

were unlikely to reach a suitable habitat for settlement.

Another species of *Discias* from off South Carolina is presently being described (B. B. Boothe, Jr., personal communication), and still another, *D. ser-ratirostris*, is known from off Vero Beach, Fla. (Wilson and Gore 1979).

Both Gurney (1942) and Bruce (1975) described the last larval stage of *D. atlanticus*.

Superfamily Palaemonoidea

Family Palaemonidae

Caridea having first 2 pairs of legs chelate, second pair usually larger than first, carpus of second pair not subdivided. Rostrum usually armed with teeth and not movable. Mandibles usually with an incisor process (Holthuis 1951a).

Key to Subfamilies

1. Posterior margin of telson with 2 pairs of spines and 2 or more setae **Palaemoninae**
- Posterior margin of telson with 3 pairs of spines (except *Anchistioides* with 1 or 2 pairs). **Pontoniinae**

Subfamily Palaemoninae

Upper antennular flagellum with both rami fused in basal part. Appendix masculina generally present on second pleopod of male, appendix interna

on second pleopod of female. Pleurobranch present on third maxilliped segment (IX). Posterior margin of telson with 2 pairs of spines and 1 or more pairs of setae (Holthuis 1952).

Key to Genera and Some Species

(Adapted from Holthuis 1952; Chace 1972)

1. Hepatic spine present, branchiostegal spine absent; chelate second legs enlarged and greatly elongated. 2
- Hepatic spine absent, branchiostegal spine present; chelate second legs not greatly enlarged. 3
2. Dactyls of last 3 legs bifurcate; marine ***Brachycarpus biunguiculatus***
- Dactyls of last 3 legs simple; fresh or brackish water ***Macrobrachium***
3. Carapace without branchiostegal groove ventral to antennal spine; endopod of first pleopod of male with accessory appendix; mandible with palp. ***Leander tenuicornis***
- Carapace with branchiostegal groove; endopod of first pleopod of male entire, without accessory appendix; mandible without palp ***Palaemonetes***

Genus *Brachycarpus* Bate 1888

Holthuis 1952:2.—Hemming 1958b:154.

Brachycarpus biunguiculatus (Lucas)

Fig. 42

Palaemon biunguiculatus Lucas 1849:45, pl. 4, fig. 4.
Brachycarpus biunguiculatus.—Holthuis 1952:3, pl. 1, figs. a-q.—Williams 1965:51, fig. 42.—Chace 1972:18.—Pequegnat and Ray 1974:251, figs. 61–62.

Recognition characters.—Rostrum well developed, rather high, directed straight forward, reaching

about to end of antennal scale; upper margin with 7 (seldom 8) teeth, first 2 placed behind orbit with first tooth at about midlength of carapace; lower margin with 3 (seldom 2 or 4) teeth. Carapace smooth; antennal and hepatic spines present; strong postorbital ridge paralleling orbit. Eyes well developed. Basal article of antennular peduncle with anterolateral spine strong, reaching beyond second article of peduncle; stylocerite small, acute, closely appressed to article; rami of inner antennular flagellum fused for 8 to 23 joints; free part of shorter ramus about as long as fused part. Antennal scale about 3 times longer than broad, outer margin concave, terminal spine overreaching lamella.

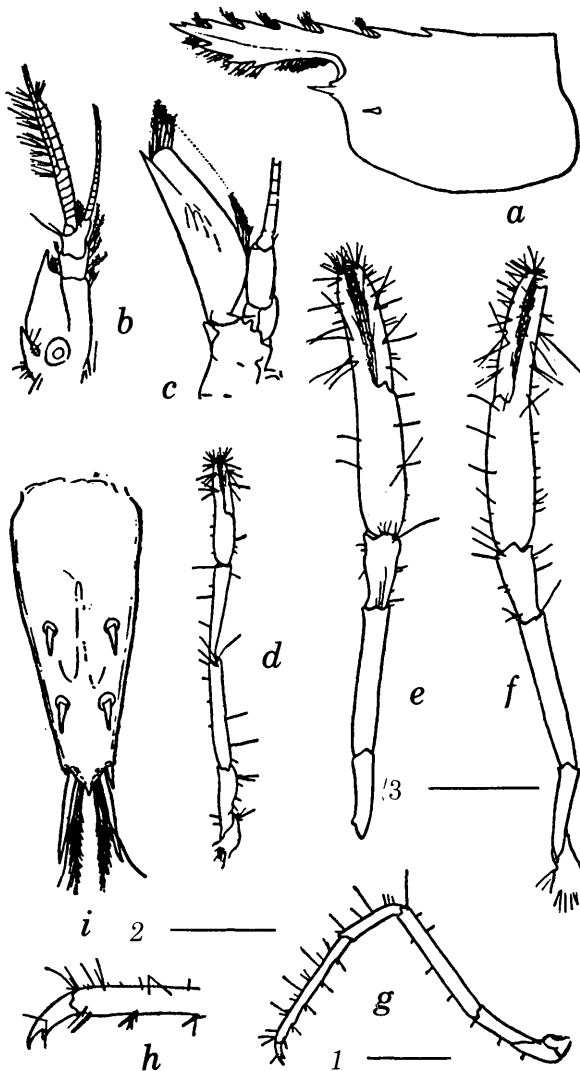


Fig. 42. *Brachycarpus biunguiculatus* (Lucas). a, Carapace in lateral view; b, antennule; c, antenna; d, first leg; e, left second leg; f, right second leg; g, third leg; h, dactyl of third leg; i, telson. Scales: 1(a, d-g)=2 mm; 2(b-c)=2 mm; 3(h-i)=1 mm (from Schmitt 1939).

First legs slender; fingers of chela longer than palm; carpus longer than chela. Second legs much stronger than first, smooth, part of carpus extending beyond antennal scale; fingers slightly shorter than palm, but in adult males sometimes only half length of palm, cutting edge of dactyl with 2 to 4, fixed finger with 2 small teeth in proximal part, adult males with fingers widely agape, opening hairy; carpus short, cup shaped, half length of merus. Last 3 legs slender, dactyls bifurcate, propodi with spines present on posterior margin.

Abdomen smooth, pleura of fourth and fifth segments pointed. Telson with 2 pairs of dorsal and 2 pairs of posterior spines; numerous setae between inner posterior spines. Appendix interna present on first pleopods in males, missing in females.

Measurements in mm.—Length of body: 65 (Holthuis 1952).

Variation.—Dorsal spines on the telson are sometimes not placed in symmetrical pairs and may be asymmetrically doubled.

Color.—Living individuals: body dark blue green mottled with white; palm of chela uniform blue green, fingers barred; fringes of antennules, antennae, antennal scale and tail fan orange; some individuals colorless, with tawny-tinged spots. Preserved specimens: pale brownish yellow, tips of fingers brownish red preceded by colorless band, then a fainter band of brownish red; antennular flagella red with white rings at articulations between joints (Holthuis 1952).

Habitat.—Found near shore among corals or rocks, on reefs (Corredor 1978), and on sea buoys; surface to 45.7 m (Pequegnat and Ray 1974).

Type-localities.—Oran and Bône, Algeria.

Known range.—Virtually pantropical (Bruce 1974); east and west American coasts, Mediterranean; West Africa; and Indo-Pacific region. Western Atlantic distribution: Cape Fear, N. C., western Gulf of Mexico (Ray 1974; Pequegnat and Ray 1974) through West Indies to Curaçao and Old Providence Island; Bermuda.

Remarks.—Gurney and Lebour (1941) described a complete series of 11 larval stages and a postlarval stage of this species from Bermuda. They pointed out that the larval life may be indefinite in length and number of developmental stages, and that this feature of development may account for the wide distribution of the species. Gurney (1943a) noted proportional changes in growth of the articles of the second legs in the last larval stage, first postlarval stage, and adult female.

The species is known to be a cleaning shrimp (Corredor 1978), having the long antennae, one pair of large chelipeds used as pruners, and smaller chelipeds used as sorters that are characteristic of these specialists. From observations on the reefs off Saint Vincent Island (West Indies), it was learned that the species is nocturnal, living as male-female pairs in smaller protected recesses than *Stenopus*, and ranging over areas about 2 m in diameter. The animals are timid, searching for sea urchins under which to hide when moving about. Although members of a pair live in the same recess, they have different though defined cleaning stations. Unlike diurnal cleaners which mount the host and concentrate on its mouth and gills, these cleaners concentrate on the surface of small fishes which present one side and then the other to the shrimp while it remains standing on the substrate, but large morays or fishes of lengths up to 100 cm are mounted for surface cleaning.

Ovigerous females were found from January to June at Saint Vincent and during the rest of the year at Santa Marta Bay, Colombia. Ray (1974) found ovigerous females in October, January, and March off Texas, and in April off Veracruz, Mexico, indicating year-round breeding.

Genus *Leander* Desmarest 1849

Holthuis 1952:167.—China 1966:213.—Carvacho 1977:100.

Leander tenuicornis (Say)

Fig. 43

Palaemon tenuicornis Say 1818:249.—Hay and Shore, 1918:392, pl. 27, fig. 6.

Leander tenuicornis.—Holthuis 1952:155, pl. 41, figs. a-g; pl. 42, figs. a-f.—Williams 1965:55, fig. 46.—Chace 1972: 19.—Pequegnat and Ray 1974:252, fig. 63.

