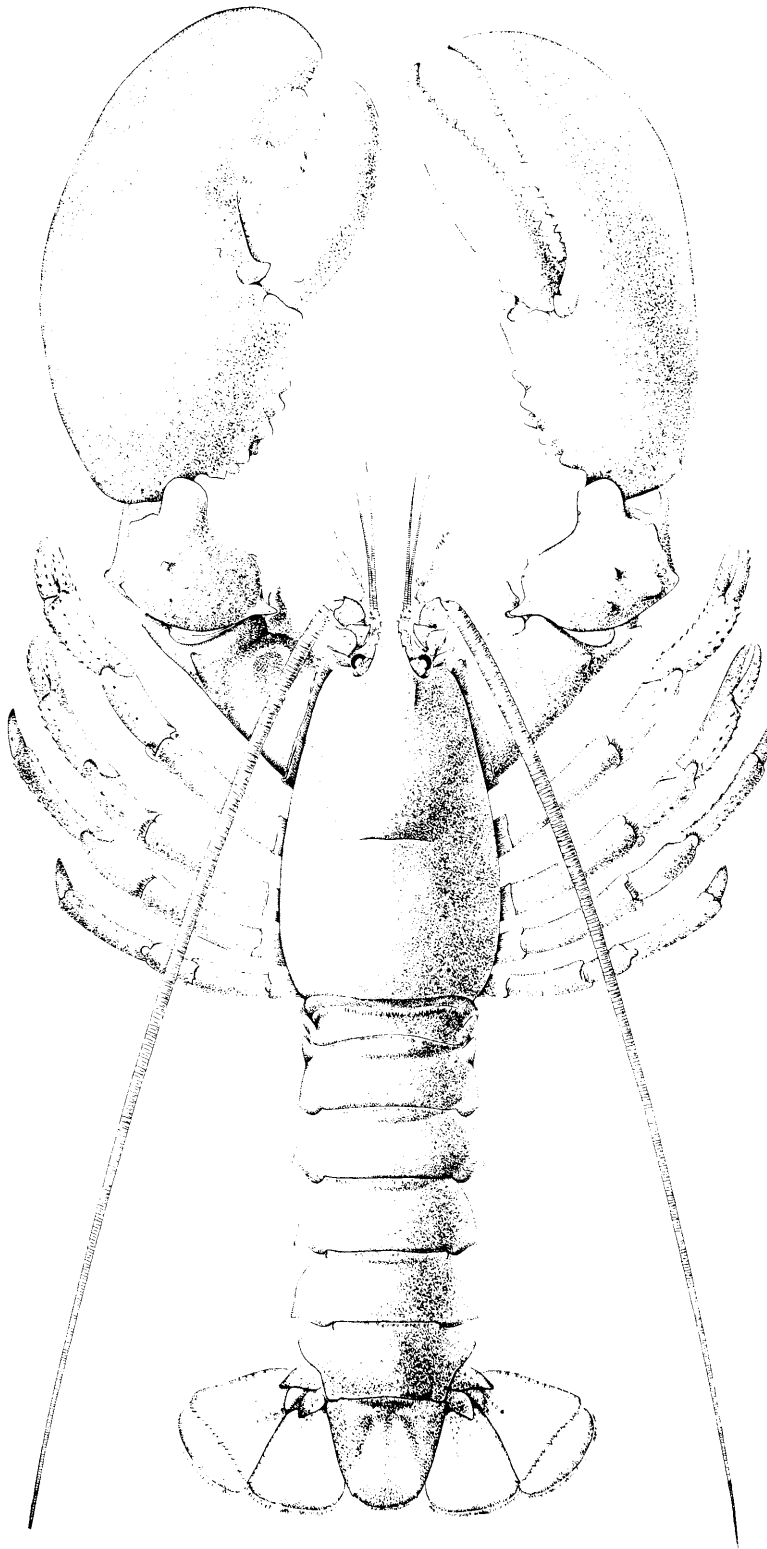


Fig. 119. *Homarus americanus* H. Milne Edwards. Male in dorsal view, much below natural size (from original by J. H. Emerton, specimen from Eastport, Maine, R. Rathbun 1884).

Infraorder Palinura

Carapace cylindrical or dorsoventrally depressed, without prominent rostrum but commonly spinose, fused laterally with epistome; antennal peduncle with 5 articles; third maxilliped pediform; abdomen well developed. (Adapted from Glaessner 1969.)

Superfamily Palinuroidea

First article of antennule fused with epistome. Antennal scale absent. All legs nearly equal in length and none chelate except subchelate last pair in females. First abdominal segment without pleopods; tail fan divided into soft membranous and striated posterior and harder anterior parts.

Family Palinuridae

Carapace subcylindrical. Eyes not enclosed in separate orbits formed by edge of carapace. Antennae not flattened but furnished with large, long, rather rigid, multiarticulate, usually spinose flagellum.

The fossil record for the family Palinuridae extends back to the Cretaceous in North America (Rathbun 1926, 1935).

Genus *Panulirus* White 1847

White 1847b:69.—Hemming 1958b:174.

Panulirus argus (Latreille)

(Spiny lobster, crawfish)

Fig. 120

Palinurus argus Latreille 1804:393.

Panulirus argus.—White 1847b:69.—Hay and Shore 1918:398, pl. 28, fig. 3.—Crawford and deSmidt 1922:291, figs. 265–271.—Schmitt 1935a:172, fig. 36.—Williams 1965:91, fig. 73.

Recognition characters.—Carapace covered with strong spines arranged more or less in regular longitudinal rows; spines above orbits very large, compressed, and curved upward and forward. Eyes large and prominent. Antennules nearly $\frac{2}{3}$ length of body; peduncles slightly exceeding antennal peduncle; outer flagellum shorter and thicker than inner, and strongly ciliated distally. Antennal segment with pair of spines in front, weaker pair about halfway to eye, strong median spine and weaker spines below insertion of antennules. Antennae very

large, heavy, exceeding body by more than length of carapace; peduncle with numerous strong spines; flagellum stout, stiff, line of cilia along inner margin and ringed with spines at intervals.

Legs rather weak, tips acute and bristly; female possessing small subchela on fifth legs with concave opposed surface formed between distal portion of propodus and proximal portion of dactyl.

Abdomen smooth, each segment crossed by furrow more or less distinctly interrupted at middle; pleural angles each produced into strong, sharp, backwardly directed tooth deeply notched and serrated on posterior margin. Pleopods absent from first segment of abdomen; exopod of pleopods broad, laminate; endopods missing in males, females with endopods of second pleopods laminate, last 3 endopods bifurcated. Proximal division of telson with rather strong spines; distal division with weak spines and setae in longitudinal lines. Uropods hard proximally, membranous distally; basal article bispinose, row of denticles along margin of hard part, and lines of minute spines and setae on upper surface of membranous part.

Measurements in cm.—Length of body from orbit to tip of telson: to approximately 45 (18 inches), occasionally larger.

Variation.—Aside from individual variations which will not be discussed here, the species exhibits marked allometric change with age as well as sexual dimorphism. These features, discussed in detail by Crawford and deSmidt (1922), are summarized here. Antennae of the young are longer in proportion to the body than in adults. Setae present on the young disappear in the adult and the sharpness of spines on the body tends to diminish with age, except for those on anterior portions of the carapace.

As pointed out in the description, only the females have chelate fifth legs. In adult males, the second pair of legs is extraordinarily developed. They are long, rarely used in walking, and the dactyl is long, curved, and provided with a brush of setae. The length of the dactyl, its curvature and setation increase with age. Sexual differences in the pleopods are given in the description.

Males have a relatively more inflated and longer carapace than females. Conversely, in females the abdomen represents a greater proportion of total length of the body than in males. Maximum lengths of the two sexes, however, are about the same (Creaser 1952). The posterior margin of the sternum in males is narrower than the comparable structure in females and the sternum is longer.

Color.—Coloration largely separable into two groups, (1) lightly colored individuals ranging from light gray and tan to shades of green and light

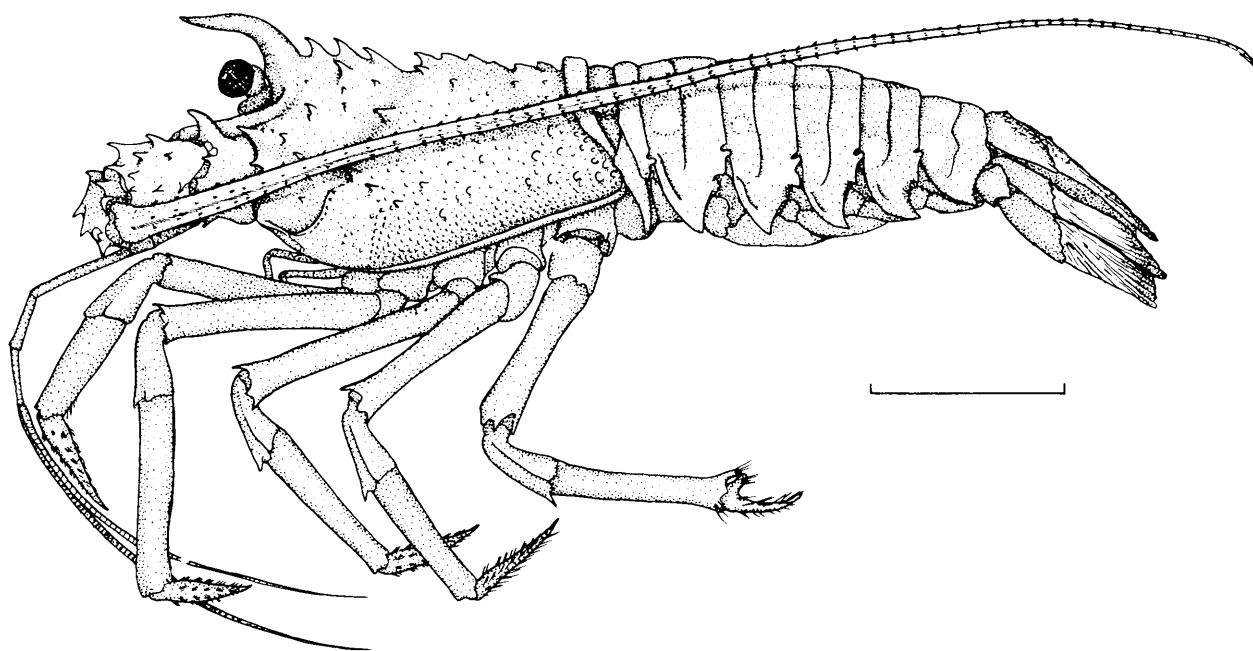


Fig. 120. *Panulirus argus* (Latreille). Female in lateral view, approx. 5 cm indicated (from Williams 1965).

brown, and (2) darkly colored individuals varying from shades of red to deep brown and blue. Abdomen spotted with yellowish ocelli; posterior margin of each segment edged with yellow or orange, lower angles of segments marked with bluish or greenish tints and sometimes additional colors. Tail fan crossed by bands of orange, yellow, and black, fringed with white. Pleopods usually orange, about half of surface covered by a black blotch. Legs striped longitudinally with blue. Ventral surfaces of body light yellow; thoracic sternum marked with irregular radiating stripes.

Young with coloration of carapace arranged in transverse bands, usually three, middle one dark; antennae frequently ringed with alternate light and dark bands; legs ringed with blue (Crawford and deSmidt 1922).

Habitat.—On reefs or among rocks, among growths of sponges or other objects which afford protection or places of concealment; low-tide mark to depths of about 91 m. Experimentally, lobsters at Bermuda have withstood depths of 457 m (Creaser and Travis 1950). Lobsters tend to aggregate in dens.

Type-locality.—Erroneously given as East Indies (“des Grandes-Indies”).

Known range.—North Carolina through Gulf of Mexico and West Indies to Rio de Janeiro, Brazil; Bermuda.

Remarks.—A number of papers have been published concerning the general ecology of *Panulirus argus*. Only a selective summary of this work can be given here. The most comprehensive single

general treatment is that of Crawford and deSmidt (1922) for the species in Florida, but substantial additions to this work have been given by Berrill (1975), Clifton, et al. (1970), Dawson (1949, 1954), Dawson and Idyll (1951), Herrnkind (1969, 1970, 1975), Herrnkind and McLean (1971), Joyce (1974), Lewis (1951), Lewis, et al. (1952), Marshall (1948), and Smith (1951). Biological notes on the species in Cuba were given by Buesa Mas (1961) and in Puerto Rico by Mattox (1952). Creaser (1950, 1952), Creaser and Travis (1950), and Sutcliffe (1952, 1953, 1957) discussed the species in Bermuda. Alves and Paiva (1976), Paiva (1971, 1973, 1976), Paiva and Pitombeira (1962), Paiva and Saraiva da Costa (1971), and Santos and Correa Ivo (1973) discussed biology and fisheries in northeastern Brazil, and Squires and Riveros (1978) discussed fishery biology of the species off Colombia. Finally, in a series of review articles, Labisky, et al., Lyons, Menzies and Kerrigan, and Simmons (1980) gave a history of the Florida spiny lobster fishery and the lobster resource, and a general summary of larval development and recruitment.

North Carolina must be regarded as the extreme northern edge of the range of this species. Concentrations of the species large enough to be exploited commercially occur in southern Florida, the Caribbean and West Indies southeast to northeastern Brazil, and at Bermuda. A population may exist in deep water in the northern Gulf of Mexico (Moore 1962). Differences in growth rate and breeding habits may exist among these areas.

Panulirus argus grows to a large size. In its first

year of life it reaches a length of about 5 cm (measurements of this species often given in inches in U.S.A.) and, though growth in the young individuals is more rapid than in older animals, increments in length after that time are about 2.5 cm a year. Adults of 41 cm length are approximately 16 years of age, the males attaining somewhat greater length than females.

After juvenile stages are past, molts average about 2 ½ times per year, occurring most frequently from March to July and from December to February, at least in the Florida area. Among captive animals, molts without growth can occur. About 12 days elapse from the first sign of molting until the new exoskeleton is hard enough to resist denting, though hardening of the new shell is not complete until the 28th day. Travis (1954, 1955a, 1955b, 1957) gave an exhaustive study of the molting process among spiny lobsters near the age of sexual maturity. This work is beyond the scope of the present summary, but her findings show that molting among captive adolescent animals is largely confined to the warmer months at Bermuda and is more frequent than among Florida specimens. Other evidence shows that growth of the young is more rapid in Bermuda than in Florida, and that sexual maturity is reached sooner.

The mating season in Florida was formerly judged to extend from March through July but evidence now indicates that it is more extended. Buesa Mas (1961) reported mating in June and November in Cuba. Sexual maturity is reached in females as small as 15 cm long, but ovigerous females under 20 cm in length are rare. Mating pairs are judged to be about the same age, and mating usually occurs in the hardshell state. At the time of mating the male places a waxy spermatophore on the thoracic sternum of the female. Prior to spawning, the female scratches the surface of this packet with the chelate fifth legs. The actual egg laying is accomplished in about one-half hour, during which the female lies partially on her back forming a trough of the underside of her abdomen with the aid of the exopods of the pleopods. Eggs extruded from the oviducts pass backward from the bases of the third legs over the spermatophore and become attached to the endopods of the last three pairs of pleopods. After spawning, the spermatophore appears eroded as if enzymatic action had partially destroyed it. The eggs hatch in about one month. A second mating and egg laying may occur about a week after the hatch of the first batch and at this time the ovary is spent and the spermatophore almost completely eroded away. Molting of females during this season occurs only after spawning.

Direct evidence from the studies in Bermuda

shows that females may lay eggs twice in a season. The number of eggs laid depends on the size of the individual, and the second brood is smaller than the first. Estimates show that a 23-cm female can lay 500,000 eggs, a 30-cm female 1,118,656, a 38-cm female 2,566,916. A second laying by a 33-cm female consisted of 1,008,788 eggs. Thus, it is estimated that a 38-cm female might lay 4 million eggs a season. Buesa Mas (1961) found that 93% of ovigerous females in Cuba exceed 18 cm total length. At Dry Tortugas, Davis (1975) found the smallest ovigerous females (cl 78 mm) to be larger than the 45 mm reported by Smith (1951) but comparable to minima given by other workers for Bahama Bank (74 mm) Bermuda (85–90 mm), Panama (69 mm) and Antigua (80–90 mm). He also found, contrary to Creaser's figures for Bermuda (1950), that reproductive activity tends to decline in females larger than 125 mm cl, and other workers have agreed.

Kanciruk and Herrnkind (1976) found that reproductive activity is greater in deeper water than in shallows. At Bimini in autumn males exceed females in size for a given depth, but females outnumber the males in the deeper range: 16–19 m, 54.8% female; 20–25 m, 65.2% female; 60% of the latter showed recent reproductive activity. The authors estimated 3.7 molt cycles per year for females of 87.4 mm cl (\bar{x}), and on this basis the animals spent 6–9 days with whole spermatophores before oviposition, 20–30 days with eggs, 38–56 days without eggs but with eroded spermatophores, for a total of 84–125 days exclusive of the days following molt before mating. In Puerto Rico, the spawning season may be similar to that in Florida, for 22% of females in the commercial catch are ovigerous in September and 18% in October.

In Bermuda and elsewhere, there is apparently a movement of females from shallow to intermediate depths and from deeper water to these depths for spawning. Aside from these movements, there is evidence in Bermuda that the lobsters exhibit considerable homing tendencies, often moving as much as 5 miles against strong tides to return to the place of original capture. Adults tagged in Florida, on the other hand, have moved as much as 100 miles in 100 days (Smith 1954). Early studies of movement in these lobsters have been augmented by observations, especially off southern Florida, of a remarkable queuing behavior (Herrnkind 1969, 1970, 1975; Herrnkind and Cummings 1964; Herrnkind and McLean 1974). Autumnal mass migrations involve diurnal movements of thousands of lobsters in single-file queues of up to 50 individuals maintained by tactile cues received through the inner antennular rami, legs and antennae. The movements are directional, but

no special animals are singled out as leaders. Individuals captured in migration maintain queues indoors for up to several weeks whereas at other times the queues last only for hours. The overlapping bodies are thought to help in protecting each other, and movements in formation reduce drag during locomotion, thus the queuing behavior may conserve energy and be a consequence of the evolutionary role of migration in the species (Bill and Herrnkind 1976).

The adaptive significance is unknown. Waning daylight in autumn seems to be a triggering mechanism. One result is redistribution to new feeding grounds. In some years the migration has been so great that lobsters spilled out of the water onto rocks. The mass marches often mean windfall profit to fishermen when hundreds are sometimes clustered in small places. *Panulirus argus* is considered to be more vagile than the relatively sedentary *P. guttatus* (see Gregory 1979).

The larva of the spiny lobster is a flattened, leaf-shaped, planktonic organism which, before its identity was known, was given the name phyllosoma. Development of the phyllosoma larvae of *P. argus* has been studied off Florida and at other points in the Atlantic Ocean from the West Indies to the southeastern coast of the United States and north of Bermuda. Bigelow and Sears (1939) found phyllosoma larvae (*P. argus?*) off Chincoteague Bay in July, 1929. Eleven stages have been described from plankton. In Florida, the bulk of freshly hatched larvae appear between June and August, the last stages being taken in December and January. The first postlarval, or puerulus, stages appear in inshore waters from January to March. Thus, larval development is judged to require six months, and during that time the larvae may be swept hundreds of miles from the spawning place. (Feliciano [1956] described a prenaupliosoma stage which may at times be freed in the water but this has yet to be confirmed.) The puerulus is shaped like a miniature adult, but is about 17 mm long, colorless, and has a soft exoskeleton. It is non-planktonic and settles in shallow water. Ten postlarval stages have been distinguished. Stages I through III avoid light, but later stages show no such reactions. At the end of the first year, at the eleventh postlarval stage, the young are approximately 5 cm long.

Aside from reactions of the very young postlarvae to light, Hess (1940) showed that freshly molted adults are sensitive to light in many regions of their bodies, but as soon as the body is again sclerotized no such reactions are apparent. Sutcliffe (1956) demonstrated that in clear, shallow water lobsters sought cover in bright moonlight. He concluded that movements attributed to tidal responses were actually responses to light.

Stridulation by spiny lobsters (Palinuridae) has been described by a number of workers (Moulton 1957) and in *P. argus* it is produced primarily by a toothed ridge mesial to the bases of the antennae and extending anteriorly from beneath each eye. A corrugated membrane at the base of each antenna is played against this ridge, producing sound when the membrane is moved proximally. Two types of sound are produced, a slow rattle normally produced by animals in small groups, and a rasp which accompanies defensive behavior. A squeaking sound is also produced in an unknown manner, by vibration of the body, when a specimen is held in the hand of an observer. The effect of these sounds on other lobsters or marine life is unknown.

Pearse (1932a) determined the freezing point of *P. argus* blood at Tortugas (range -1.86° to -2.39°C).

Panulirus argus is preyed upon by the jewfish, *Epinephelus itajara*, the Nassau grouper, *E. striatus*, and mutton snapper, *Lutjanus analis* (see Randall 1967), and other large predators (Clifton, et al. 1970). It in turn preys on a variety of invertebrates including molluscs and sea cucumbers.

Family Scyllaridae

(Spanish lobsters)

Carapace depressed; exoskeleton thick, hard, sculptured or tuberculate; orbits excavated in margins of dorsal surface. Antennae short and broad with flat scalelike, stiff articles. Mandibles with 1-jointed palp. Legs simple except minutely chelate fifth pair in female.

The fossil record for the family Scyllaridae extends from the lower Cretaceous (Glaessner 1969), and from the lower Eocene of the Gulf Coast in North America (Rathbun 1935).

Key to Genera and Species

(Adapted from Lyons 1970)

1. Exognath of outer maxillipeds without flagellum; terminal article of antennae with edge cut into deep lobes distally [*Scyllarus*] 2
- Exognath of outer maxillipeds with flagellum; terminal article of antennae with edge nearly smooth or crenulate distally *Scyllarides nodifer*

2. Gastric and all lateral prominences on carapace sharp; second article of antennular peduncles cylindrical; pleura of fourth abdominal segment sharply rectangular or acute laterally *S. depressus*
Prominences on carapace blunt; second article of antennular peduncles flattened dorsally; pleura of fourth abdominal segment rounded laterally. 3
3. Pregastric tooth on carapace nearly always bilobed, incised; first to fourth abdominal segments with deep, narrow median notch in posterior margin *S. americanus*
Pregastric tooth on carapace rounded, entire; first to fourth abdominal segments with very shallow, broad median notch in posterior margin *S. chacei*

Genus *Scyllarides* Gill 1898

Gill 1898:99.—Verrill 1922:18.—Hemming 1958b:94.

Scyllarides nodifer (Stimpson)

Fig. 121

Scyllarus nodifer Stimpson 1866:48.—Stimpson 1871b:123.

Scyllarides americanus Verrill 1922:24, pls. 5–6.

Scyllarides nodifer.—Holthuis 1960b:153.—Williams 1965:98, fig. 77.—Lyons 1970:7, figs. 3–5, 19, pl. 1, pl. 2c.

Recognition characters.—Adult carapace longer than wide, subtruncate in front, coarsely and unevenly granulate, granules elevated, not crowded, each surrounded by more or less complete circle of stiff hairs; anterolateral corners forming nearly right angle terminating in an obtuse tooth; cervical notch and groove well marked with numerous denticles on margin in front of and behind notch; posterior transverse groove deep and conspicuous; gastric area with large, broad-based, promi-

nent median ridge divided into smaller anterior and larger posterior part, each part ending in an anterior, large, conical, obtuse or bilobed tubercle with other similar but smaller tubercles and coarse granules around and behind apex; cardiac region with prominent but less elevated area with larger tubercles than on adjacent surface; similar ridge on each branchial area. Orbits large, with prominent, thick borders, anterior notch wide and deep.

Antennae with distal article broader than long, edges broadly and evenly rounded, minutely lobulate and crenulate, fringed with short, closely placed hairs; exposed portion forming a half oval, upper side covered with small, rough granules and small pits bearing tufts of short hairs in large adults, smoother in small individuals. Penultimate movable article distinctly wider than long; broader than distal article; distal lobe terminating in nearly right-angled point in large adults, armed with spine in smaller specimens; edges dentate with many small teeth and some larger ones, a larger stout tooth near inner curve of both antennae separated by space about equal to orbit of eye. First movable article irregularly 4-lobed above; small outer lateral lobe with about 3 denticles; median or distal lobe



Fig. 121. *Scyllarides nodifer* (Stimpson). Female in dorsal view, approx. $\times 0.5$. Bob Simpson photo (from Williams 1965).

swollen and coarsely granular; inner lobe swollen and coarsely granular; inner lobe obliquely oblong with inner edge truncate and denticulate; prefrontal or rostral lobe a little broader than long, widest distally, swollen laterally, with concave sides and median groove.

Outer maxillipeds large, basal articles stout. Legs projecting beyond carapace; first pair stouter than others, propodus considerably swollen, dactyl stout; fifth pair with propodus most slender; merus and carpus of all pairs, except carpus of first, with finely serrulate carina ending in sharp distal tooth; carpi, except first, with lateral carina ending in distal tooth; meri of last 4 legs with ventrolateral carina ending in sharp spine distally (carina sharpest on legs 3 and 4) and each with blunter mesial spine distally.

Underside of bases of legs and sternum roughly sculptured, 1 larger acute or pyramidal elevation on sternum opposite base of each leg.

Abdomen strongly sculptured, elevated areas coarsely granulated and hairy, much like carapace. Second to fourth segments with median, elevated, obtuse ridge, covered with large granules; fifth segment with slight ridge. Pleura large, angular; that of second segment largest, subacute, both edges with dentations about as large as adjacent granules, those of third to sixth segments more minutely dentate on posterior border, nearly smooth or minutely crenulate on anterior border. Telson broader than long, subtruncate distally; posterolateral angles broadly rounded; granulated and hairy proximally, covered with numerous forked ridges and grooves distally becoming fine near edge. Uropods broad, sculptured as telson. Sternum of second segment in males bearing sharply raised, serrate, heavily sclerotized ridge.

Measurements in mm.—Length of carapace: male, 93.8, female 103.1 (Lyons 1970); female, 127. Larger specimens have been observed.

Variation.—Smaller specimens have a smoother integument than adults, but prominences on the carapace and fourth abdominal segment are more pronounced than on adults. The carapace and fourth abdominal segment are wider than long until a length of about 30–40 mm is reached (Lyons 1970).

Color.—Body covered with irregular small brown spots on grayish brown to yellowish background; many orange-red tubercles on edges, across ridge near rear edge of carapace, base and edges of antennal lobes; darker red spots at sides of gastric region, on anterior lobes of carapace and at middle of first abdominal segment; underparts yellow with darker yellow and brown spots; legs banded with red and purple; flagella of antennules purple.

Habitat.—Mud, shell, coral, and sandy bottoms; 2 to 91 m (Lyons 1970).

Type-locality.—Florida Keys.

Known range.—Bermuda; Cape Lookout, N. C., to Florida and throughout Gulf of Mexico to Yucatan (Lyons 1970); a postlarva from S of Long Island (29°11'N, 71°56'W) was taken in the stomach of a lancetfish (*Alepisaurus*). Sims (1968) described larvae of *Scyllarides* sp. from 400 mi. E Cape Cod and 300 mi. E of Cape May, N. J., light, indicating long distance dispersal via the Gulf Stream.

Remarks.—Abstracting notes on individual scyllarid species from the comprehensive account of Lyons (1970) would be needless duplication of effort, but a few general conclusions from his work follow. There was no evidence of external fertilization from his own observations or in published accounts on *Scyllarides* or *Scyllarus*. Oviparous females of *Scyllarides nodifer* are known from late May to early August off west Florida, with some evidence for two spawnings in a single season.

In a comprehensive treatment, Lyons reviewed the confusing larval and postlarval stages of scyllarids that have been given a variety of names, including generic designations by early workers before the affinities were understood, although the life histories of these lobsters are still incompletely known. According to Lyons, development passes through larval or phyllosome stages into a transparent postlarva, and from this into pigmented juvenile stages. Juvenile *S. nodifer* was distinguished from similar *S. aequinoctialis* both by description and illustration. In *Scyllarides nodifer*, as in *Scyllarus americanus*, *chacei*, and *depressus*, there is a dramatic decrease in relative size of the pleopods at the molt from postlarva into first juvenile, and the pleopods then remain reduced in size until the genital pores appear, after which there is successive increase as the animals approach maturity. Apparently there is little need for these appendages between the early natant stage and the reproductively active stages.

Commensals of *S. nodifer* are barnacles, ectopods, hydroids, sponges, annelids, and bivalve molluscs, they being noted on all but very young individuals or recently molted adults (Lyons 1970). One stalked barnacle, *Octolasmis hoeki*, was found on oral appendages, gills, and inner lining of the carapace near the gills in 50% of the specimens examined.

Predators on *S. nodifer* noted by Lyons were grouper, red grouper, *Epinephelus morio*, gag grouper, *Mycteroperca microlepis*, and tiger shark, *Galeocerdo cuvieri*. Lyons reviewed Randall (1967) who found that scyllarid lobsters made up 1% to over 45% of food by volume in a series of West Indian fishes.

Catch of *Scyllarides* in the lobster trap fishery (Lyons 1970) and in trawl samples off Mississippi (Franks, et al. 1972) is insignificant. Lyons plotted

carapace length-weight relationships for samples of males and females.

Genus *Scyllarus* Fabricus 1775

Fabricius 1775:413.—China 1966:203.—Glaesner 1969:R475.

Carapace flattened, width at anterolateral corners equal to or slightly greater than length in midline; middorsal ridge and oblique ridge on each side prominent. Antennules with first articles broad, flattened, and immovable, second article much narrower and elongate; third and fourth articles slender; flagella short; abdomen, including telson, much longer (nearly twice) than carapace; pleura of first segment incised in center of lower edge, second broad and pointed distally. Anterior pleopods of male with both rami slender, flattened, hairy on outer border; remainder with exopods small and lamellate, endopods rudimentary. Anterior pleopods of female with both rami broad and flattened; exopods of remainder lamellate, endopods slender and with long silky hairs. Legs stout, extending beyond carapace; first legs stoutest, remainder progressively more slender; second pair longest; dactyls of first pair somewhat serrate on lower border, remainder simple; fifth legs of females subchelate. Third maxillipeds stout, basal articles prismatic.

Scyllarus americanus (Smith)

Fig. 122

Arctus americanus Smith 1869b:119.

Scyllarus americanus.—Bouvier 1925:448–450 (part).—Holthuis 1960b:152.—Williams 1965:96, fig. 75.—Lyons 1970:25, fig. 9.