Recognition characters.—Rostrum well developed; high in female, more slender in male, reaching about to end of antennal scale; upper margin with 8 to 14 regularly spaced teeth, first 2 behind orbit; lower margin with 5 to 7 teeth partially concealed by double row of setae. Carapace smooth; antennal spine present, branchiostegal spine

placed some distance behind anterior margin; branchiostegal groove absent. Eyes well developed, rounded; 2 dark-colored bands visible on cornea, especially in fresh material. Basal article of antennule with stylocerite large and pointed, reaching beyond middle of article, and with anterolateral spine reaching almost to end of second article of peduncle, anterior margin of basal article between spine and second article straight or only slightly convex; second and third antennular articles shorter and narrower than first; upper flagellum with fused part of rami shorter than free part of shorter ramus. Antennal scale 3 to 5 times longer than broad; outer margin about straight; terminal tooth strong, as long as lamella; antennal peduncle not reaching middle of scale; strong external spine near base of scale. Mandible with 2–3 jointed palp.

First pair of legs slender; reaching about to end of scale; fingers longer than palm. Second legs more robust than first, equal in size and shape; chelae reaching beyond scale; fingers longer than slightly swollen palm, cutting edges of fingers entire except for small basal tooth in males; carpus shorter than chela and about as long as merus. Last 3 legs slender, dactyls simple, slender; propodi armed with posterior spinules; fifth leg more slender than third.

Abdomen smooth; first 3 pleura broadly rounded; pleura of fourth and fifth segments narrower, ending in minute, acute tooth. Sixth segment lightly longer than fifth and about $\frac{2}{3}$ length of telson. Telson with 2 pairs of dorsal spines, first pair at midlength, second at $\frac{3}{4}$ length; inner 2 pairs of posterior spines overreaching acute tip of telson, pair of strong feathered setae between inner pair of spines.

Measurements in mm.—Length of body: 47; males generally smaller than females; ovigerous females 26 (Holthuis 1952).

Variation.—Length of the second legs is variable, and the palm of the chela is more swollen in some specimens than in others. Length of the terminal tooth of the antennal scale is variable.

Color.—Green or olive, with opaque spots (Schmitt in Holthuis 1952, for specimens from Tortugas); color plate (Sivertsen and Holthuis 1956). Brown in varying shades; mature females with ocelli on pleura of first and third abdominal segments (Manning 1961a).

Habitat.—Found in floating sargassum, on wharf pilings, and among submerged vegetation.

Type-locality.—Newfoundland Banks.

Known range.—Tropical and subtropical waters all over world except for west coast of Americas; Newfoundland Banks (occasionally mouth of Bay

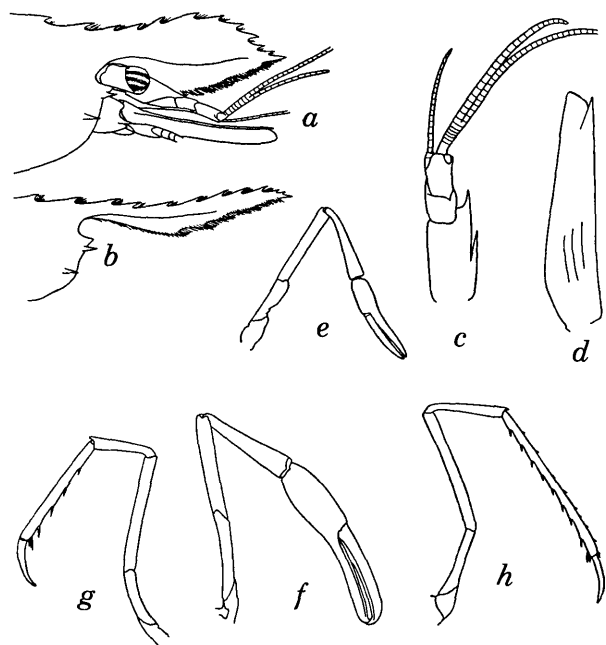


Fig. 43. *Leander tenuicornis* (Say). a, Female, anterior part of body in lateral view; b, male, anterior part of carapace in lateral view; c, antennule; d, antennal scale; e, first leg; f, second leg; g, third leg; h, fifth leg (from Holthuis 1952).

of Fundy and New England, Wigley 1970; Williams and Wigley 1977) to Falkland Islands in western Atlantic (Holthuis 1952; Bruce 1974).

Remarks.—Wigley (1970) considered the New England and Canadian occurrences to represent tropical vagrants that soon perish when temperatures drop in autumn. Ovigerous females have been observed from July to October in the Carolinas, in August in the Bay of Fundy, in June in the middle and western Atlantic (Sivertsen and Hol-

thuis 1956), and in August at Old Providence Island (Schmitt 1939). Gurney (1939) described the fifth(?) larval and first postlarval stages and compared them to related forms, with remarks on the statocyst in adults.

Genus *Macrobrachium* Bate 1888

Holthuis 1952:45.—Chace and Hobbs 1969:89.

Key to Species

(Adapted from Holthuis 1952)

1. Carpus of second legs with maximum length as great or greater than merus 2
 Carpus of second legs distinctly shorter than merus *M. carcinus*
2. Palms of chelae on second pair of legs cylindrical, not greatly swollen; fingers not noticeably gaping but may be hairy 3
 Palms of chelae on second pair of legs greatly swollen; prehensile surfaces of noticeably gaping fingers thickly set with long, stiff setae *M. olfersii*
3. Fingers of chelae on second pair of legs thickly pubescent throughout length; rostrum with teeth extending to tip *M. acanthurus*
 Fingers of chelae on second pair of legs with scattered hairs, except thicker on fingers along cutting edges; rostrum with toothless daggerlike tip *M. ohione*

Macrobrachium acanthurus (Wiegmann)

Figs. 44–45

Palaemon acanthurus Wiegmann 1836:150.

Macrobrachium acanthurus.—Holthuis 1952:45, pl. 9, figs. a-b.—Williams 1965:52, figs. 43–44.—Chace and Hobbs 1969:89, figs. 20, 25a, g.—Bonnely de Calventi 1974:44, fig. 13.

Recognition characters.—Rostrum almost straight, reaching slightly beyond antennal scale; upper margin slightly arched basally, with 9–11 teeth, proximals closer together than distals, first 2 teeth on carapace behind orbit, second tooth sometimes partly over posterior margin of orbit and separated from first tooth by distance greater than that between other proximal teeth; lower margin with 4 to 7 (generally 6) teeth, proximals closer together than distals. Carapace smooth, with short hairs especially on anterolateral region; antennal spine a little below orbit and slightly removed from margin; hepatic spine behind and a little below antennal spine. Antennal scale about 3 times longer than broad; outer margin straight or convex.

First legs with chela and sometimes part of carpus reaching beyond scale; fingers as long as palm; carpus $\frac{1}{3}$ longer than merus. Second legs equal,

with carpus and sometimes part of merus reaching beyond scale; fingers slender, thickly pubescent throughout length, slightly shorter than palm, cutting edges with tooth on each finger in proximal $\frac{1}{4}$ (that of dactyl more advanced) preceded by row of about 4 denticles; palm elongate, cylindrical, with several longitudinal rows of spinules, largest and farthest apart on inner and lower regions; carpus and merus spinulose like palm. Articles of last 3 walking legs with numerous densely placed small spinules.

Abdomen smooth; pleura of fifth segment ending in acute point. Telson 1.5 times length of sixth segment, with pairs of dorsal spines at middle and $\frac{3}{4}$ of length; posterior margin ending in sharp median point flanked by 2 pairs of spinules, inner pair overreaching median point.

Measurements in mm.—Length of body: male 179; ovigerous females 36 to 110.

Variation.—The rostrum may vary in length and shape. Adult females and young males have second legs shorter, more slender, and less spinulose and pubescent than adult males.

Color.—Green or pale yellow with red speckles; carapace with middorsal stripe of red or brownish orange and occasionally with irregular red bands laterally; chelipeds greenish becoming blue dis-

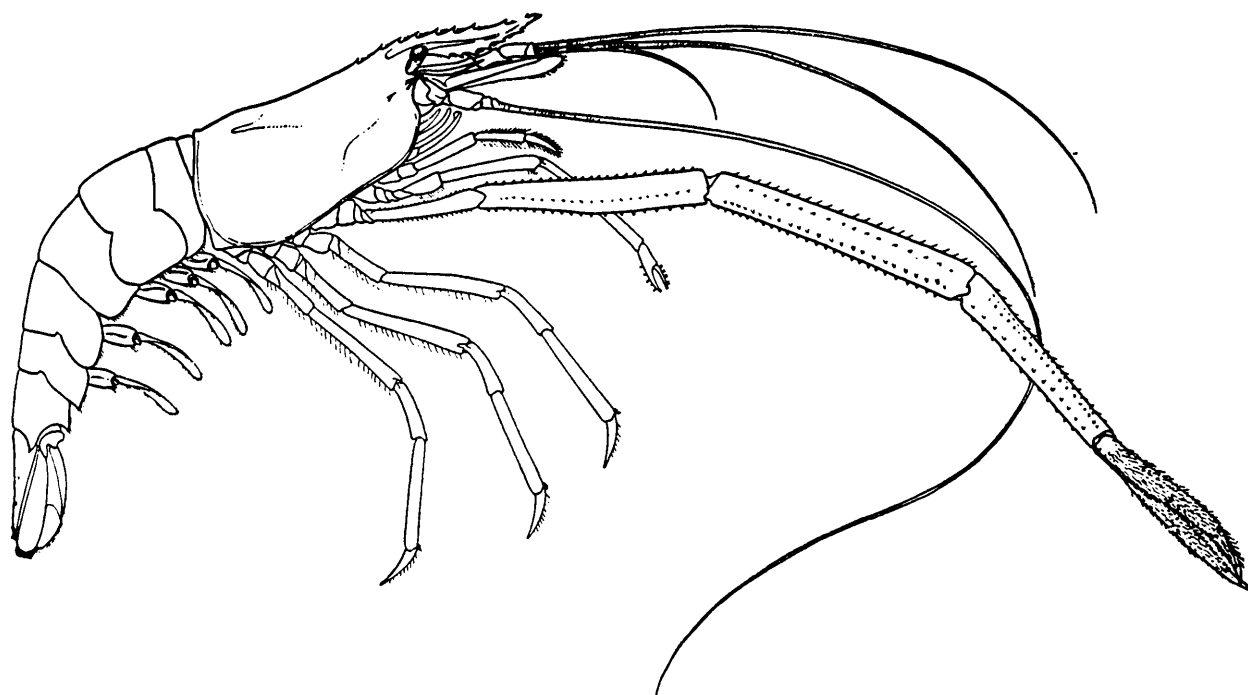


Fig. 44. *Macrobrachium acanthurus* (Wiegmann). Animal in lateral view (from Hedgpeth 1949).

tally, articulation orange; abdomen with middorsal stripe similar to carapace, pleura green with blue edges and striped with red; eggs green (Hedgpeth 1949; Schmitt *in* Holthuis 1952).

Habitat.—The species lives in coastal rivers and bays, usually near brackish water, but sometimes quite far upstream; 97 mi. (156 km) from mouth of Rio Grande River in Texas (Hedgpeth 1949).

Type-locality.—Brazilian coast.

Known range.—Neuse River estuary, N. C., to Rio Grande do Sul, Brazil.

Remarks.—North American records from the Carolinas are more numerous than in 1965. Two females, 44 and 48 mm total length, have been taken from intake screens of the Brunswick Nuclear Power Plant near Southport, N. C. (USNM), as well as other individuals from South Carolina localities.

Chace and Hobbs (1969) gave an excellent description and short ecological summary, pointing out that in Dominica the species frequents comparatively quiet waters near the mouths of streams that enter the Caribbean over a bed below sea level or lacking riffles. During the day the animals lie hidden among debris and roots of shoreline plants, but after dark they move by the thousands into open water on to the tops of debris accumulations. Carrillo (1968) discussed morphological variation in populations from Veracruz which fall within the normal range for the species.

In Colombia, females spawn throughout the year, bearing eggs 25%–45% of the time, although an

intense reproductive period lasts from August to October, with a massive spawning in September when most females at ages of 6 to 12 months have a body length of about 90 mm (Martinez 1975). Ovigerous females were reported to bear 150,000 to 250,000 eggs, although Paiva and da Costa (1962) found only ca. 4500 eggs on females 64 mm long; larvae hatch at a length of 2 mm; postlarval development lasts two months, development progressing best in 20‰ salinity. Martinez found that males in El Totumo swamp were larger than females, some reaching lengths of 179 mm (an unspecified individual reached 213 mm) and a weight of 89 g. Weight of individuals in his samples increased geometrically, 2.96 g for each mm increase in total length, the latter increasing at a mean of 1.87 mm; and for individuals between 12 and 130 mm long, increase in total weight was 2.33 g for each g weight of abdomen. Beyond 130 mm total length, total weight made a major increase to 3.86 g for each g increase in weight of abdomen. Martinez discussed other details on growth of adults and larvae.

Both Martinez and Choudhury (1971) observed mating in captivity, the latter remarking that it is always preceded by a pre-mating molt of the female and prolonged courtship display in which the strongest males dominate other males. Egg-laying occurs 4–12 h after mating, the female bringing the abdomen near the genital opening on the coxae of the third legs to extrude eggs at the bases of pleopods 1–4, to which they become attached. Un-

mated females will also deposit unfertilized eggs, but they drop off the pleopods within 5 days. Incubation lasts 16–18 days.

Choudhury (1970) described and selectively illustrated 10 larval stages, first and second juveniles, and a 1-month-old juvenile hatched from ovigerous females collected in the Cabarita River, Jamaica, and transported to Kingston in aerated containers. The larvae, reared in 60‰ seawater in mass culture on a diet of brine shrimp nauplii, developed to Stage VIII in 22–29 days, and to Stage X in 32–42 days. In other experiments Choudhury (1971) transferred newly hatched larvae by slow acclimation to an array of salinities (fresh, 5, 10, 15, 20, 25, and 34‰) and reared them at ambient temperatures on a variety of diets. Though adults live and breed in freshwater, salinity of 15–20‰ was best for larval development; those in waters outside this range died during development. Starved larvae, living on stored yolk, died in two days; those fed detritus died in 14 days at Stage III; those fed boiled rice and a combination of vegetables died in 13 days at Stage III; of those fed fish, shrimp and crustacean muscle, five Stage IV larvae were alive on day 16 at termination of the experiment; larvae fed brine shrimp nauplii lived 18 days through Stage V when the experiment was terminated. Dobkin (1971), from ovigerous females trapped in canals near Boca Raton, Fla., and maintained in 1:1 seawater and canal water, hatched larvae and reared them in plastic boxes at 12, 23.5, and 35‰ salinity at 26° and 30°C on a diet of *Artemia* nauplii. He found molting frequent, survival best in the higher two salinities, mortality before metamorphosis in the lower salinity, and illustrated zoeal stages 1–4.

Current chamber experiments have indicated that gravid females of *M. acanthurus* tend to swim consistently downstream whereas nongravid females tend to swim consistently upstream (Hughes and Richard 1973). This behavior suggests a mecha-

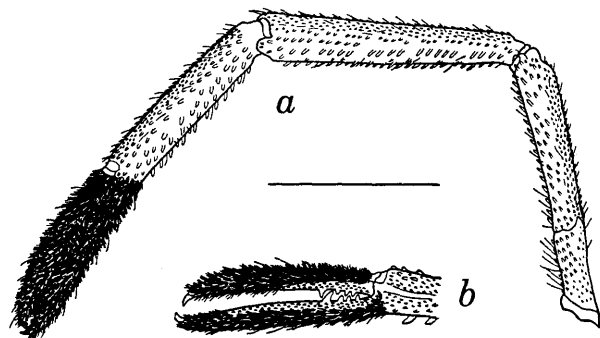


Fig. 45. *Macrobrachium acanthurus* (Wiegmann). Adult male: a, second leg; b, fingers of second leg (part of hairs removed); 3 cm indicated (from Holthuis 1952).

nism for insuring that larvae will hatch where they can survive. A similar experiment showed that larvae held in brackish water will drop to a position low in the water column when salinity is reduced (simulating ebb tide) and revert to swimming higher in the water column when salinity is increased (simulating flood tide). These responses are interpreted as a mechanism helping to prevent larvae from being carried out to sea, thus facilitating their eventual migration upstream to a freshwater environment where adults spend most of their lives.

Macrobrachium carcinus (Linnaeus)

Cancer Carcinus Linnaeus 1758:631.

Macrobrachium carcinus.—Holthuis 1952:114, pl. 30; pl. 31, figs. a-c.—Chace and Hobbs 1969:93, fig. 21.—Chace 1972:20.

Remarks.—Distribution of this species lies largely beyond the temperate east coast of the United States. The range extends from St. Augustine, St. Johns County, and Silver Glen Springs, Marion County, Fla., southward around the Gulf of Mexico and Caribbean Sea to Santa Catarina, Brazil. Hedgpeth (1949) gave a good short account of its occurrence in Texas rivers and bays, and Chace and Hobbs (1969) provided additional and more detailed observations from Dominica.

Macrobrachium ohione (Smith)

Fig. 46

Palaemon Ohionis Smith 1874:640.

Macrobrachium ohione.—Holthuis 1952:62, pl. 14, fig. b.—Williams 1965:54, fig. 45.

Recognition characters.—Rostrum high and straight, tip curving somewhat upward and reaching to between end of antennular peduncle and end of antennal scale; upper margin with 9 to 13 teeth, 3 or 4 teeth behind orbit, first 3 more widely separated than remainder; lower margin with 1 to 3 teeth; distal 2/5 of rostrum unarmed. Carapace smooth; antennal spine slightly remote from anterior margin; hepatic spine below antennal spine. Antennal scale about 2.5 times longer than broad; outer margin straight or slightly concave.