Recognition characters.—Carapace with surface squamose in part dorsally, a little squamose below lateral borders posteriorly, lightly tuberculate toward epistome, with feathered setae (some darkened) between squames; middorsal ridge with anterior (pregastric) eminence large, bilobed anteriorly, gastric eminence sharper and more elevated, cardiac eminence not so sharp, bilobed; 2 coalesced blunt spines over each orbit large and somewhat separated from ridges over branchial areas. Rostrum short, rounded at tip, blunt keel-like middorsal tubercle above. Anterior border of carapace emarginate. Orbits deeply excavated, margins broad, with broad anterior notch; blunt tooth on proximal (fixed) antennal article in center of notch. Anterolateral corners of carapace spini-



Fig. 122. *Scyllarus americanus* (Smith). Ovigerous female in dorsal view, approx. $\times 1.5$. Bob Simpson photo (from Williams 1965).

form, lateral borders roughened with squames; rather deep notch behind orbit and another one farther back. Area between posterior marginal groove and posterior margin of carapace faintly squamose and traversed almost always by single distinct groove.

Second antennular article elongate, flattened above, anterior margin obliquely truncate. Antennae spatulate, somewhat punctate, surface variably covered with feathered setae; distal article with irregularly rounded anterior border cut into 6 somewhat separated lobes, edges ciliated, mesial lobe short, spiniform, next much larger and less pointed, following 3 about equal in length, tips rounded, lateral lobe about twice width of intermediate lobes; penultimate article short, bilobed in dorsal view; proximal movable article triangular in outline, edges spinose, 2 lateral spines larger than 4 variably sized mesial spines, prominent ridge running to apical spine nearly dividing article in half.

Second, third, and fourth tergites of abdomen (and to some extent first) with arborescent furrows running inward and forward toward midline. First to fourth segments with median notch in posterior margin fairly deep and narrow; fourth segment

elevated, more or less ridgelike in midline. Third to fifth pleura rounded distally, sixth with narrowly rounded anterolateral lobe. Sternum triangular, broad at base; smooth with furrows ciliated; male with low tubercle in center of fifth sternite, female similar.

Measurements in mm.—Ovigerous female: length of carapace 25, width 29; length of abdomen 45. Females larger than males (Lyons 1970).

Habitat.—Low-tide mark to 46 m (Lyons 1970); many taken in 2–6 m by bait shrimpers in Biscayne Bay and off central west Florida.

Type-locality.—Egmont Key, Fla.

Known range.—Off Bogue Inlet, N. C., to Campeche Banks off Mexico, and Venezuela.

Remarks.—Ovigerous females have been reported from southern Florida in January, March and April (Robertson 1968b), and in September (Williams 1965). Sims (1966) found them off west Florida from February to May, and Lyons (1970) reported them from Cuba in May and September. From numerous records, Robertson thought that spawning may occur throughout the year, at least in southern parts of the range, with a peak in spring and summer.

Robertson (1968b) gave a detailed, illustrated descriptive account of larval development in the laboratory, finding that it passed through six or seven stages to reach postlarva in 32 to 40 days at 25°C, and maybe less than 30 days at 30°C, on a diet of brine shrimp nauplii. Final stage phyllosomas were obtained in various salinities ranging from 23.2 to 38.6‰. Larval life is lengthened at lower temperatures (20°C), but such larvae did not metamorphose to postlarvae. Larval life of *S. americanus* is probably shorter than that of other genera in the family, including *Scyllarides*, its success in culture owing to an ability of all stages to feed well on *Artemia* nauplii. Feeding is a problem in the culture of phyllosomas, for the latter stages seem to have more difficulty than earlier ones in catching brine shrimp nauplii, and it seems that changing morphology of the larvae indicates a change in food with increasing age. Mouthparts of larger phyllosomas are relatively small in relation to overall size. Some authors have indicated that food of these later stages is scyphozoan medusae.

Robertson, agreeing with some previous authors, thought that distribution of both larvae and adults indicates a relatively inshore habitat where in some areas salinity may fluctuate. Evidence for this distribution is further offered by presence of *S. americanus* in the stomach of a snakefish and *Scorpaena brasiliensis* at an 18 m station (Lyons 1970).

Scyllarus americanus has been found fouled with serpulid worms, balanoid barnacles, and once with

the holdfast of an alcyonarian coral on the carapace, but is much less frequently burdened with such animals than *Scyllarides nodifer* (see Lyons 1970).

Scyllarus chacei Holthuis

Fig. 123

Scyllarus americanus.—Hay and Shore 1918:399, pl. 28, fig. 2.—Bouvier 1925:448–450 (part), pl. 7, fig. 3.—Boone 1930:84, pl. 23, fig. A.—Schmitt 1935a:174 (part), fig. 39.—Holthuis 1959:126.

Scyllarus chacei Holthuis 1960b:152.—Williams 1965:95, fig. 74.—Lyons 1970:27, fig. 10.

Recognition characters.—Carapace with surface squamose in part dorsally, lightly squamose below lateral borders, with feathered setae (some darkened) between squames; middorsal ridge with anterior (pregastric) eminence large, rounded, gastric eminence higher, upturned, cardiac eminence somewhat smaller than pregastric; 2 coalesced



Fig. 123. *Scyllarus chacei* Holthuis. Male in dorsal view, approx. $\times 2$. Bob Simpson photo (from Williams 1965).

spines over each orbit large and somewhat separated from ridges over branchial areas. Rostrum short, rounded, sides nearly parallel. Anterior border of carapace emarginate. Orbits deeply excavate, with broad anterior notch, blunt tooth on proximal (fixed) antennal article in center of notch. Anterolateral corners of carapace spiniform, lateral borders roughened and another spine farther back; area between posterior marginal groove and posterior margin of carapace nearly smooth but traversed by 2, seldom 3, distinct parallel grooves.

Second antennular article elongate, flattened above, anterior margin obliquely truncate. Antennae spatulate, somewhat punctate; distal article with irregularly rounded anterior border cut into 7 elongate, somewhat separated, lobes with rounded ends, edges ciliated; mesial 2 lobes shortest and sharpest, lateral lobe obliquely truncate and broadest; penultimate article short, bilobed in dorsal view; proximal movable article cordate, a prominent ridge throughout length to spiniform tip, a less conspicuous and irregularly shaped mesial ridge, edges spinose.

Second, third, and fourth abdominal tergites (and to some extent first) with arborescent furrows running inward and forward toward midline; first to fourth segments with median notch in posterior margin very shallow, fourth segment not elevated in midline. Third to fifth pleura rounded distally, sixth with rounded anterolateral lobe. Sternum triangular, broad at base, smooth with furrows ciliated; male with slight midventral elevation on fifth plate, elevation less evident in female.

Measurements in mm.—Length of carapace: male 21.6, female 24.2 (Lyons 1970); 19, length of abdomen 35 (Williams 1965).

Habitat.—“On bottoms composed primarily of sponge, dead and living coralline algae, and dead shell, with little sand but much silt” (Lyons 1970); 11 to 329 m.

Type-locality.—North-northwest mouth of Marowijne River, about 20 miles off coast of Surinam.

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

Remarks.—Ovigerous females have been reported from Florida in late January (Lyons 1970) and March, South Carolina in July, Surinam in August and September, and northeast Brazil in November (USNM).

Robertson (1968a) hatched and reared phyllosomas of *S. chacei* in the laboratory until transformation of postlarvae; both phases were identical to analogues from plankton and indistinguishable from developmental stages of *S. americanus*. Lyons (1970) agreed with this judgment. Lyons noted

considerable variation in exopod development on postlarvae of *S. chacei*, finding development more prominent in planktonic than in benthic animals, but seemed to suggest that this may result from staging variations in metamorphosing from larva to postlarva.

Lyons further characterized *S. chacei* as one of the most common and widely ranging western Atlantic scyllarids, occurring mainly beyond depths frequented by *S. americanus*; samples throughout the range indicate general abundance. He plotted carapace length-weight relationships for samples of males and females.

Scyllarus depressus (Smith)

Fig. 124

Arctus depressus Smith 1881:429.

Scyllarus arctus paradoxus Rathbun 1900:309 (part).

Scyllarus depressus.—Bouvier 1915:291.—Lyons 1970:30, figs. 11–13.—Robertson 1971:841 ff., figs. 2–33.

Scyllarus americanus.—Bouvier 1925:447, pl. 8, fig. 2.

Scyllarus nearctus Holthuis 1960b:151.—Williams 1965:97, fig. 76.

Recognition characters.—Carapace with surface squamose in part dorsally, but only on or near ridges and sides, smooth below except sinuous submarginal row of tubercles and lightly granulate area posteriorly, densely ciliate above between squames and on smooth areas. Rostrum short and acute; pregastric tooth above it about same size, gastric tooth larger, acute, all 3 of these directed forward. Cardiac eminence blunt, bilobed at apex. Gastric tooth and cardiac eminence with squames at base, rostrum and pregastric tooth in smooth area. Lateral ridges ending anteriorly in forwardly directed spine. Front emarginate with small projection about halfway between rostrum and orbit. Orbits deeply excavated, upper border composed of 2 spines coalesced at base, lower border an inflated ridge more or less interrupted by 2 subequal spines at anterolateral corner; anterior notch partially occupied in middle by large serrulate tooth on first (fused) antennular article and another eminence forming articulation of second antennal article. Anterolateral corners of carapace drawn out to strong spine, lateral border with notch behind eye and another less definite notch behind anterior end of branchial ridge. Posterior margin of carapace with sharp but broadly opened notch in midline; area between posterior marginal groove and posterior margin of carapace traversed by 2 rows of squames.



Fig. 124. *Scyllarus depressus* (Smith). Male in dorsal view, approx. $\times 1.5$. Bob Simpson photo (from Williams 1965).

Anterior border of first antennular article with low teeth or irregularities; second article cylindrical with flattened, rounded distal projection; succeeding articles slender, flagella short. Antennae fairly smooth, ciliated, edges densely covered with longer feathered setae; distal article semi-elliptical in outline, edge broken into 6 well-separated lobes with narrowly rounded tips, inner lobe smallest, outer broadest and subtruncate, suggestion of seventh lobe mesially; penultimate article short, irregularly spined and lobed; first movable article roughly triangular with apex formed by strong spine, 2 spines on outer border and 3 spines on inner border, apical spine and first 2 inner spines with small spurs on mesial borders, third spine at posteromesial border smaller, definite ridge running across article from articulation to apex.

Second to fifth abdominal segments (and to some extent first) with arborescent furrows running inward and forward toward midline. First to fourth segments with median notch in posterior margin deep and narrow. Third and fourth with distal edge

of pleura rounded anteroventrally, angled at posteroventral corner; fifth broadly rounded distally; sixth with anteroventral lobe broad and rounded. Telson with 4 flattened spines at distal edge of hard portion. Each ramus of uropods with spine at same level on outer margin.

Sternum triangular, narrower in males than in females, smooth, a little pubescent in grooves. Males with strong, shelflike protuberance on sternite between last pair of legs, and with strong sharply ridged shoulder extending over genital pore. Female with low eminence on sternite between last pair of legs.

Measurements in mm.—Ovigerous female: carapace length 24, width 26; abdomen, length approximately 50. Male carapace length 23.8 (Lyons 1970, in part).

Habitat.—Bottom associations similar to those of *S. chacei*; 29 to 263 m (Lyons 1970).

Type-locality.—South of Martha's Vineyard, $40^{\circ}05'39''N$, $70^{\circ}23'52''W$, 157.3 m, *Fish Hawk* Stn. 872.

Known range.—Off Martha's Vineyard, Mass.; off Cape Hatteras, N. C., through Gulf of Mexico and West Indies to State of São Paulo, Brazil.

Remarks.—Both Lyons (1970) and Robertson (1971) reviewed the history of this species, agreeing that Smith's specimen of *Arctus depressus*, originally acknowledged as a probable immature stage, is the holotype of *Scyllarus depressus*. The larval description of Bouvier (1925) agrees both with Smith's specimen and with the results of modern work.

Ovigerous females are known from southern Florida in January and October (Lyons 1970), and off North Carolina in June (Williams 1965) and November (Sandifer 1971). Lyons (1970) entertained the possibility that spawning occurs throughout the year. Planktonic phyllosomas were taken in Florida Straits from January through May, the final stages in April and May (Robertson 1971); from this the spawning season was judged to be fall-winter-spring. Seven larval stages were reared from eggs that hatched and developed in the laboratory. Later phyllosomas were obtained from plankton and some of these metamorphosed into postlarvae. The complete series of nine or ten phyllosoma stages plus postlarvae, described and illustrated, were estimated to have a minimal life span of about 2.5 months in water temperature of $25^{\circ}C$, and longer in lower temperatures. Sandifer (1971) also reared the first two phyllosomas of *S. depressus* in the laboratory from eggs of a female taken off Cape Lookout, N. C.

Lyons (1970) noted that postlarvae have been taken mostly in depths inhabited by adults, but one studied by him occurred at a station where bottom

depth was 2400 m, and another was from off Cape Charles, Va. Sims (1968) gave records of *Scyllarus* sp. larvae from 600 mi. east of Cape Cod, showing that phyllosomas can be transported great distances in oceanic currents.

Infraorder Anomura

Section Thalassinidea

Superfamily Thalassinioidea

Family Callianassidae

Carapace elongate, slender, separated by cervical groove into long anterior (gastric) and short posterior (cardiac) region. Rostrum little developed, nearly always unspined. Linea thalassinica present (Callianassinae) or absent (Callianideinae). Without pleurobranches. Ocular peduncles more or less dorsoventrally depressed, contiguous, cornea usually subdistal. Antennal scales reduced. First maxilliped with large foliaceous exopodite, non-flagellated, reduced endopodite and well-developed epipodite generally composed of anterior and posterior lobe; second with often foliaceous exopodite and epipodite reduced or absent; third frequently without exopodite, endopodite pediform, subpediform or operculiform and epipodite reduced or absent. First legs chelate, usually unequal; second legs chelate; third simple; fourth simple or subcheliform; fifth subchelate or chelate. Pleopods 1 and 2 present in both sexes (except some

males), 3–5 foliaceous, provided with appendix interna. (After de Saint Laurent 1973.)

Genus *Callianassa* Leach [1814]

Leach [1814]:400.—Hemming 1958b:142.—Biffar 1971a:648.—de Saint Laurent 1973:514.

The genus *Callianassa* has a fossil record extending back to the Upper Cretaceous (Glaessner 1969). Fossil chelae of *Callianassa* are occasionally found in fossil burrows called *Ophiomorpha* by paleontologists, and *Ophiomorpha* is known to range at least as far back as the Permian (Frey and Mayou 1971), although there is no suggestion that these two entities are always associated with each other.

Biffar (1971a) regarded Stimpson's (1866, 1871b) genus *Callichirus* "to be subgeneric at best," but de Saint Laurent (1973) divided the family Callianassidae into two subfamilies (Callianassinae and Callianideinae) and subdivided the Callianassinae into eight genera including *Callichirus* Stimpson. According to de Saint Laurent, the known species from the western Atlantic formerly placed in *Callianassa* belong in *Callichirus*. The differences between *Callianassa* and *Callichirus* depend upon mouthparts and seem somewhat overlapping. For the time being, therefore, I am retaining the well-known name *Callianassa* for these species, awaiting further research which may place de Saint Laurent's system on a firmer basis.