First legs with chelae reaching beyond scale; chelae slender; fingers about as long as palm; carpus twice length of chela. Second legs in adult female stronger than in male, with carpus and chela reaching beyond scale; fingers somewhat shorter than palm, cutting edges pubescent and with 4 to 8 small denticles of equal size on proximal half, remainder of surface with scattered hairs; palm

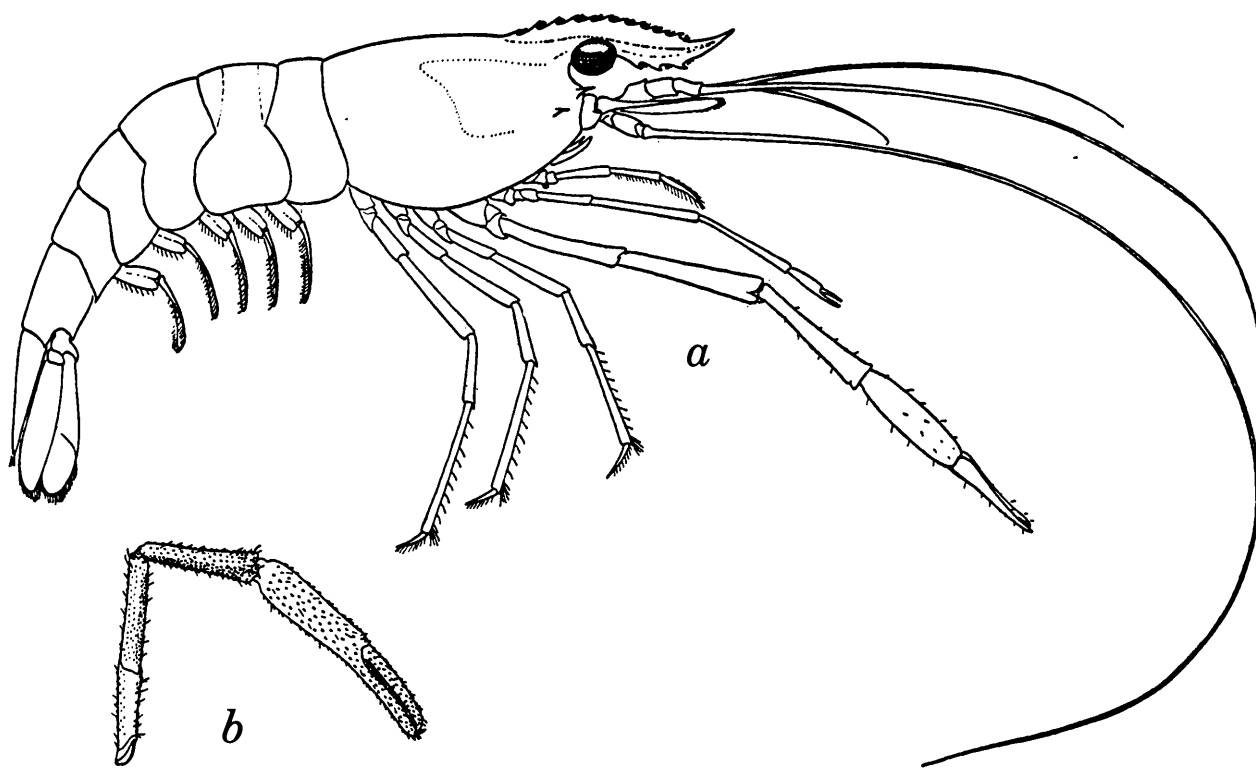


Fig. 46. *Macrobrachium ohione* (Smith). a, Animal in lateral view (from Hedgpeth 1949); b, second leg of adult male (from Holthuis 1952).

elongate, cylindrical, entirely pubescent, most conspicuous pubescence along lower surface; carpus, merus, and palm of equal length, these articles and fingers with longitudinal rows of small spinules, carpus most pubescent anteroventrally; merus somewhat pubescent anteroventrally.

Abdomen smooth; pleura of fifth segment ending in acute point. Telson about 1.5 times length of sixth segment; pairs of dorsal spines at middle and $\frac{3}{4}$ length; posterior margin ending in an acute tip overreached by inner pair of posterior spines.

Measurements in mm.—Length of body: male 68; female 102.

Variation.—Juveniles (10 mm and larger) have the same number of rostral spines as adults but fewer spines behind the orbit. In such juveniles, the hepatic spine is very close to the anterior margin of the carapace, similar in position to a branchiostegal spine.

Color.—Pale gray flecked with small blue spots; uropods pale blue (Hedgpeth 1949).

Habitat.—Rivers and estuaries.

Type-locality.—Ohio River at Cannelton, Ind.

Known range.—A narrow zone along Atlantic seaboard from James River, Hopewell, Va. (Hobbs and Massmann 1952), to southern Georgia; widespread from coastal Alabama to Aransas Bay, Tex.; Mississippi River and tributaries upstream to

McCurtain County, Okla.; Fort Smith, Ark.; St. Louis, Mo.; Washington County, Ohio (Hedgpeth 1949).

Remarks.—This species is distributed chiefly in brackish and fresh water, ranging far inland in the Mississippi River drainage. It is abundant enough to provide a fishery, especially in Louisiana, though the exact magnitude is not known. Gunter (1937) described the Louisiana fishery and gave information on ecology of the species. Commercially, the shrimp are taken in traps made of wooden slats, similar to lobster traps, baited with meat scraps or cotton seed cake. The shrimp are sometimes captured by lifting submerged willow branches from the water and catching the animals as they drop off. Such catches are best made at night. Commercial shrimping is done in the warmer months, as the animals are scarce in winter. The shrimp will attack fish kept in live boxes in the river, and, though feeding habits of the species are not known completely, stomachs of animals examined have contained 50% finely ground detritus and bits of organic matter, 20% sand, and 30% clams (*Rangia*), miscellaneous plant, invertebrate, and vertebrate remains (Darnell 1958).

During a period of study from November to early July, Gunter found that ovigerous females first appeared in mid-April, and were still present when

the work was terminated in July. Ovigerous females have been found in April and May in North Carolina. McCormick (1934) stated that eggs in various stages of development were found in females at the same time that they were in berry, which indicates a long egg-laying season. Gunter (1937) found females to outnumber males by more than 3 to 1. However, this ratio varied. When females were carrying eggs, males made up only 9% of the captured individuals, but prior to the egg-laying season males made up 31.8% of the total. He concluded that this indicated a change in sex ratio at the egg-bearing period.

Thirteen percent of the females caught were ovigerous, and these ranged in length from 38 to 76 mm. Eggless females ranged from 23 to 93 mm in length. From November to December, the population was made up of individuals 60–80 mm long. In January, shrimp below 30 mm average length predominated, but from then until April the average length increased to about 50 mm, and thereafter the range of variation widened as smaller animals came into the catch.

Gunter found ovigerous females in bay water with salinities ranging from 1.38 to 14.24‰. He noted that when the river was on the rise, with turbidity high, few shrimp were taken in water over 6 m deep, and these were sometimes dead. He conjectured that because these shrimp were not buried in mud, high turbidity in deep water during flood may have an adverse effect on respiration. Hedgpeth (1949) suggested that silt causing interference with respiration may drive the shrimp from rivers to estuaries during such seasons, but he also suggested that in regions such as the Atlantic seaboard, where the species is apparently a comparatively recent immigrant, it may still depend on bay waters to complete its breeding cycle. In any case, it is thought

that these shrimp and other species of the genus move from river to river through the estuaries at the river mouths (Gunter 1937).

This species and *M. acanthurus* are forms which may be advanced in the process of moving from the sea to fresh water. Few such examples exist.

Bridgeman (1969) found *M. ohione* to be the second intermediate host for the trematode, *Carneophallus choanophallus*, whose natural definitive hosts are the raccoon and black rat, and first intermediate host is the snail, *Lyrodes parvula*.

Macrobrachium olfersii (Wiegmann)

Figs. 47–48

Palaemon Olfersii Wiegmann 1836:150.

Macrobrachium olfersii.—Holthuis 1952:95, pl. 24; pl. 25, figs. a, b.

Recognition characters.—Rostrum straight or bent slightly downward, reaching about to end of antennular peduncle; upper margin bearing 12–15 evenly spaced teeth, 4 or 5 on carapace behind orbit; distance between first tooth and orbit somewhat less than $\frac{1}{3}$ total length of carapace excluding rostrum; lower margin with 3 (rarely 4) teeth. Carapace smooth; hepatic spine smaller than antennal spine. Antennal scale less than 3 times as long as broad; outer margin nearly straight.

First legs with $\frac{1}{3}$ or less of carpus reaching beyond antennal scale; fingers about as long as palm; carpus twice length of chela; merus $\frac{1}{3}$ length of carpus. Second legs very unequal. Larger leg reaching with all of carpus and small part of merus beyond antennal scale; palm and fingers bearing longitudinal row of spines or spinules, as do carpus and merus, longitudinal row of strong spines

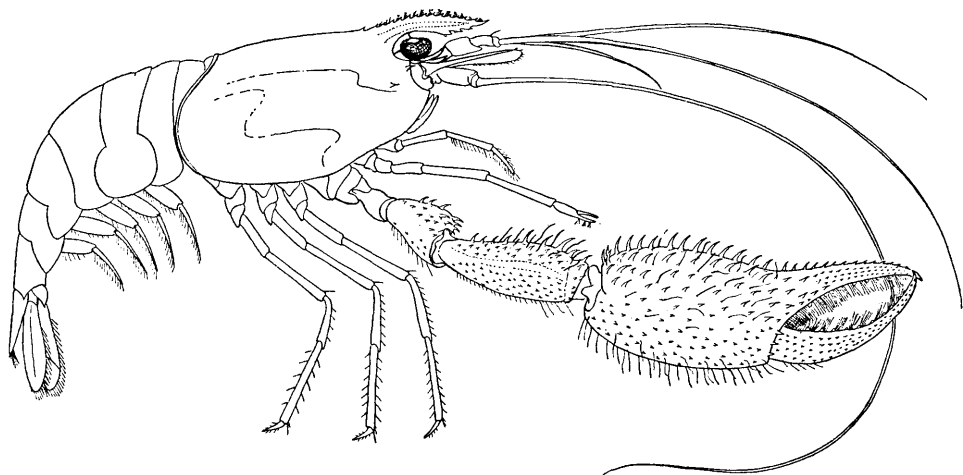


Fig. 47. *Macrobrachium olfersii* (Wiegmann). Animal in lateral view (from Hedgpeth 1949).

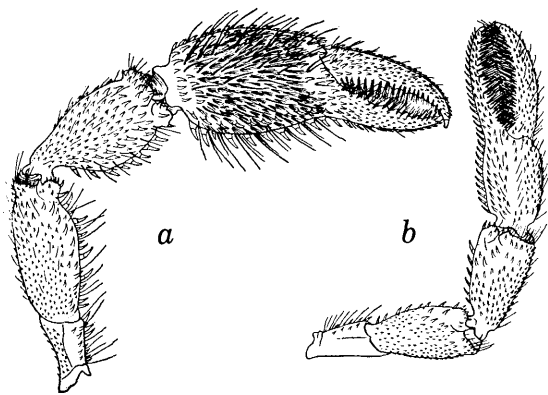


Fig. 48. *Macrobrachium olfersii* (Wiegmann). *a*, Larger, *b*, smaller second leg of adult male (from Holthuis 1952).

along lower margin; fingers (especially dactyl) curved and gaping, cutting edges with rather large proximal tooth succeeded by 2–4 smaller ones followed in turn by a number of denticles, stiff inwardly directed long hairs along cutting edges; palm slightly compressed, both upper and lower margin convex, about as long as fingers, dense pubescence on inner, outer, and lower surfaces plus scattered stiff hairs; carpus shorter than palm, about as long as merus, swollen distally but constricted near base. Smaller second leg with part of carpus reaching beyond antennal scale; fingers with 1 proximal tooth on cutting edge; ornamentation as in larger leg. Articles of last 3 legs much smaller and smoother; row of posterior short spinules on merus of third leg; otherwise with scattered spinules.

Abdomen smooth; pleura of fifth segment rectangular or slightly acute distally. Telson 1.5 times length of sixth segment, with pairs of dorsal spines at middle and $\frac{3}{4}$ length; posterior margin ending in acute median point flanked by 2 pairs of spinules, inner pair overreaching median point.

Measurements in mm.—Length of body: male 90; ovigerous female 30 to 65 (Holthuis 1952).

Color.—Male dark brown, some individuals overlain with bistre or olive, others speckled muddy brown; hazy lines of cream buff on carapace, especially laterally, and on first and third abdominal segments, extending down almost to top line of epimera. Large cheliped of bistre individuals bluish dark green, of muddy speckled individuals blackish brown, with remainder of limb black. Smaller chela dark brown. Walking legs more or less transparent; first type having faint bands of blue spots, but second type speckled with moderate brown.

Females more russet in color, marked like male; larger chela faint pea green mottled with rather large patches of light marine blue on inner and outer margins and fingers; walking legs almost white with few dark mottlings on anterior side; abdomen with dark, blackish area posteriorly on segments 1

and 3. (Abridged from notes by Schmitt in Holthuis 1952.)

Habitat.—Fresh and low salinity waters.

Type-locality.—“Brazilian Coast.”

Known range.—Lower Cape Fear River near Southport, N. C.; Florida; Louisiana; Texas; Veracruz, Mexico, to Santa Catarina, Brazil. Villalobos F. (1969) gave a distributional map for this and related species.

Remarks.—Holthuis and Provenzano (1970) acknowledged long-standing records of the species from St. Augustine, St. Johns County, and Silver Glen Springs, Marion County, Fla., and added a record from Dade County, Fla. They attributed these occurrences to introduction from South America, probably with water plants or fishes. Since then, J. O. Lee (personal communication and USNM) found *M. olfersii* (a 31-mm male) on intake screens of the Brunswick Nuclear Power Plant, Southport, N. C., in 1975. Horne and Beisser (1977) documented its occurrence in Texas in the Gaudeloupe River and Rio Grande River at Brownsville, suggesting that larval drift might account for its spread. White (1977) found a male at the confluence of Little Pecan Bayou and the Mermentau River, Cameron Parish, La., in 2.4‰ salinity water influenced by tide.

Dugger and Dobkin (1975) collected ovigerous females with males in a Lake Worth, Palm Beach County, Fla., drainage canal. Maintained in an environmental chamber on a 12 h light-dark cycle at 30°C in an aerated jar in which salinity was gradually raised during two weeks to 21‰, the eggs of one female hatched 17 days after capture, releasing 150–200 larvae. These were reared in 21 and 35‰ salinity in partial isolation and mass culture. Stages and development were described (similar to *M. acanthurus*), the largest larvae undergoing 12 molts without metamorphosing, but developing pleopod buds. Larvae in 35‰ salinity were 85% dead in seven days, and all dead by day 50, whereas those in 21‰ showed gradual mortality over 27 days. The authors thought that the species may be present throughout the east coast drainage of Florida.

Genus *Palaemonetes* Heller 1869

Holthuis 1952:199.—Hemming 1958b:158.—Chace 1972a:12.—Bray 1976:66.

Diagnosis.—Carapace with branchiostegal spine and groove but lacking supraorbital spine. Without appendix interna on first pleopod of males.

Subgenus *Palaemonetes* Heller

Holthuis 1952:207.

TABLE 2.—Determination of *Palaemonetes* species in marine waters of eastern United States (from Holthuis 1952 and Fleming 1969).

Structure	<i>P. vulgaris</i>	<i>P. intermedius</i>	<i>P. pugio</i>
Rostrum:			
dorsal teeth	up to tip	usually up to tip	tip unarmed
ventral teeth	generally 4 or 5	generally 4 or 5	generally 2 or 3 (but up to 5)
teeth behind orbit	2	1	1
Shape upper margin	often concave	often concave	usually straight (directed up-ward)
Second legs:			
carpus of male	1.1 × palm; 0.8 × merus	almost = chela; = to merus	almost = chela; = to merus
carpus of female	shorter than palm; 0.7 × merus	longer than palm; = to merus	longer than palm; = to merus
Teeth of chela (usual):			
dactyl	2	1	0
fixed finger	1	0	0
Male second pleopod, appendix masculina:			
shape	straight	straight	somewhat curved distally
apical setae	4	4	5
subapical setae	2	2	1-2
exceeds appendix interna	0.25	0.33	0.33

Key to Species

1. Rostrum with 2 teeth of dorsal series behind posterior margin of orbit, teeth reaching to tip, 3 to 5 ventral teeth; carpus of second leg in adult female shorter than palm, in male slightly longer or shorter (1.1 times); dactyl of second leg with 2 teeth, fixed finger with 1 on cutting edge
P. (P.) vulgaris
Rostrum with only 1 tooth of dorsal series behind posterior margin of orbit; carpus of second leg in adult female much longer than palm (1.3-1.5 times), in male almost as long as whole chela; dactyl of second leg with or without single tooth, fixed finger without tooth on cutting edge2
2. Rostrum with dorsal teeth reaching to often bifurcate tip, 4 or 5, seldom 3, ventral teeth; dactyl of second leg with tiny and sometimes blunt tooth
P. (P.) intermedius
Both margins of rostrum with unarmed stretch before dagger-shaped tip, 2 to 5, generally 3, ventral teeth; fingers of second leg without teeth on cutting edge
P. (P.) pugio

Palaemonetes (Palaemonetes) vulgaris Say

Fig. 49

Palaemon vulgaris Say 1818:248.*Palaemonetes carolinus*.—Hay and Shore 1918:393, pl. 27, fig. 4.*Palaemonetes (Palaemonetes) vulgaris*.—Holthuis 1952:231, pl. 54, figs. f-1.—Williams 1965:56, fig. 47.—Fleming 1969:445 ff., figs. 4, 10.

Recognition characters.—Rostrum reaching to or slightly beyond end of antennal scale; tip directed upward making upper margin more or less concave; dorsal margin with 8 to 11 teeth, first 2 behind posterior orbital margin and separated more widely than other proximal teeth, all teeth rather regularly distributed along rostrum but proximals generally closer together than distals, no unarmed space behind often bifurcate tip; ventral margin with 3 to 5 teeth (usually 4, rarely 2). Carapace smooth; antennal spine present; branchiostegal spine on anterior margin just below branchiostegal groove. Eyes well developed. Antennular peduncle with slender stylocerite reaching slightly beyond middle of basal article, anterolateral spine of basal article strong, overreaching rounded anterior margin; upper antennular flagellum with both rami fused for 7 to 9 joints; free part of shorter ramus with 10 to 17 joints, at least 1.5 times as long as fused part. Antennal scale 3 times longer than broad; terminal tooth strong, reaching almost to end of lamella.