Key to Species of *Callianassa*

1. Uropods narrow, about 4 times longer than broad *C. major*
 Uropodal endopods not much longer than broad 2
2. Eyestalks with pointed tips slender, curved outward and upward; uropodal
 exopods composed of 2 fused parts, shorter, narrower anterior and
 underlying broader posterodistal parts both terminating in dense fringe
 of marginal setae *C. atlantica*
 Eyestalks with obliquely rounded tips lacking projection; uropodal exopods
 bilobed, underlying posterodistal parts having posterior lobe fringed with
 single row of plumose setae and larger anterior lobe with compound fringe
 of plumose setae *C. biformis*

Callianassa atlantica Rathbun

Fig. 125

Callianassa stimpsoni Smith 1873c:549, pl 2, fig. 8.—
 Hay and Shore 1918, pl. 29, fig. 5.

Callianassa atlantica Rathbun 1926:107.—de Man
 1928a:37.—Rathbun 1935:104.—Schmitt 1935b:
 4.—Williams 1965:102, fig. 79.—1974c:16, figs.
 43A-B (key).

Recognition characters.—Integument smooth, shining, thin, almost membranous. Carapace about $\frac{1}{3}$ length of abdomen, thin but with oval thickened plate on gastric region. Rostrum small, acute, flanked by small triangular prominence at each side on frontal margin. Eyestalks small, flat, contiguous mesially; pointed tips slender, curved outward and upward; cornea small, situated on outer border. Antennular peduncles about $\frac{1}{2}$ length of cara-

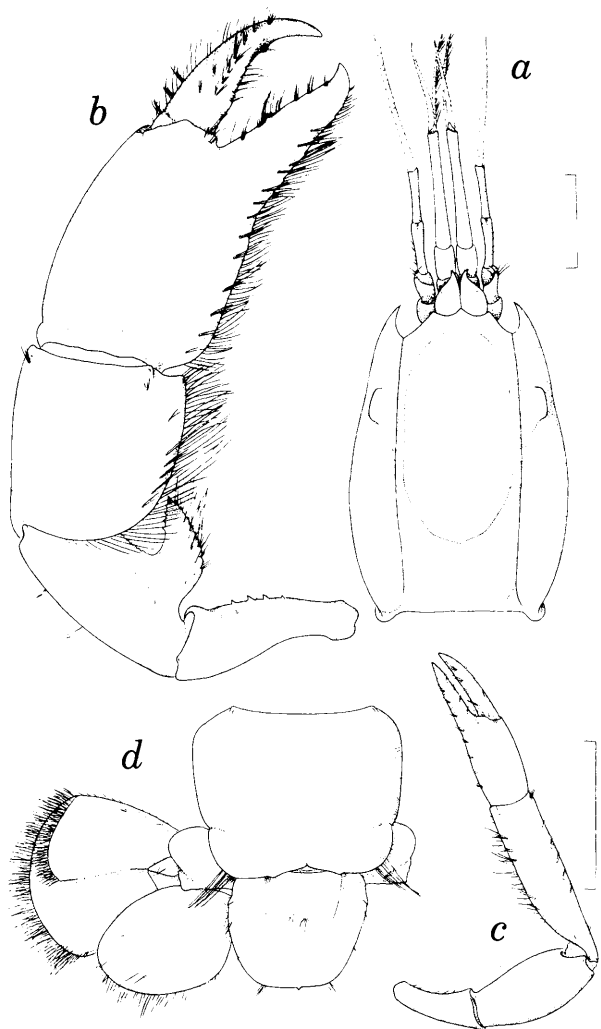


Fig. 125. *Callianassa atlantica* (Rathbun). Male: a, carapace, eyes, antennules, antennae in dorsal view; b, major (right) cheliped, c, minor (left) cheliped, external view; d, sixth abdominal segment with telson and left uropods; a, d, 5 mm; b-c, 1 cm indicated (USNM 14096).

pace; flagella about as long as distal article of peduncle, densely hairy below. Antenna slender, longer than carapace; peduncle much shorter than that of antennules, bent between second and third articles. Third maxilliped operculiform; dactyl slender.

Chelipeds unequal, showing sexual dimorphism. Larger cheliped of male with fingers about equal in length, hairy, tips incurved; cutting edge of dactyl with long, low, truncate tooth at base, smaller teeth distally; fixed finger with small teeth; palm hairy below, upper border ridged along proximal $\frac{2}{3}$; carpus as wide as but shorter than palm, upper and lower border ridged; merus articulating with carpus by extreme upper angle, prominent denticulate tooth on lower border

proximally; ischium with 6 or 7 subacute teeth on lower border. Smaller cheliped of male slender with fingers little longer than palm; carpus 4 times as long as broad distally, little longer than palm, half again as long as merus; merus twice as broad as long. Larger cheliped of female less toothed than in male; smaller cheliped as in male.

Abdomen with third to fifth segments about equally wide, each with small patch of fine hairs on posterolateral angle; sixth segments broader than long. Male with no pleopods on first and second segments. Female with uniramous pleopods on first segment; remainder well developed in both sexes. Telson nearly as long as broad; subtruncate distally, corners rounded. Exopods of uropods broader than endopods; exopod composed of 2 fused parts, anterior lobe shorter and narrower than its much larger underlying posterodistal lobe, both lobes fringed with dense marginal setae.

Measurements in mm.—Length of body: male 59; female 68.

Habitat.—Muddy shores and bottoms (Sumner, et al. 1913a, b); shoreline to approximately 38 m.

Type-locality.—“Our species ranges from the coast of the Southern [United] States north to Long Island Sound” (Smith 1873c).

Known range.—Bass River, Nova Scotia, to Georgia; Franklin County, Fla.

Remarks.—Both de Man (1928) and Schmitt (1935b) pointed out that Rathbun renamed this species because the name *stimpsoni* was preoccupied by a fossil species of *Callianassa*. To *Callianassa atlantica* itself is attributed a fossil record extending from first appearance in the Upper Miocene of North Carolina and Virginia, and a later occurrence in the Pleistocene of Maryland to the Recent (Rathbun 1935).

The species has been collected in areas ranging from salty estuaries to offshore fishing banks. Frankenberg and Leiper (1977) reported it as dominant from June through November in grab samples from fine sand off Georgia, apparently in association with *Pinnixa chaetoptera*.

Ovigerous females have been taken in Massachusetts and South Carolina in July. Sandifer (1973c) described two zoeal stages from plankton near the mouth of Chesapeake Bay that he attributed to this species. Sandifer (1973d) found these larvae in samples from July to September, and most abundantly near the bottom. Fish (1925) reported larvae (as *C. stimpsoni*) at Woods Hole from July to October, and Deevey (1960) found a *Callianassa* larva (considered *C. atlantica*) in Delaware Bay during January, March, and July to October. Sandifer considered all identical larvae from New England to be this species.

Callianassa biformis Biffar

Fig. 126

Callianassa biformis Biffar 1971b:225, fig 1.

Recognition characters.—Integument smooth, shining, thin, almost membranous. Carapace about $\frac{1}{4}$ length of abdomen, thin but with oval thickened plate covering anterior $\frac{3}{4}$. Rostrum small, acute; front broadly rounded at base of antennae. Eye-stalks flattened, shorter than first antennular article, irregularly rounded at tips; cornea small, central and subterminal. Antennular peduncle shorter than antennal peduncle, fringed with long, sparse setae laterally.

Chelipeds unequal, showing sexual dimorphism. Males with major cheliped showing 2 forms. Stronger form having palm smooth and round externally, little longer than carpus, margins entire. Opposed margin of propodal finger with broad, rounded tooth centrally, inconspicuously serrate distally, tip upturned and subacute; rounded notch at base of finger near articulation of dactyl. Dactyl hooked distally, cutting edge finely serrate and with broad, rounded proximal tooth. Carpus little longer than merus, similar to palm, margins entire except for few tubercles proximoventrally. Merus with strong proximoventral hook, margin of hook serrate and setose, acute distally, remainder of ventral

margin with irregular denticles, dorsal margin with rounded denticles on proximal half separated by tufts of fine elongate setae. Ischium with distinct, distally directed spur or hook on proximodorsal margin; distodorsal margin with tufts of fine, long setae separated by rounded denticles; ventral margin with 5 to 7 subacute spines along proximal half.

Weaker form with propodus proportionally narrower; fixed finger deeper proximally, cutting edge with series of rounded denticles and lacking median tooth; notch between fingers shallower; dactyl narrow, hooked distally, cutting edge with series of small rounded teeth but lacking large proximal tooth.

Small cheliped of male identical to both chelipeds of female. Palm subquadrate, width increasing distally, propodal finger deep proximally, acute at tip, series of acute denticles on cutting edge; dactyl curved, slightly longer than palm and equal to fixed finger, cutting edge entire or with few serrations. Carpus narrow, elongate, a bit longer than merus. Merus with midventral spine; ischium without spur, spines or dorsal elongate hairs. First walking legs chelate.

Abdomen long, gradually widening from anterior end to almost equally broad third to fifth segments, sixth narrower. Uropods broad; exopod composed of 2 fused parts, narrow anterior lobe nearly as long as its much larger underlying posterodistal lobe, latter lobe composed of 2 parts separated by marginal indentation, anterior part and fused anterior lobe both densely fringed with plumose setae, but posterior part fringed with single row of plumose setae. Telson slightly wider than long, truncate posteriorly, lateral margins convex, 2 small spinules at each posterolateral corner.

Measurements in mm.—Length of body: males 32; ovigerous females 27.

Habitat.—Primarily intertidal, occasionally subtidal, in fine mud or sand and in salinities ranging from 10 to 30 but usually around 25‰ (Biffar 1971b). Dörge (1977) found it both on protected mud flats in high salinity estuaries and from 10-m depths seaward on nearshore bottoms in Georgia.

Type-locality.—South end of Sapelo Island, mouth of Doboy Sound, McIntosh County, Ga.

Known range.—Bass River, Yarmouth and Nantucket Sound, Mass. (Williams and Wigley 1977); Chesapeake Bay (?); North Inlet, S. C. (Holland and Polgar 1976), to McIntosh County, Ga.; Franklin County, NW Fla. (USNM).

Remarks.—Biffar (1971b) pointed out that this species has been confused with juveniles of *C. atlantica*. He named the species for the two forms of large chelae found in the males. The cause for this condition is not known; “the full range of variation

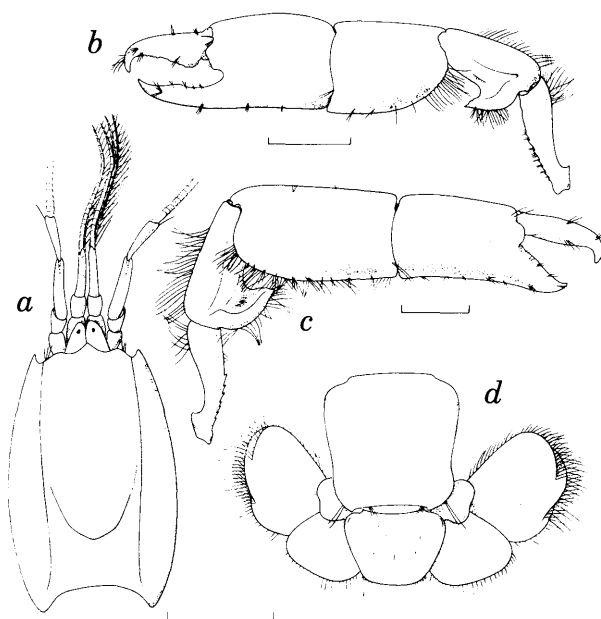


Fig. 126. *Callianassa biformis* Biffar. Male: a, carapace, eyes, antennae in dorsal view; b, major (strong form) cheliped, c, major (weak form) cheliped, external view; d, sixth abdominal segment with telson and uropods. a-b, d, USNM 135053 (paratype); c, USNM 135052 (holotype); a, c, d, 3 mm; b, 2 mm indicated.

in sizes of the chelipeds of both forms clearly shows that differences between juvenile and adult morphology are not sufficient to explain the situation." These and other polymorphic conditions are known in other species of *Callianassa* (Poore 1975).

Ovigerous females are known in June and July. Sandifer (1973c) described four zoeal stages of a *Callianassa* (species A) that he referred questionably to *C. biformis*. These zoeae were identical to stages Kurata (unpubl.) reared from *C. biformis* in Georgia. Sandifer (1973d) found the larvae in low concentrations in bottom samples from lower Chesapeake Bay over a temperature range of 18.8° to 27.6°C and salinities of 25.7 to 32‰ during July to September.

Callianassa major Say

Fig. 127

Callianassa major Say 1818:238.—Schmitt 1935b.—Williams 1965:100, fig. 78.—Rodrigues 1971:192, figs. 1–20.—Coelho and Ramos 1972:161.
Callichirus major.—Hay and Shore 1918:407, pl. 29, fig. 10.—de Man 1928a:30.

Recognition characters.—Integument more or less thin and membranous, chelipeds and oval plate covering anterior $\frac{3}{4}$ of carapace being most hardened parts. Rostrum minute, somewhat obtuse; similar projecting lobe at each side on margin of front. Cornea minute, situated at about middle of outer margin of flattened and pointed ocular peduncles. Antennular peduncles about $\frac{2}{3}$ as long as carapace, stout, densely hairy below; each with 2 flagella about as long as distal article of peduncle. Antenna slender, longer than carapace, peduncle bent between second and third article.

Chelipeds unequal, showing sexual dimorphism. Males with major cheliped rather large; granular along proximal lower edge of carpus, lower surface of merus and over most of ischium; propodus and carpus about equal in length, twice as broad as merus and more than 3 times as broad as ischium; merus with strong tooth on lower proximal border; fingers strong, dactyl hooking over outside fixed finger, strong tooth near base. Major cheliped of female weaker, not granular; propodus and carpus proportionately shorter than in male; merus without tooth on lower proximal border; dactyl hooking over inside fixed finger. Minor cheliped of male and female similar, small; fingers weak, meeting only at tips; carpus as long as hand and somewhat wider. Chelipeds and first 3 pairs of walking legs much compressed; margins of distal articles on first 2 pairs especially sharp; first walk-

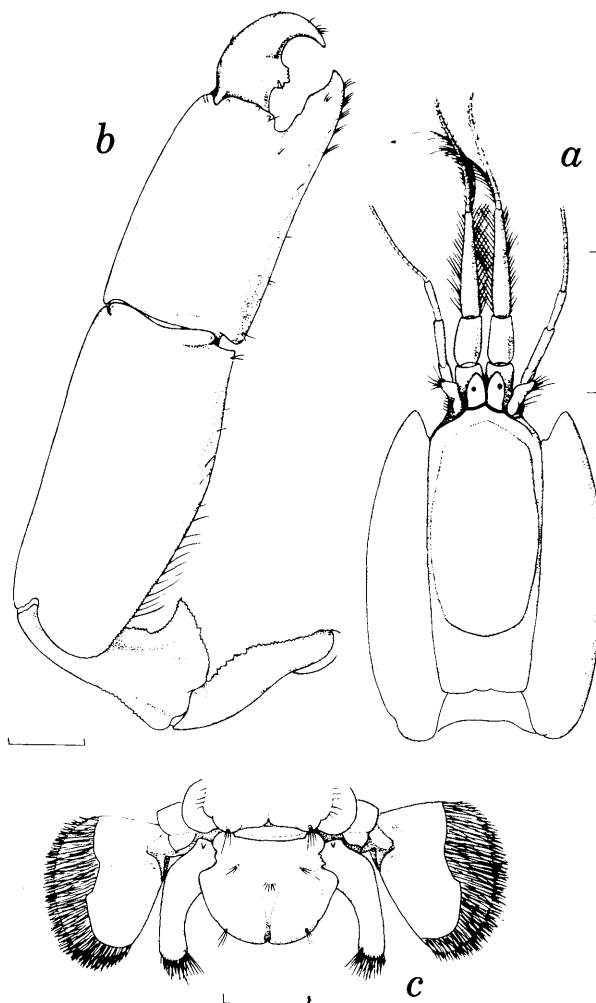


Fig. 127. *Callianassa major* (Say). Female: a, carapace, eyes, antennules, antennae in dorsal view; b, major (right) cheliped, external view; c, sixth abdominal segment with telson and uropods; a, 1 cm; b-c, 3 mm indicated (USNM 122451).

ing legs chelate, long hairs on lower margin; second legs with propodus transverse, it and small triangular dactyl densely hairy along margins; third and fourth walking legs with last 2 articles hairy, last legs subcylindrical.