First leg usually not reaching to end of antennal scale; fingers about as long as palm; carpus 1.3 to 1.7 times as long as chela and slightly longer than merus. Second leg longer and stronger than first,

stronger in adult females than in males, fingers and sometimes entire palm reaching beyond scale; fingers a little over half length of palm, cutting edge of dactyl with 2 small proximal teeth, fixed finger with 1 similar tooth fitting between those of dactyl; carpus shorter than palm and about $\frac{3}{4}$ length merus. Second leg of male not so large as in female; teeth on fingers indistinct. Third leg with propodus less than twice length of carpus. Fifth leg with propodus about 3 times length of dactyl, twice length of carpus.

Abdomen smooth; fifth segment with tip of pleura rectangular or slightly acute. Sixth segment 1.5 times length of fifth, shorter than telson. Male with appendix masculina on endopod of second pleopod straight, bearing 4 apical and 2 subapical setae and exceeding length of appendix interna by $\frac{1}{4}$ its length. Telson with 2 pairs of dorsal spines; anterior pair somewhat behind middle; second pair halfway between these and tip; posterior margin with strong median point flanked by 2 pairs of spines, inner pair longest, and between them 2 feathered setae. Outer margin of uropodal exopod with strong terminal tooth flanked mesially by slender movable spine.

Measurements in mm.—Length of body: male 30; ovigerous females 22 to 42.

Variation.—Every character given in the key and table of comparisons for this species is subject to some variation, but most specimens fit the standard described.

Color.—Transparent in life.

Habitat.—Estuarine waters, especially in beds of submerged vegetation; water's edge to (rarely) 15 m. In North Carolina, *P. vulgaris* is usually found in waters of 15 to 35‰ salinity; Wilson (1969) found that it preferred saltier areas of the Louisiana canal-lake area, especially flowing canals. Bowler and Seidenberg (1971) showed that extremely low salinity is not tolerated well and may be fatal, confirming the findings of Nagabhusanam (1961), but in salinities of 36–40‰ this species is much more tolerant than *P. pugio*, indicating that this tolerance may help to separate niches of these species which otherwise are apparently similar. Thorp and Hoss (1975) confirmed these findings but thought predator-prey interactions, competition, or behavioral differences rather than physiological tolerances may help to explain coexistence of the species.

Type-locality.—Atlantic coast of United States.

Known range.—Southern Gulf of St. Lawrence from northern Cape Breton Island (Bousfield 1956) through Northumberland Strait (Bousfield, personal communication) to St. Simons Inlet and Miscou Harbor near Portage Bay (Bousfield and Laubitz 1972), southward to Cameron County,

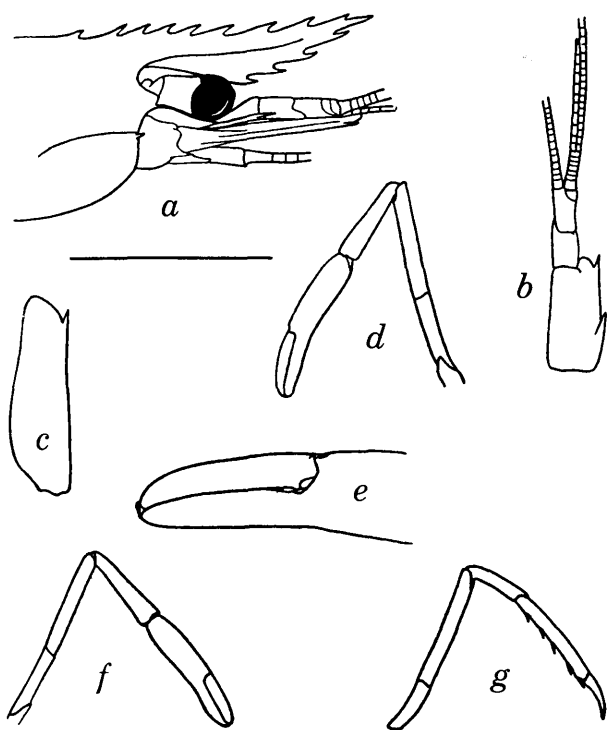


Fig. 49. *Palaemonetes (Palaemonetes) vulgaris* (Say). a, anterior part of body in lateral view; b, antennule; c, antennal scale; d, second leg of female; e, fingers of second leg of female; f, second leg of male; g, third leg; 5 mm indicated (from Holthuis 1952).

Texas. Published records also from Rio Champoton and near Progreso, Yucatan, Mexico (Holthuis 1952).

Remarks.—Correct identification of the species of *Palaemonetes* occurring on the east coast of the United States was not possible until Holthuis (1949) introduced his key. Two closely related species, *P. intermedius* and *P. pugio*, occupy much the same habitat and geographic range as *P. vulgaris*. An unfortunate but natural result of such confusion is that the voluminous older literature on *P. "vulgaris"* undoubtedly concerns all three species in unknown ways, hence must be viewed with reserve. Breeding experiments have shown that there is no natural hybridization among these species (Boston and Provenzano 1978).

Jenner (1955) showed that both *P. vulgaris* and *P. pugio* occur in the Woods Hole, Mass., region where much of the experimental work on *Palaemonetes* has been done. His useful field character for differentiating the two species is color of the eyestalks, those of *P. pugio* being generally much more yellow than the more red-brown *P. vulgaris*. The source of *Palaemonetes* for the Marine Biological Laboratory is thought to have been principally the dock, where only *P. vulgaris* has been found; Jenner suggested that most of the experimental work at Woods Hole was correctly referred to *P. vulgaris*.

In southern North Carolina, overt development of ovaries in largest females of *P. vulgaris* begins in February, egg deposition in early April. These events occur later in progressively smaller females. Zoeae begin to appear in plankton around the first of May. Peak egg production occurs in May when virtually all females are ovigerous. Breeding is continuous through summer; new eggs are deposited within 1 to 2 days after hatching of a previous brood. Larval development is rapid, juveniles appearing in early June. Sexual maturity is attained in animals having about a 5-mm carapace length. Females of the spring-hatched generation spawn in later summer and at a smaller size than overwintering 1-year-olds (in spring) which disappear from inshore areas by August. Reproductive activity wanes during September and hatching ceases by mid-October. Larvae are common in plankton throughout the breeding season, up to late November. Growth of adults largely stops during winter, resuming in spring (Knowlton and Williams 1970).

Larvae occur in much the same pattern in Chesapeake Bay (Sandifer 1973d), and a similar breeding season is inferred for other parts of the range, with allowance for latitudinal differences in temperature. Near northern extremes, ovigerous females are reported from southern Nova Scotia in early July (Bousfield 1958).

Burkenroad (1947a) showed that male *P. vulgaris* respond only to females which have molted to breeding form recently. After mating, the female resists further courtship. Males recognize such females only upon contact of the antennae with any surface of the female. The spermatophore will adhere to any part of the integument of either sex, but becomes non-adhesive almost immediately after exposure. Burkenroad stated that the sperm-bearing matrix of the spermatophore dissolves about a half-hour or less before spawning, and he thought that some substances freeing the sperm cells must be released by the female at the approach of spawning.

Eggs are released simultaneously from both oviducts in a continuous stream. Fertilization is external and, because sperm cells of decapod crustaceans in general are non-motile, Burkenroad suggested that entry of the sperm cell precedes development of the egg membranes in all decapods. All parts of the eggshell are produced by the ovum or the embryo. The first membrane is developed upon contact with water, the second about half an hour after spawning, and the third about 12 hours after spawning in fertile eggs only. The fourth and last membrane is an embryonic molt skin.

In *Palaemonetes*, the eggs are not adhesive when laid and first adhere to each other about half an hour after spawning. No attachment surface other than the first membrane of the egg develops. The eggs become fused, apparently by their own membranes, to the special setae in the brood pouch of the female. Egg stalks are drawn out by stretching movements of the pleopods. It is possible that the membrane is activated to become adhesive by the secretion of an enzyme-like material released among the eggs by the female from the pleopodal glands during attachment. Only near sources of this secretion would such attachment occur; therefore, the eggs usually do not stick to each other but rather to the setae.

Under experimental conditions *P. vulgaris* larvae tolerate a wide range of temperature and salinity, provided sufficient food is available. Salinity alone at five levels from 15 to 35‰ was found to have no effect on development of larvae but temperature profoundly affected both molting frequency and rate of growth. As temperature increased, growth and molting frequency increased, but the former decreased with respect to the latter. Thus, the average amount of growth per molt varied inversely with temperature, resulting in an increasing number of instars. Increased amounts of *Artemia* nauplii accelerated growth. Temperature and amount of food are important factors affecting rate of larval development, and growth and molting are semi-independent processes (Knowlton 1965).

Knowlton (1974) amplified this idea hypothesizing that food energy is utilized for maintenance activities at the expense of molting processes, which in turn have priority over growth and morphogenesis, considered to be roughly at the same level of demand. In a factorial experiment Sandifer (1973a) examined larval development of the species at 20°, 25° and 30°C in a different range of salinities (5–30‰). Lowest survival was in 5‰ at all temperatures. Time of development was twice as long at 20°C as at 25° and 30°C in most salinities, but a general retarding influence was noted at 5 to 10‰. Sandifer found metamorphosis as early as the 5th and late as the 12th molt. Salinity and temperature-salinity interaction had no detectable influence on number of instars, but the effect of temperature on number of instars was statistically significant at the 1% level. He concluded that optimal conditions for survival, rate of development and number of instars are at 25°C over a salinity range of 10 to 30‰.

For adults, McFarland and Pickens (1965) found no changes in rate of oxygen consumption related to salinity. They did, however, find moderate seasonal acclimation to temperature such that although metabolic rates did not change markedly, warm-adapted shrimp swam faster per unit of oxygen consumed when exposed to warm temperature than did intermediate or cold-acclimated shrimp. The reverse condition prevailed for cold-acclimated shrimp.

Since the early 1930s, much experimental work has been done on the endocrine system in relation to color control in *Palaemonetes*, mostly assumed to be *P. vulgaris*. The shrimp has been found to have four kinds of pigment under independent hormonal control—red, yellow, white, and blue. These pigments are mediated through the eyes by the background on which the animal is found. The source of the hormones is principally the sinus gland complex in the eyestalk and the central nervous system. Literature on this subject is beyond the scope of this paper. Kleinholz (1961) and Fingerman (1968) gave comprehensive reviews.

Palaemonetes vulgaris and *P. pugio* are both eaten by hakes, *Urophycis regius* and *U. floridanus* (Sikora, et al. 1972), and probably by many other predatory fishes.

Palaemonetes (Palaemonetes) intermedius Holthuis

Fig. 50

Palaemonetes (Palaemonetes) intermedius Holthuis 1949:94, fig. 2 j-l.—1952:241, pl. 55, figs. a-f.—Williams 1965:58, fig. 48.—Fleming 1969:445 ff., figs. 3, 11.—Chace 1972:22.

Recognition characters.—Rostrum reaching to or somewhat beyond end of antennal scale, tip directed upward making upper margin more or less concave; dorsal margin with 7 to 10 (usually 8 or 9) teeth, first tooth placed behind posterior orbital margin, second before or just over posterior orbital margin, proximal teeth more closely spaced than distal ones leading to often bifurcate tip; ventral margin with 4 or 5 (occasionally 3) teeth. Carapace smooth; antennal spine present; branchiostegal spine on anterior margin just below branchiostegal groove. Eyes well developed. Antennular peduncle with slender stylocerite reaching about to middle of basal article; anterolateral spine of basal article strong, overreaching rounded anterior margin; upper antennular flagellum with both rami fused for 7 to 10 joints; free part of shorter ramus with 7 to 12 joints, longer than fused part. Antennal scale slender, 3 to nearly 4 times longer than broad in females, even more slender in males; outer margin straight or slightly concave; terminal tooth not overreaching end of lamella.

First leg almost reaching tip of antennal scale; fingers as long as palm; carpus twice length of chela and slightly longer than merus. Second leg in adult female with fingers or almost entire chela reaching beyond antennal scale; fingers a little over half length of palm, cutting edge of dactyl with 1 proximal tooth, remainder of cutting edges of both fingers entire; carpus 1.2 to 1.5 times length of palm and as long as merus. Second leg of male somewhat more slender than in female; only fingers reaching beyond scale; carpus as long as merus. Third leg with propodus about 3 times as long as dactyl, twice as long as carpus.

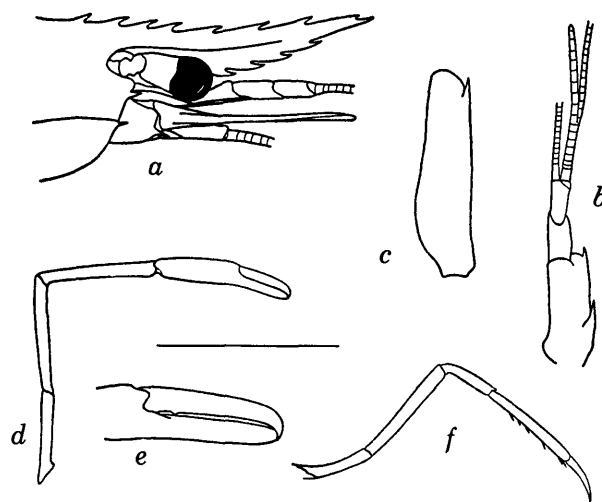


Fig. 50. *Palaemonetes (Palaemonetes) intermedius* Holthuis. a, Anterior part of body in lateral view; b, antennule; c, antennal scale; d, second leg of female; e, fingers of second leg of female; f, third leg; 5 mm indicated (from Holthuis 1952).

Abdomen smooth; pleura of fifth segment with tip rectangular or slightly acute; sixth segment 1.5 times length of fifth, somewhat shorter than telson. Male with appendix masculina on endopod of second pleopod straight, bearing 4 apical and subapical setae and exceeding length of appendix interna by $\frac{1}{3}$ its length. Telson with 2 pairs of dorsal spines; anterior pair somewhat behind middle, second pair halfway between these and tip; posterior margin with strong median point flanked by 2 pairs of spines, inner pair longest, and between these 2 feathered setae. Outer margin of uropodal exopod with strong terminal tooth flanked mesially by slender movable spine.

Measurements in mm.—Length of body: male 30; ovigerous females 20–42.

Variation.—Other than variations indicated in the description, the legs reach less far forward in males and juveniles than in ovigerous females (Holthuis 1952), and the second chelae of some females have one tooth on the cutting edge of each finger.

Color.—Transparent in life.

Habitat.—Estuarine waters, especially in beds of submerged vegetation.

Type-locality.—Iron Box Bay, Chincoteague Bay, Va.

Known range.—Vineyard Sound, Mass., to Port Aransas, Tex. (Holthuis 1952); Bahía de la Ascension, Quintana Roo, Mexico (Chace 1972).

Remarks.—The taxonomic status of this species is discussed in the account for *P. vulgaris*, in which a table of comparisons with closely allied species is given, and dealt with in more detail by Holthuis (1952).

Palaemonetes intermedius is variably abundant in south and southwestern Florida where it is more abundant than *P. pugio* and found in higher salinities (Tabb and Manning 1961; Rouse 1970). In studies of osmotic concentration of body fluids determined by freezing point depression, Dobkin and Manning (1964) found that *P. intermedius* is able to regulate over a wide range of salinities whereas regulation in *P. paludosus* (Gibbes) breaks down in salinities above 20‰. Odum and Heald (1972) found food habits of the latter two species similar in mangrove ecosystems except for the salinity range occupied. Both were considered opportunistic omnivores whose guts contained 22% unrecognized fine particles, 41% fine inorganic particles, 8% microalgae, 7% animal (invertebrate) remains, and 22% vascular plant detritus from which important food source bacteria, protozoa and fungi are removed.

Ovigerous females are reported in southern Florida from January to April and August to November (Tabb and Manning 1961; Rouse 1970). They are known from February to April in

(Hedgpeth 1950) and May to September in the Carolinas and Virginia. Hubschman and Broad (1974) described six larval forms and a postlarva in experimental rearings from females taken near Beaufort, N. C. Development closely resembles that of related species, size and number of molts being intermediate between marine and freshwater species (fewer molts) in the genus.

Palaemonetes (Palaemonetes) pugio Holthuis

Fig. 51

Palaemonetes (Palaemonetes) pugio Holthuis 1949:95, figs. 2 m-o.—1952:244, pl. 55, figs. g-l.—Williams 1965:59, fig. 49.—Fleming 1969:445, ff., figs. 7, 9.

Recognition characters.—Rostrum reaching to or slightly beyond end of antennal scale; straight, sometimes slightly upturned at tip; dorsal margin with 7 to 10 teeth (usually 8 or 9), first tooth placed behind posterior orbital margin, distal tooth placed at distance from tip leaving space before tip unarmed, distal teeth more widely spaced than proximal ones; ventral margin with 2 to 4 teeth (rarely 5 and usually 3), distal tooth also placed at distance from dagger-shaped tip. Carapace smooth; antennal spine present; branchiostegal spine on anterior margin just below branchiostegal groove. Eyes well developed. Antennular peduncle with slender stylocerite reaching slightly beyond middle of basal article, anterolateral spine of article strong, overreaching rounded anterior margin; upper antennular flagellum with both rami fused for 10 to 14 joints; free part of shorter ramus with 12 to 18 joints, longer than fused part. Antennal scale 2.5 to 3 times longer than broad (3 times breadth in males); lateral margin convex; terminal tooth strong, almost reaching end of lamella.

First leg not quite reaching tip of antennal scale; fingers as long as palm; carpus nearly twice length of chela and slightly longer than merus. Second leg of adult female stronger than first; fingers more than half length of palm, reaching beyond scale, cutting edges of both fingers with no teeth, often gaping proximally; carpus 1.3 to 1.5 times length of palm but shorter than entire chela; merus as long as carpus. Male with second leg more slender and shorter than in female; fingers shorter than palm; carpus nearly as long as whole chela and as long as merus. Third leg with propodus twice length of carpus.