Abdomen long, gradually widening from anterior end to third segment, then narrowing slightly to sixth; sixth segment deeply grooved above. First 2 pleopods small and slender in male, larger and definitely biramous in female; remaining pleopods broad and overlapping. Uropods with exopod broad, rounded distally; distal half covered with mat of dense short hair becoming longer on border; endopod narrow, obliquely truncate, hairy at tip only. Telson with inflated area on each side giving notched or fissured appearance.

Measurements in mm.—Length of body: males 95; females 92; ovigerous females 80 (Lunz 1937b).

Color.—Transparent gray except for porcelain

white chelipeds and hardened portion of carapace (Lunz 1937b). Yellowish digestive glands and red female or orange male gonads show through integument (Rodrigues 1971).

Habitat.—Burrows in sandy shores on or near open ocean; intertidal zone to 2 m.

Type-locality.—Bay shore of St. Johns River in east Florida, near low-water mark.

Known range.—Beaufort Inlet, N. C., to Cape Canaveral, Fla.; Grand Terre Island to Timbalier Island, La.; Espírito Santo and São Paulo, Brazil (Rodrigues 1965, 1971).

Remarks.—Biffar (1971a) gave a key to the western Atlantic species of *Callianassa* along with a summary of biological literature. Ovigerous females are known from Georgia in June, North Carolina in June and July, and Louisiana in June.

For many years *C. major* was known only from a single specimen from Beaufort, N. C., and early descriptions of specimens from South Carolina and Florida, but new investigations have supplied much detail. Burrowing habits of the form prevent easy detection by the casual observer using conventional methods of collection. Such habits no doubt also enhance chances for fossilization, for the genus is abundant in Cretaceous through Cenozoic deposits of the Gulf coastal plain, and somewhat less abundant in later deposits down to the Recent (Rathbun 1935; Weimer and Hoyt 1964).

Lunz (1937b) determined the habitat and abundance of the species in South Carolina and his studies were closely followed by those of Willis (1942) in Louisiana, Pearse, et al. (1942) and Pohl (1946) in North Carolina, and recently Rodrigues (1971) in Brazil. Weimer and Hoyt (1963, 1964) and Hoyt and Weimer (1964), from studies in Georgia, linked modern environments of the animal to Pleistocene and older deposits containing fossil tubes like those of *Callianassa*.

The animals live in deep burrows on sandy beaches that either face the open ocean or are close to it. In Louisiana, the burrows occupy a band from the intertidal zone to a distance of over 30 m from shore in 5 to 6 feet (2 m) of water, and in Georgia in similar parts of the foreshore to perhaps greater depths. Estuaries are tolerated to some degree in Brazil. Felder (1978) showed that the lower lethal limits of salinity are 7–8‰ and that blood osmotic regulation fails below 20‰. Blood magnesium is slightly hyperregulated at acclimation salinities less than 30‰. The tubular burrows, usually vertical to the surface, are divided into three parts. The mouth, about 5 mm in diameter, opens into the upper part, 5 to 20 cm long and 5 to 8 mm in diameter. From this the middle part, 10 to 15 cm long and often angled, widens gradually to approximately 20 mm.

The third part, 20 mm wide, is the longest. An approximate average depth of the whole burrow is 146 cm with variations usually from 60 to over 210 cm. Frey and Mayou (1971) reported living shrimp from burrows as deep as 4 m in Georgia. Branches are common and arise most often from the middle part. Characteristically, the burrows are lined with a brown material secreted by the animal (Weimer and Hoyt 1964), apparently collophanite (amorphous calcium phosphate) which is thinnest in the upper and thickest (3 to 7 mm) in the lower part. The burrows often end in an enlarged pocket lined with crushed shell, and in some the lined tube extends below the pocket. Say's (1818) general account agrees well with this description. (Some collections have been made by removing the mouth of the burrow, dropping pebbles or debris down the hole, waiting for the animal to appear at the exposed surface, then jabbing a shovel into the sand below the animal thus cutting off escape into the burrow.)

In captivity, the animals burrow in sand head-first with the anterior appendages until a shallow pit is constructed, then they reverse themselves and continue to burrow tail-first. Though the shrimp emerge voluntarily from their burrows at times, such behavior is probably infrequent and may be confined to the breeding season (Lunz 1937b). The species is well fitted for a fossorial life by virtue of the slender, elongate body, thin exoskeleton, and flattened hairy appendages adapted for burrowing, carrying sand, sifting food, and pumping water for feeding and respiratory currents. Examination of gut contents has shown an amorphous mass containing sand grains, diatoms and other algae, and many bacteria.

Burrow mouths are often surrounded by fecal pellets which resist rapid disintegration in water. On some South Carolina beaches, such pellets were washed together in patches measuring up to 3 × 15 m and piled to a depth of about 0.5 m; wave action sometimes concentrates the pellets along the beach to form thin layers of clay (Weimer and Hoyt 1964). Mouths of burrows are not uniformly scattered but tend to be clumped in patches or tracts, often as dense as three or four openings per square foot (.09m²). Chimneylike structures at the mouths of burrows noted by Say (1818) apparently are formed when shifting sand exposes the main portion of the burrow. A small, raised ridge of sand often surrounds burrow mouths, but many are not marked or may be located in a depression.

Frankenberg, et al. (1967) investigated the trophic significance of fecal pellets by measuring rates at which the material was produced, its content of organic carbon and nitrogen, and its ingestion by other

animals. Results indicated deposition of 456 ± 46 to $2,600 \pm 670$ pellets/m²/day, depending on population density, and that a *C. major* population occupying an area of about 200,000 m² produces about 280×10^6 pellets/day. Carbon and nitrogen contents of the pellets were 3% and 0.3% of dry wt. Aging the pellets had no effect on carbon content but halved the nitrogen in 48 hrs. Ingestion experiments indicated that pellets were eaten by hermit crabs, probably by blue crabs, and possibly by several other beach inhabitants. This fecal material may concentrate carbon in a readily exportable state.

Thompson and Pritchard (1969) considered species of *Callianassa* to have limited euryhalinity.

In Brazil, one or two specimens of *Pinnixa angeloi* are frequently found in the upper narrow part of

the burrows of *C. major*, and a bivalve (*Ceratobornia cema*) and reddish copepod (*Hemicyclops* sp.) inhabit deeper parts of the gallery (Rodrigues 1971). The same author reported ovigerous females nearly year round in São Paulo, Brazil, and also worked out the larval development of the species (1966), describing and figuring three zoeal stages.

Family Axiidae

Carapace with rostrum and cervical groove, lacking linea thalassinica. Antennular flagella well developed, both movable and fixed antennal thorns present though sometimes minute. First legs with large chelae, second legs with small chelae. (After Borradaile 1903; Glaessner 1969.)

Key to Genera and Species

1. Uropodal exopod lacking transverse suture *Axius serratus*
Uropodal exopod with transverse suture distally 2
2. Eyes normal with pigmented, rounded cornea; antennal thorn long
. *Axiopsis jeneri*
Eyes lacking pigment, stalks short and flattened obliquely on distal surface;
antennal thorn very short. *Calocaris templemani*

Genus *Axiopsis* Borradaile 1903

de Saint Laurent 1972:347, 354.

Both Borradaile (1903) and de Man (1925) separated *Axiopsis* from *Calocaris* on the basis of degree of arch in the dorsal surface of the carapace. That unsatisfactory distinction has been followed by most workers, but de Saint Laurent (1972) separated these taxa on a firmer basis in discussing the characters differentiating subgenera of *Calocaris*, which she raised to generic rank (*Calocaris* and *Calastacus*). Both of the latter lack pigmented eyes whereas *Axiopsis* (*Axiopsis*) has mobile, pigmented eyes.

Axiopsis jeneri (Williams), new combination

Figs. 128–129

Calocaris (*Calastacus*) *jeneri* Williams 1974d:451, figs. 1–10.

Recognition characters.—Carapace compressed, nearly smooth, almost straight along middorsal line in lateral view but gradually deflexed from gastric region to tip of rostrum; midline sharply rounded and elevated posteriorly but not keel-like; scattered setae in densest tufts on gastric region. Gas-

tric region with 4 interrupted and spiny dorsal carinae parallel to middorsal keel. Rostrum slightly exceeding eyes, tip upturned, 1–3 marginal spines on each side, low median dorsal keel extending to cephalic groove, notched at base (orbit) for reception of eyes in erect position. Eystalks cylindrical, cornea well developed. Antennular peduncle with second article equaling rostrum. Antennal peduncle with terminal article exceeding antennular peduncle, strong dorsolateral spine of second article reaching proximal border of cornea; antennal thorn (scale) slender, curved, exceeding cornea.

Chelipeds strong, asymmetrical and clothed with numerous tufts of conspicuous, silky, plumose setae obscuring fingers and portion of hands. Major chela stout; fixed finger nearly straight, crushing edge with strong tooth proximally or at midlength, and some smaller teeth; dactyl curved, with strong tooth more or less opposing teeth of fixed finger; crest of propodus with few spines and tubercles, inner face with patch of tubercles near base of fixed finger; merus with row of spines on proximoven-tral margin. Minor chela more slender, fingers agape proximally but distal half of opposed edges straight and finely serrate, prominent triangular tooth at middle of fixed finger diverging outward from cutting edge and opposite it an internal

shoulder on dactyl; external row of coalesced tubercles and/or spines parallel to proximal margin of fixed finger near articulation of dactyl.

Abdomen and telson nearly twice length of carapace; segments smooth and almost uniformly arched; pleura of short first drawn to acute posteroventral point, anteroventral margins of 2–5 broadly rounded, their posterior corners nearly rectangular, of sixth broadly rounded. Tail fan with thick, long, plumose setae on caudal margin. Telson longer than broad, evenly rounded caudally, lateral margin with proximal lobate process and marginal spines distal to it as well as submarginal spines, unequal pair near distolateral corners movable. Uropodal endopods with 2–4 lateral marginal spines; exopods with transverse distal suture bordered by row of strong, fixed spines and movable one at distolateral corner, lateral margin with 2–4 spines.

Measurements in mm.—Length of carapace including rostrum: male 12.4; female 10.5.

Variation.—Ornamentation (setae, tubercles,

spines) increases in size with increasing size of the animal. The rostrum is often asymmetrically toothed. Fingers of the chelipeds gape less in smaller specimens. The major chela may be on either right or left sides with no indication of regeneration when it is on the left.

Color in life.—“Ground color ‘flesh’ to off-white (pinkish white) with longitudinal trending, cross-banded maculations of orange red. Most dense orange-red color on posterior part of carapace where red is also deepest in intensity. Abdomen with first segment quite light, others progressively darker caudad; lightest areas at articulations dorsally, deepest colors at pleural junctures. Basal articles of antennules and antennae with bands of color equal in intensity to darker parts of abdomen. Color on legs more washed out. Pubescence light greenish tan.” (From Williams 1974d.)

Habitat.—Near edge of continental shelf; 85–232 m (Wenner and Read 1982).

Type-locality.—E Cape Lookout, N. C., 34°18'N, 76°01.2'W–34°17.1'N, 76°01.3'W.

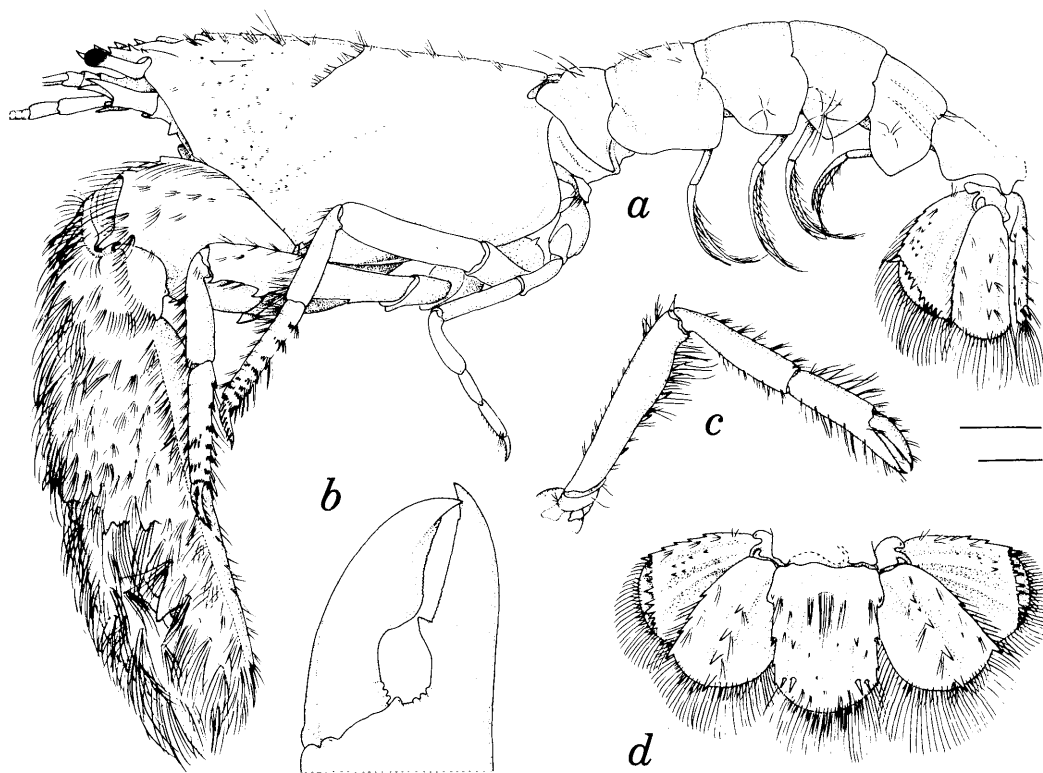


Fig. 128. *Axiopsis jenniferi* (Williams). Male: a, lateral view; b, fingers of chela with setae removed, inner view; c, second leg; d, telson and uropods; 2 mm indicated, upper a, c, d; lower b (from Williams 1974d).

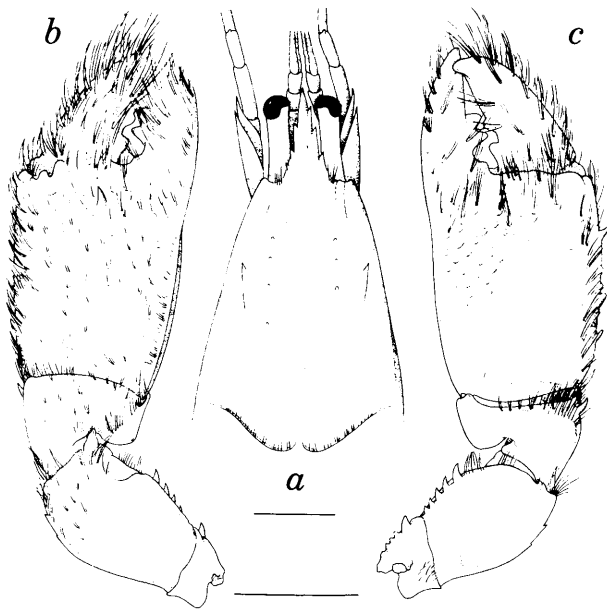


Fig. 129. *Axiopsis jenneri* (Williams). Male: *a*, anterior carapace, eyes, antennules, antennae in dorsal view; major (right) chela, *b*, external, *c*, internal view; *a*, 2 mm, *b*, *c*, 5 mm indicated (from Williams 1974d).

Known range.—Off Cape Lookout, N. C.

Remarks.—The species closely resembles *Axiopsis* (= *Calocaris* [*Calastacus*]) *hirsutumana* and *oxypleura* from the Gulf of Mexico and northern South America (Boesch and Smalley 1972; Williams 1974d).

Genus *Axius* Leach 1815

de Man 1925:8.

Fossil members of the genus range back to the Oligocene (Glaessner 1969).

Axius serratus Stimpson

Fig. 130

Axius serratus Stimpson 1852:222.—Smith 1879:55, pl. 10, figs. 4, 4a.—1881:435.—Rathbun 1929:25, fig. 32.—Williams 1974c:17, figs. 46A-B (key).

Recognition characters.—Carapace smooth, few scattered setae; compressed and drawn to rounded ridge posteriorly; cervical groove deep; lateral carinae on gastric region continuous with rostral margin and mesial to them a pair of shorter carinae. Rostrum elongate triangular, about 5–8 forward trending spines on each side and upturned spine at tip, prominent median carina. Eyestalks

with pigmented cornea nearly hidden beneath rostrum. Antennal peduncle with terminal article partly exceeding rostrum and reaching about to middle of penultimate article of antennal peduncle; antennal thorn (acicle) long, extending about to end of penultimate article.

Chelipeds asymmetrical, sparsely setose, dactyls hooking over ends of fixed fingers; upper and lower margins of palms crested, lower crest flattened ventrally and ornamented under both inner and outer crenate edges with row of long setae; lower crest continued and becoming obsolescent on carpus; upper edge of merus smooth, lower margin with 3 or 4 spines; tips of fingers calcareous on major, corneous on minor chela. Second legs flat-

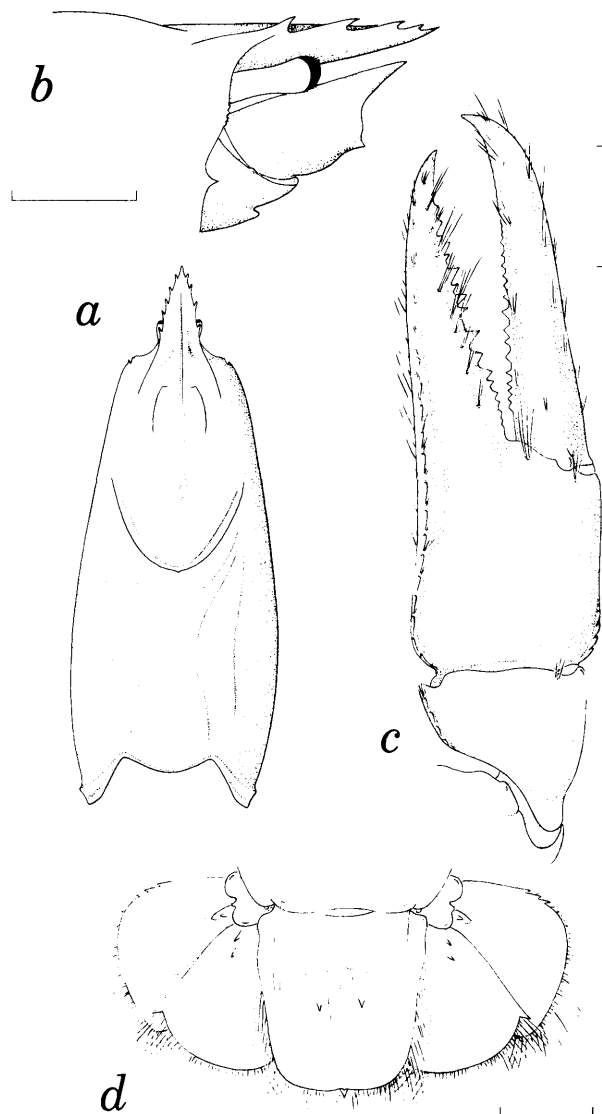


Fig. 130. *Axius serratus* Stimpson. Male: *a*, carapace, dorsal view; *b*, rostrum, eye, base of antenna, lateral view; *c*, chela and carpus, left, external view; *d*, telson and uropods; *a*, *c*, *d*, 5 mm; *b*, 3 mm indicated (USNM 20864).

tened, chelate, especially long silky setae on lower margin and moderately long ones on upper margin; last 3 legs with distal articles densely setose.

Abdomen broad, depressed and smooth; pleura of first segment drawn to fairly acute point, of segments 2–5 more or less rounded, sixth rounded but with 1 or 2 small marginal spines. Telson somewhat truncate, distal margin with median spine. Uropods with stiffening ribs; endopod with prominent proximal spine, smaller ones at distolateral corner and submarginally on central rib; exopod with about 3 small marginal spines distally.

Measurements in mm.—Carapace length including rostrum: male 30; ovigerous female 33. Total length: male 82; ovigerous female 83.

Variation.—The major chela may be on the right or left side; spines on pleura of the sixth abdominal segment may be absent.

Habitat.—Mud or sand (a burrower); 20–100 m.

Type-locality.—Off Scituate, Mass., 37 m.

Known range.—Strait of Canso, Nova Scotia, to Long Island Sound.

Remarks.—Almost nothing has been known of the biology of this species until recently. In 1954, a causeway constructed across the Strait of Canso between Nova Scotia and Cape Breton Island led to alteration of the environment in a harbor associated with industrialization and development (Pemberton, et al. 1976). Study of the area showed that *Axius serratus* constructed burrows more than 2.5 m deep with openings up to 3 cm in diameter in water depths of 7.5 to 11.5 m, most abundantly in polluted sediments barren of living Foraminifera, molluscs, and ostracods. Average density of the burrows, often interconnected, was 9/m². Shrimp retreated more than 2.5 m deep to avoid suction dredges, then reestablished burrows overnight in overburden freshly filling the excavated area.

An ovigerous female is known from the Sheepscot River, Me., in October (USNM 80514). Juveniles and larvae are known from Long Island Sound in August and September in depths of 23–30 m (R. N. Reid, personal communication). Smith (1879) gave the location of the dry type-specimen at the time he wrote, made from it the illustrations reproduced in part by Rathbun (1929), and reported the species from the stomach of a flounder (*Glyptocephalus cynoglossus*) taken 5 mi. SE Cape Ann, Mass.

Genus *Calocaris* Bell 1853

de Saint Laurent 1972b:354.

Calocaris templemani Squires

Fig. 131

Calocaris macandreae.—Rathbun 1929:25, fig. 33.
Calocaris templemani Squires 1965:2, figs. 1; 2A-B, CtC, CtD; 3Ct; 4; 5Ct; 6.—Williams 1974c:17, figs. 47A-B (key).

Recognition characters.—Carapace with middorsal carina extending full length and continuing well out on rostrum; cervical groove distinct; gastric region with carina on each side converging to merge with rostral margin and bearing 3–4 spines. Rostrum angled downward, 4–5 spines on each side pointing upward and forward. Eyestalks rudimentary, lacking pigment, with flat oblique surface facing anterolaterally but anterior edge almost rectilinear. Antennular peduncle with terminal article exceeding antennular peduncle; second article with very short lateral spine and antennal thorn (acicle) equally small.

Chelipeds essentially similar, sometimes slightly unequal in size; fringed with many long setae; dactyl with ridge on each side fringed with setae for its whole length, cutting edge with 2 large teeth separated by gap; propodus with 6 or 7 smaller

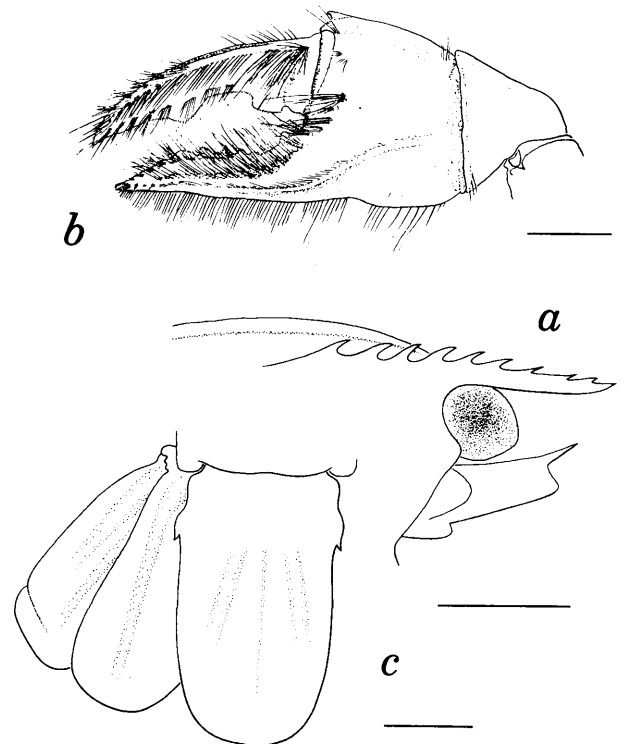


Fig. 131. *Calocaris templemani* Squires. *a*, Ocular region, lateral view; *b*, left first chela and carpus, external view; *c*, telson and left uropod. *a*, *c* (from Williams 1974c), 2 mm; *b* (from Squires 1965), 1 mm indicated.

teeth increasing in size proximally, prominent ridge on inner and outer surface of lower margin forming somewhat flattened edge, upper margin with prominent ridge ending in distal spine.

Abdomen with rounded pleura fringed with long simple setae and few setae near edge especially on segment 5, dorsal tuft of long simple setae at each side of midline on segments 2–5. Telson and uropods rounded terminally, few small carinal and lateral spines.

Measurements in mm.—Holotype: total length 44; carapace 14.

Color.—Pale pink.

Habitat.—Soft mud; 200–600 m [?], 650–700 m.

Type-locality.—Hermitage Bay, Newfoundland, 260 m.

Known range.—(Greenland?); the type-locality; Gulf of Maine; SE Cape Lookout, N. C., 34°14.8'N, 75°46.7'W–34°16.2'N, 75°44.9'W, 650–700 m.

Remarks.—This rare species was confused for years in published reports with *C. macandreae* Bell of the eastern Atlantic until Squires (1965) described it as new and clearly distinguished the two. Because few specimens have been taken, the depth range is largely unknown. The type is a mature hermaphrodite from 4.9°C water. Both sexual condition and habitat suggest a biology similar to that of *C. macandreae* in which eggs are carried 8–9 months, larvae have no significant pelagic phase, 1- to 3-year-olds have both testis and ovary, testes peak in the third year and degenerate in the fourth leaving the vas deferens filled with sperm, ovaries continue to develop and first eggs are laid at age 5 years, next eggs are laid at age 7 and possibly another clutch at age 9, animals molt annually after the fifth year and may attain an age of 10 (Buchanan 1963).

The species may occur in deeper water in the southern part of its range.

Family Laomediidae

Carapace longer than broad; rostrum well developed; linea thalassinica present. Fixed antennal thorn absent, scale reduced to flattened vestige or absent. First legs large, equal, chelate or subchelate. Abdominal pleura well developed, sutures usually present on rami of uropods. (After Borradaile 1903; de Man 1928b; Goy and Provenzano 1979.)

Genus *Naushonia* Kingsley 1897

Chace 1939b:524–530.

Naushonia crangonoides Kingsley

Fig. 132

Naushonia crangonoides Kingsley 1897:96, pl. 3, figs. 8–10.—Thompson 1903a:2, pls. 1–3.—Chace 1939b:529, figs. 1–14.—Williams 1974c:16, figs. 42A–B (key).—Goy and Provenzano 1979:352–357, figs. 1–5; 6A, E; 7A; 8A, G, H.

Recognition characters.—Carapace somewhat cylindrical, arched downward and depressed anteriorly, slightly granulate; cervical groove well marked in middle but not reaching well-impressed line (linea thalassinica) extending from anterolateral angle to posterior margin; pair of low anterolateral crests on each side of gastric region, lateral one more anterior than mesial and almost merging with rostral margin. Rostrum flattened, extending slightly beyond eyes, broadly rounded, margin tipped with small corneous spine and minutely spi-

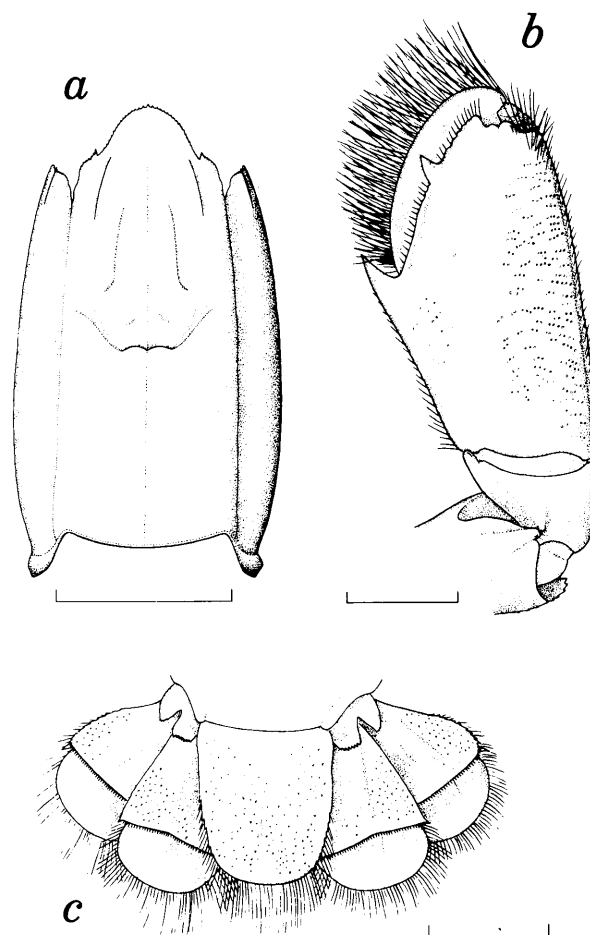


Fig. 132. *Naushonia crangonoides* (Kingsley). Female: a, carapace in dorsal view; b, chela, carpus and distal merus, inner surface; c, telson and uropods; a, 5 mm; b, 2 mm; c, 3 mm indicated (USNM 102278).

nulose elsewhere; anterior margin of carapace similarly spinulose. Eyes not visible from above, pigmented part of cornea tiny. Antennules with short flagella, inner ramus shorter than outer. Antennae with broad scale spinulose on outer margin, tip reaching to or beyond base of terminal antennular article.

Chelipeds flattened, subchelate, raised crest along external margin from propodus to ischium; dactyl regularly curved, tapered to sharp point and toothless, folding to reflexed position when closed, outer margin with fringe of dense, long setae; propodus covered with many low, transverse rugae, twice as long as broad, prehensile margin with large, acute terminal tooth, prominent central tooth and variable smaller ones largest distally; carpus triangular; merus about twice length of ischium, spinulose on distal margins. Second legs shortest, somewhat flattened, dactyls setose. Remaining legs slender, dactyls slightly curved, almost hairless, lacking spines on outer surface but comb of spinules on ventral surface.

Abdomen about $\frac{1}{3}$ longer than carapace, smooth; telson $\frac{1}{3}$ longer than broad, tip regularly and broadly rounded, posterolateral margins variably spinulose; uropods broadly rounded, transverse suture on both rami, proximal part of exopod with slightly spinulose lateral margin ending in strong movable spine.

Measurements in mm.—Length of body: male 26; female 36.

Variation.—The rostrum is variably spinulose, the tip not always spined, and the anterior part of the carapace is usually more granulate than other parts. Rugation of the chelipeds is variable.

Habitat.—Sand and mud near shore to 14 m.

Type-locality.—Naushon Island, Mass.

Known range.—Bass River, Vineyard Sound and Elizabeth Islands, Mass., to Bogue Sound, N. C.

Remarks.—Thompson's (1903a) complete account of this species at Woods Hole includes a well-illustrated, detailed description of adult and larval stages as well as biological notes and comparisons with other thalassinideans. She studied the type male and an ovigerous female dug from "a burrow with a peculiar funnel-shaped mouth" in sand at a depth of about 10 inches at Ram Island, Woods Hole Harbor, in July, 1899. From plankton she reconstructed a larval development consisting of five stages, the first appearing in mid-July but the last not until near the end of August. Fish (1925) found larvae at Woods Hole in July-September. Sandifer (1973d) reported larvae in plankton from Virginia coastal waters and lower Chesapeake Bay at least in July and August, and summarized the above published accounts of larvae as well as others in Narragansett Bay in August (Hillman 1964) and

Delaware Bay in August-October (Deevey 1960). Goy and Provenzano (1978) reared first stage zoeae taken in the mouth of Chesapeake Bay off Cape Henry, Va., in June and July to early juvenile stages in the laboratory in salinity of 25‰ at 25°C in a darkened incubator. Six or seven zoeal stages and a postlarva (described and illustrated) developed on a diet of *Artemia salina* nauplii, but early juveniles fed only on detritus and did not burrow. Thompson (1903a) also recorded notes on the first two postlarval stages (6 and 10 mm long). These colorless stages crawled on the bottom, hid but did not burrow in sand supplied them, and ate considerable diatomaceous matter but did not take animal matter during the period of observation. In all movements, the abdomen was extended and the chelipeds held stiffly in front, "thumbs" pointed inward and "elbows" not flexed. She pointed out that these stages closely resemble the adult.

The record from North Carolina is based on a postlarval specimen 10 mm long, lacking all legs except one of the fifth pair, that was taken in nocturnal surface plankton on flood tide at the UNC-IMS pier, 22 May 1966.

From larval stages reared in the laboratory, Goy and Provenzano (1979) followed subsequent development to the fifth juvenile stage, describing and illustrating their material as well as comparing it with existing museum collections in a general review of the genus, and revising Chace's key.

Langton and Brodeur (1978) reported and illustrated remains of three specimens of *N. crangonoides* taken along with *Callianassa atlantica* Rathbun and other organisms from the stomach of a roughtail stingray, *Dasyatis centroura* (Mitchell), caught in October off the mouth of Chesapeake Bay at a depth of 16 m. They felt that this confirmed Sandifer's (1973d) suggestion that a breeding population of *N. crangonoides* must exist near the mouth of Chesapeake Bay.

Specimens of *N. crangonoides* are by far the largest recorded for this rare genus. Adults of only four species are known, the one listed here, one from Puerto Rico and Yucatan (USNM), one from southern California, and one from French Somaliland, that were discussed and keyed out by both Chace (1939) and Goy and Provenzano (1979). Goy and Provenzano (1978) compared larvae of *N. crangonoides* to those of other Laomediidae that are recorded.

Family Upogebiidae

Carapace with rostrum well developed, spinous, cervical groove delimiting anterior and posterior region of about equal size; linea thalassinica present. Ocular peduncles cylindrical, cornea terminal.

Antennal scale reduced. First maxilliped with slender exopod provided with terminal flagellum, endopod short and epipod rudimentary or absent; second with slender exopod and very short epipod turned internally; third with exopod, endopod pediform, without dentate crest, epipod vestigial or absent. Neither pleurobranchs nor epipods on legs; first legs equal, chelate, subchelate or simple; second to fourth legs simple; fifth subchelate or chelate. First pleopod present in female only, second to fifth similar, foliaceous, without appendix interna. Exopod of uropods not lobed. (After de Saint Laurent 1973.)

Genus *Upogebia* Leach [1814]

Leach [1814]:400.—Hemming 1958b:143.

The genus *Upogebia* has a fossil record extending back to the Upper Jurassic (Glaessner 1969).

Upogebia affinis (Say)

Fig. 133

Gebia affinis Say 1818:241.

Upogebia affinis.—Hay and Shore 1918:408, pl. 29, fig. 9.—Schmitt 1935b:196.—Williams 1965:103, fig. 60.—1974c:16, figs. 44A-B (key).—Thistle 1973:23 (key).

Recognition characters.—Integument, except dorsal part of carapace and of legs, more or less membranous. Carapace about half as long as above, anteriorly rugose and covered with short, rigid hairs. Rostrum large, flanked on each side at base by large spine, spiny beneath in midline. Small upcurved spine behind eye on anterior margin, and minute lateral spine behind cervical groove. Eyestalks concealed, pubescent above; corneal surface small. Antenna little less than twice as long as carapace.

Chelipeds stout, fringe of long hairs below; hands with external, dentate ridge above, median row of acute spines and internal line of stiff hairs; fixed finger curved, dactyl longer, denticulate above at base, cutting edges of both fingers toothed near base; carpus grooved on outer face with row of small teeth on inner margin, and 6 acute spines along distal margin above; merus with small spine above and row of spines beneath. First pair of walking legs hairy at tips and along lower margin; merus with strong spine at base. Remaining legs hairy at tips.

Abdomen gradually increasing in width from first to fourth segment, fifth narrower posteriorly, sixth subquadrate; lateral portions of third and fourth segments densely pubescent and all with pleura

marked off by an impressed line. Tail-fan densely hairy distally. Uropodal endopods truncate, with median rib and costate outer border; exopods rounded distally and with 2 ridges. Telson broad, subquadrate, with impressed median line.

Measurements in mm.—In an analysis of sexual dimorphism, Thistle (1973) found no difference in overall length of mature males and females; mature shrimp ranged from 27 to 60. Slightly larger specimens are known.

Variation.—Schmitt (1935b) mentioned variability in spination of the lower border of the rostrum and multiple spination or lack of spines behind the cervical groove. Juveniles often lack these spines.

Color.—Gray, blue or yellowish gray dorsally, tinged with light blue medially on tail-fan and on fifth abdominal segment, interlaced with uniform light lines; and oblique blue spot on side of carapace at base of antenna extending posterodorsally; underparts light (various authors).

Habitat.—Burrows on estuarine mud flats and in shallow estuaries; intertidal to 29 m.

Type-locality.—Georgia.

Known range.—Wellfleet, Mass., to Rockport, Tex. (Hedgpeth 1950); through West Indies to Estado de São Paulo, Brazil (Coelho 1966b, 1970; Gomes Corrêa 1968).

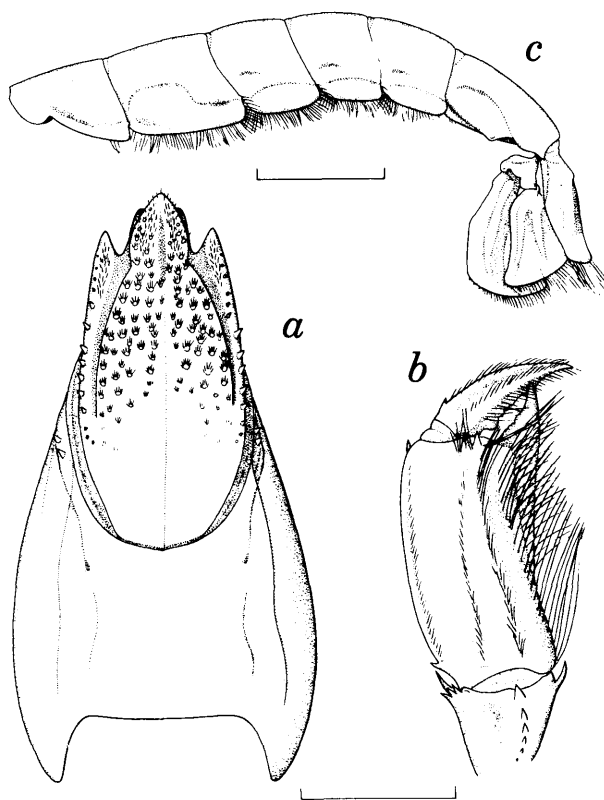


Fig. 133. *Upogebia affinis* (Say). Female: a, carapace in dorsal view; b, chela and carpus, right external view; c, abdomen, lateral view. a-b, USNM 66612; c, USNM 41747; 5 mm indicated.

Ecological observations on *U. affinis* in North Carolina were reported by Pearse (1945). The species inhabits muddy situations in estuaries where salinities are fairly high; experiments show that it is an osmo-conformer above 75% seawater, and a strong hyperosmotic regulator in lower salinities down to a lethal limit of 10% seawater (Thompson and Pritchard 1969). Its burrowing habits are similar to those of *Callianassa*. Wass (1955) found burrows prevalent in Florida where the marine grass *Halodule wrightii* stabilizes muddy substrates. Dörge (1977) found it associated with marsh creek banks and the marsh side of point bars close to the ocean in Georgia. Burrows examined by Pearse were 30 to 50 cm deep with openings about 30 cm above low-tide mark (McCloskey and Caldwell [1965] reported 60 cm depths). Burrows were often branched, containing several individuals, each in its own branch, and showed one to eight small openings at the surface. In communal burrows Pearse often found two or three ovigerous females and one or two juveniles. Like the burrows of *Callianassa*, those of *U. affinis* are narrowest in the upper part, and Pearse concluded that the animals seldom leave their confines.

In captivity, *U. affinis* made only feeble attempts to burrow. In nature, however, the animals are active and pump water vigorously from the anterior to posterior end of the body by flapping movements of the pleopods. Food is apparently strained from the water by the hairy mouthparts and walking legs, and probably consists largely of organic materials swept in the water current.

Rouse (1970) found ovigerous females nearly year round in southwestern Florida. Hay and Shore (1918) reported them throughout the summer in Bogue Sound, N. C., and they are known from Georgia in March. Sandifer (1973b) described four zoeal stages from plankton in lower Chesapeake Bay and York River, Va., in a salinity range of 13.02 to 32.34‰, and reviewed work of other students of the larvae, mentioning occasional occurrence of a fifth zoeal stage in culture. He found planktonic larvae to be common to fairly abundant from June to October, with peak numbers in July when temperatures ranged between 25° and 27°C. Hay and Shore (1918) found juveniles in plankton tows from early April to late October in North Carolina; and Fish (1925) reported larvae at Woods Hole from

mid-July to the latter part of October, but most abundant in early August. A single female may produce about 10,000 eggs at a time. They are borne on the first four pairs of pleopods. In captivity, more zoeae were hatched at night than in daytime. Pearse cited MacGinitie (1934) for evidence that *U. affinis*, like members of the genus *Callianassa*, may live several years, though there is no evidence supporting this idea for the former.

The commensal alpheid, *Leptalpheus forceps*, occurs in burrows of *U. affinis* (see Williams 1965). *Upogebia affinis* is one item in the diet of two species of hake in Georgia estuaries (Sikora, et al. 1972).

Upogebia affinis is commonly parasitized in North Carolina by the bopyrid, *Pseudione upogebiae*. Pearse (1952a) described a parasitic isopod, *Phylloporus robustus*, from a Florida specimen. McCloskey and Caldwell (1965) reported a parasitic fungus, *Enteromyces callianassae*, from the gut of *U. affinis* near Beaufort, N. C., suggesting a link between presence of the fungus and muddy environment, whereas *Callianassa major* in clean sandy habitats nearby contained none.

Section Paguridea

(Hermit crabs)

The hermit crabs have a nomenclatural history as contorted and diverse as their body forms. Modern workers such as Provenzano (1959), Forest and de Saint Laurent (1967), Mayo (1973), and McLaughlin (1974), on the basis of both adult and larval morphology, have followed MacDonald, et al. (1957) in organizing the family categories. This system is followed here, although it raises the categories one grade above that used by Glaessner (1969) and leaves the term Paguridea between infraorder and superfamily.

A bibliography of this group was published by Gordan (1956), compiling most references since Alcock (1905). The pagurids have a long fossil record in North America, species of *Paguristes*, *Petrochirus*, and *Pagurus* being known from the Cretaceous, and *Dardanus* from the Eocene (Rathbun 1935; Glaessner 1969), as well as these and other horizons in other parts of the world; *Clibanarius* may occur in the Eocene of Egypt (Glaessner 1969).

Superfamily Coenobitoidea

Family Diogenidae

Key to Genera and Some Species

1. Abdomen coiled for housing in gastropod shells; chelae and distal articles of walking legs not forming opercular face 2

- Abdomen secondarily straightened for housing in rock cavities or sponges; chelae and distal articles of walking legs forming opercular face *Cancellus ornatus*
2. Paired appendages present on first 2 abdominal segments of male and first abdominal segment of female; fingers opening and closing horizontally *Paguristes*
- No paired appendage on anterior abdominal segments in either sex. 3
3. Fingers of chelipeds opening and closing horizontally *Clibanarius vittatus*
- Fingers of chelipeds opening and closing obliquely or almost vertically 4
4. Chelipeds markedly unequal, left much larger than right. *Dardanus*
- Chelipeds not markedly unequal, right usually slightly larger than left *Petrochirus diogenes*

Genus *Cancellus* H. Milne Edwards 1836

Mayo 1973:6.

Cancellus ornatus Benedict

Fig. 134

Cancellus ornatus Benedict 1901b:772, figs. 1–2.—
Mayo 1973:18, figs. 5–8.

Recognition characters.—Anterior shield of carapace shorter than maximum width. Inflated anterior margin with rounded postorbital indentations between lateral projections and rostrum, occasionally 1 or more tiny spinules at lateral terminations; a crescentic depression behind this, its anterior border running parallel to rim, but becoming wider behind ocular peduncles and diamond shaped behind rostrum. Rostrum broadly triangular with slightly concave sides, barely exceeding blunt lateral projections. Central gastric region relatively smooth, but with light transverse sculpturing anterolaterally and behind frontal depression. Round to oval gastric pits near posterolateral margin of shield. Calcified portion of cardiac region broader than long, posterior margin straight but corners rounded. Eyestalks $\frac{2}{3}$ to $\frac{3}{4}$ length of shield, nearly parallel sided in dorsal view but broadening proximally, narrowest at point even with antennal acicle; triangular part of eyescales armed with distal spinule. Antennular peduncle reaching cornea when extended. Antennal flagellum longer than eyestalk; acicle reaching about $\frac{1}{3}$ length of eyestalk and armed with usually 3 anterior or anterolateral teeth and 1 on inner margin behind these.

Chelipeds and first pair of walking legs with carpi, propodi and dactyls forming irregularly tuberculate opercular face; propodi of each with longitudinal concavity, that of second legs bound on each side, and that of chelae mesially, by series of compound tuberculate lobes separated by narrow transverse fissures, and of chelae laterally by rounded reticulate face bearing transverse ridges

or irregularly spaced tubercles; carpi rimmed by raised margins of more or less coalesced tubercles; corneous tips on fingers broad and on dactyls of walking legs spinelike.

Abdomen ellipsoidal, covered with many short setae. Female with 4 biramous pleopods on either right or left side, large females with hardened strips at base of and mesial to pleopods. Sixth abdominal tergite broadly hexagonal, $\frac{1}{3}$ broader than long, anterior part larger than posterior, rounded transverse carina extended to blunt triangular lateral projection. Ridge on each side of anterior margin armed with 8–11 strong uneven spines, single spine (sometimes bifid) anterior to each lateral projection, and more or less toothed ridges on posterior and posterolateral borders.

Measurement in mm.—Anterior shield: males and females, length to 9.4.

Variation.—Spinination and tuberculation become less accentuated with increasing age (Mayo 1973).

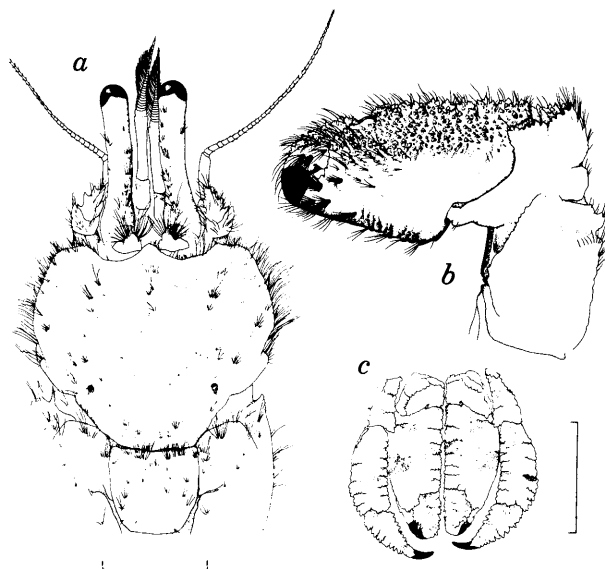


Fig. 134. *Cancellus ornatus* Benedict. Male: a, anterior part of body in dorsal view. Female: b, right cheliped; c, chelipeds and second legs in frontal view; 5 mm indicated (from Mayo 1973).

There are minor sexual differences in ornamentation of the opercular face, the longitudinal groove of the palm being more distinct in females and the tubercles more irregular. These and other minor differences have suggested the existence of a similar second species to some authors, but Mayo took a conservative view. Pleopods of females may be on either side of the abdomen.

Color.—In recently preserved specimens, dark violet on a cream-colored background with scattered red and orange markings, mainly in depressions. Large dark violet patches on carapace, particularly on anterior sculptured areas; a distinct red spot on each side of shield just anterior to gastric pit, and a broad pigmented spot on side of thorax below lateral margin of carapace; anterolateral corners of cardiac region also with a concentration of color.

Opercular surface with somewhat rectangular areas of pigmentation creating checkerboard effect with legs drawn together; undersurface of legs and coxal segments cream with scattered red markings, ambulatories generally cream with violet spots and banding, and some red spots.

Dorsal surface of ocular peduncles violet with small diffuse patches of red and white or cream-colored tubercles; undersurface white with orange patches and an indistinct longitudinal line along lateral surface. Maxillipeds with pigmented band around most segments. Antennules pale orange or cream with yellow flagella. Eye scales with patches of color on cream background; antennal acicles with red markings and a pigmented band around middle of fifth peduncular article.

Symmetrical red patches on sixth abdominal tergite and telson; uropods cream and slightly nacreous with light red patches.

One striking female had brownish violet on brownish red instead of violet. In preservation the violet seems to fade quickly, but other colors persist longer (paraphrased from Mayo 1973).

Habitat.—Members of this secondarily almost symmetrical hermit crab species are not associated with mollusk shells. Of the 10 specimens reported here or elsewhere, 8 are females, 2 are males. Each was a solitary specimen. Both males were associated with siliceous sponges at depths of 55–366 m; females associated with housing were in calcareous rock at 73–110 m.

Type-locality.—Northeast Gulf of Mexico between Mississippi Delta and Cedar Keys, Fla., 28°45'N, 85°02'W, 55 m.

Known range.—Off Cape Fear, N. C., 33°43'N, 76°40'W to 33°42.7'N, 76°40.2'W, 90–110 m (*Eastward* Stn. 1087, UNC-IMS 2397) (Herbst, et al. 1978) through eastern Gulf of Mexico, Greater and Lesser

Antilles, to near Los Abrolhos off central Brazil in a depth range of 37–366 m.

Remarks.—Mayo (1973) gave a full review of the genus *Cancellus*, pointing out probable close relationships among *C. ornatus* and *C. viridis* of the western Atlantic and *C. tanneri* of the eastern Pacific Ocean. The ovigerous female from North Carolina was collected in April in porous calcareous rock.

Genus *Clibanarius* Dana 1852

Dana 1852:122.—China 1966:254.

Clibanarius vittatus (Bosc)

(Striped hermit crab)

Fig. 135

Pagurus vittatus Bosc [1802]:78, pl. 12, fig. 1.

Clibanarius vittatus.—Hay and Shore 1918:410, pl. 30, fig. 9.—Provenzano 1959:371, fig. 5D.—Holthuis 1959:141, figs. 26, 27.—Williams 1965:120, fig. 97.—Forest and de Saint Laurent 1967:104.—Coelho and Ramos 1972:170.—Felder 1973:32, pl. 3, fig. 20.

Recognition characters.—Anterior shield of carapace subquadrate, distinct groove behind anterior margin, few tufts of hairs along lateral margin. Front with rostrum acute, triangular, slightly more prominent than lateral projections. Eyestalks almost as long as width of shield, nearly cylindrical, cornea not dilated, right eyestalk occasionally slightly shorter than left; eye scales narrow, approximate at tips but well separated at bases, margin with 1 to 4 spines, terminal largest. Antennal peduncles reaching to at least $\frac{3}{4}$ length of eyestalks; acicles acute, with 3 to 5 spines on inner margin, flagella reaching tips of walking legs.

Chelipeds equal, sparsely hairy; hands thick, inflated, twice as long as broad, covered thickly above, sparingly below, with variable, somewhat blunt spines, few darker than color of hands and with tufts of setae springing from bases; fingers opening horizontally, heavy, toothed and somewhat gaping at base, distal cutting edges corneous, extending along upper side; carpus as long as palm. Walking legs (legs 2 and 3) exceeding chelipeds by over half length of dactyls, tips corneous; 2 distal articles with numerous bundles of hairs.

Measurements in mm.—Anterior shield: male, length 17.4, width 14.4; female, length 14.9, width 12.5.

Color.—Greenish to dark brown with longi-
tudi-

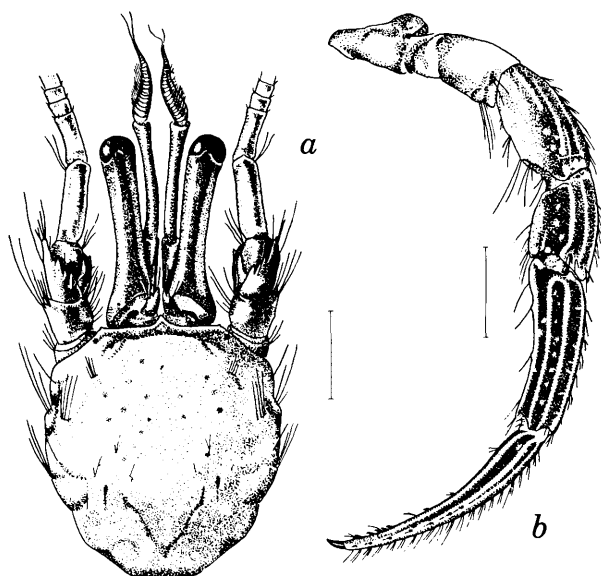


Fig. 135. *Clibanarius vittatus* (Bosc). *a*, Anterior part of body in dorsal view; *b*, third leg; *a*, 1 cm; *b*, 5 mm indicated (from Holthuis 1959).

nal stripes of gray to white; antennular peduncles light above, dark laterally, with orange flagella; tubercles on outer surface of chelae bluish white; propodus of walking legs with 4 pairs of light, longitudinal stripes continuous with similar stripes on dactyl and carpus, 1 of ventral stripes usually somewhat diffuse (Provenzano 1959; Holthuis 1959).

Habitat.—Common on harbor beaches, especially on borders of mud flats (Pearse, et al. 1942) in a variety of gastropod shells (Holthuis 1959); often on rock jetties or high on bay shores (Whitten, et al. 1950); near water line to 22 m.

Type-locality.—"Les côtes de la Caroline."

Known range.—Potomac River, Gunston, Va., to Florianopolis, Santa Catarina, Brazil (Forest and de Saint Laurent 1967).

Remarks.—This large species is one of the commonest conspicuous hermit crabs of the shore region of the Carolinian Province. Holthuis (1959) gave a history of its early recognition by explorers and naturalists, and Forest and de Saint Laurent (1967) discussed variation.

Ovigerous females have been reported from Surinam in July and August, North Carolina in June (Kircher 1967), South Carolina in July and August (Lang and Young 1977), Florida in October (Provenzano 1959), and spring in Texas (Fotheringham 1975). In one experiment at 25°C in salinities ranging from 15 to 40‰ (Kircher 1967) there were usually 5 zoeal stages (occasionally 4) and a glaucothoe. Survival to first crab stage occurred at salinities of 25, 35 and 40‰, was highest at 20‰,

but low in all cases. Total development time to first crab stage ranged from 57 days at 35‰ to 91 days at 25‰. Lang and Young (1977) studied larval development in South Carolina in filtered 25‰ sea water at 25°C under light conditions of 15 L/9 D hours, describing and illustrating larval stages as found by Kircher and passed through in about 76 days. Young and Hazlett (1978) showed by experiment in an array of salinities (15–30‰) and temperatures (15°–35°C) that no development occurred in any salinity at 15°C, but that partial development occurred in all other test conditions. Metamorphosis to juvenile crab was noted only at salinities of 25 to 30‰ in combination with temperatures of 25° to 30°C. Development time was decreased at higher temperatures, and it was suggested that the geographic distributional limits in the north are governed not by adult tolerances (survival at 5°C) but by inability of the species to establish a breeding population where time for larval development and metamorphosis is not sufficient. Larvae require two months to reach metamorphosis at 25°C, a condition not met north of Virginia.

In Texas populations the largest crabs, almost all of which are males, begin to leave the shore in early summer, but the smaller females remain until autumn (Fotheringham 1975). In spring, smaller crabs return to the shore area one month in advance of large crabs. The species aggregates in the shallow sublittoral zone in winter; individuals have been found buried in the substrate at 4°C when air temperature was subfreezing. Also in this zone a large hermit is more likely to find a large shell than in the littoral. Fotheringham (1976; 1976a) showed that *C. vittatus* maintained in shells smaller than preferred grow more slowly than those in shells of preferred size and that clutch size is highly correlated with crab size. Shell shortages may limit population size by denying room for growing young, stunting growth, or forcing females into shells that restrict brood size. *Clibanarius vittatus* females bore 1,481–30,520 eggs. Commensals, including polychaetes, gastropods, a hydroid, and xanthid crabs, consumed eggs or zoeae in the laboratory. Such egg predators were encountered in large shells occupied by males more frequently than in shells of the size range occupied by females, however. Fotheringham found a 1:1 overall sex ratio and implied, along with other evidence (1976b), that males monopolize large shells, thereby stunting females and holding down their egg production, thus influencing population structure. The species may migrate to the littoral in spring to breed.

Wright (1973) showed that *C. vittatus* is stung by the hydroids *Podocoryne carnea* and *Hydractinia*

echinata, and almost always avoids shells harboring them.

Behavior studies (Hazlett 1968a) show that aggressiveness in *C. vittatus* increases with size and that interacting crabs probably react to absolute size rather than relative size differences. If two animals are very different in size and their paths cross, they probably will not alter their behavior. If they do react, the larger will not execute a display (Hazlett 1972) nor will it react to execution of display by the smaller. If either retreats, it will almost certainly be the smaller. If the two are similar in size, they will probably interact and probability of the larger winning will not be much above chance. From experiments, it is clear that feeding behavior can be initially elicited by chemical stimuli which affect receptors in the antennules (Hazlett 1968b). Sight of a piece of fish does not act as a stimulus, though it can act as a stimulus for orientation once the response has been elicited chemically. Grasping ac-

tion is oriented primarily by visual stimulus; dark objects seem more effective than light colored. Hazlett (1966b) also briefly described courtship and mating.

Caine (1975), analyzing the relationship between feeding and masticatory structures, found stomach contents of *C. vittatus* to be composed of 40% scavenged material, 40% detritus, and the remainder presumably of muddy substratum.

Clibanarius vittatus is far more capable of resisting desiccation than are *Pagurus longicarpus* and *P. pollicaris*, an adaptation that enables it to survive intertidal exposure, especially during high daytime temperatures in summer (Young 1978a).

Genus *Dardanus* Paulson 1875

Paulson 1875:96 (translation).—Hemming 1958:163.—Provenzano 1959:372.

Key to Species

1. Propodus of second left walking leg conspicuously hairy, with lateral longitudinal ridge paralleled by groove; ridge crossed by rugae . . . *D. fucosus*
Propodus of second left walking leg not hairy, without lateral longitudinal ridge or groove; rugae arranged in herringbone pattern . . . *D. insignis*

Dardanus fucosus Biffar and Provenzano

Fig. 136

Pagurians insignis.—Benedict 1901b:141(part).

Dardanus venosus.—Verrill 1908a:441, text-figs. 58, 59; pl. 26, figs. 4a, 5a.—Schmitt 1935a:201, fig. 62 (part).—Provenzano 1959:374, fig. 6 (part).—Holthuis 1959:153.—Cerame-Vivas, Williams, and Gray 1963:157.—Williams 1965:123, fig. 99.

Petrochirus diogenes.—Provenzano 1963c:242, figs. 1–8.

Dardanus fucosus Biffar and Provenzano 1972:782, figs. 1A–4A, 5B, 6B.

Recognition characters.—Anterior shield of carapace slightly longer than width of front, nearly smooth but shallow cordate depression behind front, few tufts of hairs near sides and scattered elsewhere; anterior margin lacking rostrum, lateral projections between bases of eyestalks and antennae prominent, roughly triangular, blunt, surmounted by blunt spinule, and hairy on frontal edge. Eyestalks stout, slightly constricted in middle, extending to tips of antennal peduncles or slightly beyond, tuft of setae just behind dilated cornea; eye scales widely separated, inner margins straight, tips bearing several spines. Antennular peduncles

exceeding cornea by $\frac{1}{3}$ length of terminal peduncular article. Acicles short, reaching midlength of eyestalks, armed with small sharp spines.

Chelipeds unequal, left much larger than right; opposed edges of fingers with low white teeth, tips dark, corneous, spooned. Major chela with outer surface covered by scalelike tubercles separated by fan-shaped fringes of appressed hairs, inner surface smooth, mesial margin bearing row of about 7 sharp at least partially horny-tipped spines continued as row of decreasing appressed spines on dactyl and as well-developed spines on carpus; carpus with smaller sharp spines and few setae scattered over surface. Minor chela narrower, lacking scalelike tubercles on outer surface and with long setae rather than appressed bristles. Walking legs (legs 2 and 3) with dactyls longer than propodi, longest in first pair; second left walking leg markedly different from others, with dactyl and propodus broadened, fringed with hairs and with lateral longitudinal ridge paralleled by groove, ridge crossed by numerous rugae; dactyl with shallow groove on ventral margin bounded at each side by row of setae in tufts.

Measurements in mm.—Anterior shield: male, length 18.8, width 17.8; ovigerous female, length 11.7, width 11.