Abdomen smooth; fifth abdominal segment with occurring in fresh water (Beeston 1971; Bowler and pleura ending in acute tooth, sometimes extremely

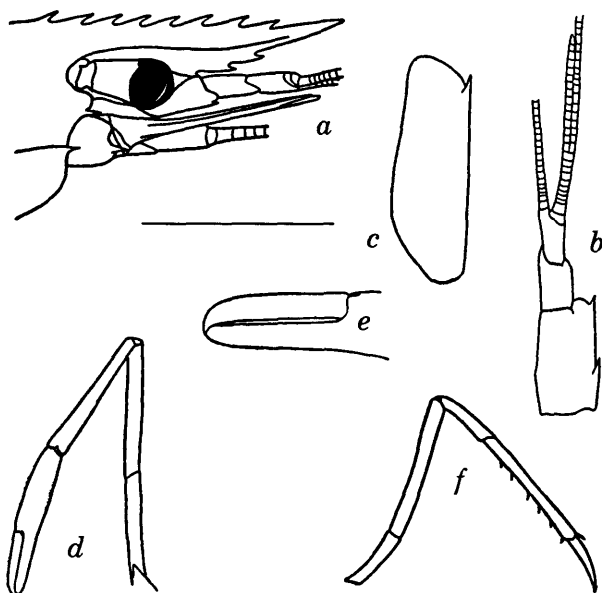


Fig. 51. *Palaemonetes (Palaemonetes) pugio* Holthuis. a, Anterior part of body in lateral view; b, antennule; c, antennal scale; d, second leg of female; e, fingers of second leg of female; f, third leg; 5 mm indicated (from Holthuis 1952).

small; sixth segment half again as long as fifth, somewhat shorter than telson. Male with appendix masculina on endopod of second pleopod somewhat curved laterad distally, bearing 5 apical and 1–2 subapical setae and exceeding appendix interna by $\frac{1}{3}$ its length. Telson with 2 pairs of dorsal spines; anterior pair somewhat behind middle; second pair halfway between these and tip; posterior margin with strong median point flanked by 2 pairs of spines, inner pair longest, and between them 2 feathered setae. Outer margin of uropodal exopod with strong terminal tooth flanked mesially by slender movable spine.

Measurements in mm.—Length of body: male 33; ovigerous females 30 to 50.

Variation.—Males further differ from females as follows: smaller size, more slender rostrum, free part of shorter ramus of upper antennular flagellum longer in relation to fused part, somewhat shorter legs, and carpus of second leg longer in relation to chela. Juveniles resemble males (Holthuis 1952). The second chelae of a few females have one small tooth on the cutting edge of the dactyl.

Color.—Transparent in life.

Habitat.—Estuaries, especially in beds of submerged vegetation (Marsh 1973). *Palaemonetes pugio* seems more tolerant of low salinity than *P. vulgaris*, being most abundant in the 10 to 20‰ range but Seidenberg 1971; Thorp and Hoss 1975; Wilson 1969; Wood 1967) as well as higher salinities. Welsh (1975) linked its abundance in estuaries to toler-

ance of poor flushing rather than to low salinity.

Type-locality.—Lagoon near Cove Point Light, Chesapeake Bay.

Known range.—Probably intermittent from Verte R., 3 mi. W St. Modeste (47°51'N, 69°26'W) Quebec, to near Yarmouth, Nova Scotia, Newcastle and East Brunswick, Maine (Bousfield, personal communication; Bousfield and Laubitz 1972; Knowlton 1973a; Williams 1974c), southward to Corpus Christi, Tex. (Holthuis 1952).

Remarks.—The taxonomic status of this species is discussed in the account for *P. vulgaris* where a table of comparisons with closely allied species is given, and dealt with in more detail by Holthuis (1952).

Breeding in *P. pugio* is comparable to that in *P. vulgaris*, varying with latitude. Rouse (1970) reported ovigerous females all year round in southwestern Florida in salinities varying from 0 to 43‰, but usually 10 to 15‰, at temperatures of 15° to 32°C; Hoese (1972) reported them from the Chandeleur Islands, La., in June in what must be high salinity for the species; and Knowlton (1973a) found them in Maine in mid-September.

Broad (1957) first worked out the larval development of *P. pugio* and *P. vulgaris*. He found that mature individuals of both species were abundant in the Beaufort, N. C., area from April until mid-October. Larval development is similar, 10 zoeal stages and a postlarval stage being described for both. The chief difference between larvae of the two is the presence of a pair of chromatophores on the second abdominal sternite of *P. pugio*, but absence in *P. vulgaris*. The number of larval stages and length of developmental period may vary, and one apparent cause of such variation is availability of suitable food. In rearing *Palaemonetes* with artificial diets, Broad (1957a) found that algae alone were not sufficient to promote survival; mixtures of plant and animal food were better, but best survival was obtained by feeding living *Artemia* nauplii. This was one of the pioneer experiments with this food in the rearing of decapod crustacean larvae. Frequency of molting and rate of development were directly correlated with amount of suitable food available.

Little (1968) showed that *P. pugio* could be induced to breed in winter. In November, two groups of animals whose water temperature was raised from 10° to 25°C over a period of 20 days and then held constant, one group being maintained at day lengths of 10.5 h and the other group at day lengths increased from 10.5 to 14.5 h in a month, spawned after two months, producing eggs which hatched into viable larvae. Animals in a similar experiment initiated in February spawned in five weeks. Eggs from the latter, maintained in 33‰ seawater and

22°–23°C, hatched in 15–19 days and larvae were reared to metamorphosis in 25–47 days. Both normal and abnormal larvae were produced.

Aspects of the physioecology of *P. pugio* have been studied in both field and laboratory. Wood (1967) found shrimp active throughout the year in Texas, with greatest abundance in July and October, mainly in salinities of 10–20‰. Growth to maturity there takes two to three months in summer and four to six months during the rest of the year. He found no appreciable variation in the length or weight associated with differences in salinity or temperature, but the most rapid increases occurred in temperatures over 30°C and the lowest ones at 11°–14°C. Welsh (1975), in Rhode Island, found an annual cycle with spawning in May–July, most rapid growth in late summer–fall, and over wintering in deep holes. Adams and Angelovic (1970) experimentally demonstrated what Odum and Heald (1972) found in the field, i.e., that *P. pugio* ingests and assimilates detritus with associated bacteria and that this material is perhaps one of their main sources of energy. Welsh (1975) amplified these findings, elaborating on the energetics of the species in the tidal marsh ecosystem. The shrimp macerate detritus into a heterogeneous assortment of uneaten particles by plucking away cellular matrix from surfaces of large detrital fragments. Resulting cavities in the detrital mass become heavily invaded by pennate diatoms, particles suspended in the water column and bacteria. Nutrient analyses indicate that the shrimp excrete large quantities of ammonia and phosphate which together with release of dissolved organic matter is presumably responsible for the heavy microfloral growth and in-

creased protein fraction in both feces and large and small uneaten detrital fragments. The shrimp while supporting their own trophic requirements accelerate breakdown of detritus. Welsh extended the finding of Johannes and Satomi (1966) that feces of these shrimp are rich in assimilable organic matter, particularly protein, and that a considerable fraction of energy in marine communities is channeled into feces to be consumed by the shrimp themselves and other organisms. Fecal pellets are thus a component of marine ecosystems, contributing to energy flow and nutrient cycles in a quantitatively significant way.

A number of parasites have been reported from *P. pugio*. Pearse (1952b) reported *Probopyrus pandicola* from the gill chamber of specimens from Texas, and Bousfield (personal communication) found bopyrids associated with it in Nova Scotia. Bridgeman (1969) described a microphallid trematode, *Carneophilus choanophallus*, whose definitive hosts in southern Louisiana are the raccoon and black rat (as well as other mammals in experiments) and second intermediate host is *P. pugio*. Sprague (1970) reported microsporidians in metacercariae from *P. pugio* in Georgia as well as from muscles of the shrimp.

Subfamily Pontoniinae

Upper antennular flagellum with both rami fused in basal part. Appendix masculina generally present on second pleopod of male; appendix interna on second pleopod of female. Pleurobranch absent from third maxilliped. Posterior margin of telson with 3 pairs of spines (Holthuis 1951a).

Key to Genera and Some Species

(Adapted from Holthuis 1951a; Chace 1972a)

- | | |
|--|------------------------------------|
| 1. Third maxilliped with well-developed exopod | 2 |
| Third maxilliped without exopod | 4 |
| 2. Hepatic spine present. | <i>Periclimenes</i> |
| Hepatic spine absent | 3 |
| 3. Rostrum compressed, with distinct teeth. | <i>Periclimenaeus</i> |
| Rostrum depressed, with at most 2 small teeth near tip | <i>Pontonia</i> |
| 4. Second maxilliped with exopod | <i>Anchistioides antiguensis</i> |
| Second and third maxilliped without exopods | <i>Neopontonides beaufortensis</i> |

Genus *Anchistioides* Paulson 1875

Holthuis 1951a:175.

Anchistioides antiguensis (Schmitt)

Fig. 52

Periclimenes antiguensis Schmitt 1924a:84.

Periclimenes barbadensis Schmitt 1924a, pls. 3–4.

Anchistioides antiguensis.—Holthuis 1951a:175, pl. 57, legend on p. 310 facing pl. 55.—Coelho and Ramos 1972:148.

Recognition characters.—Rostrum large, toothed part nearly triangular in lateral view, reaching

somewhat beyond antennal scale; upper margin bearing 8–10 teeth on anterior $\frac{2}{3}$ of margin; lower margin bearing 5–8 teeth. Carapace smooth; large and conical postorbital tubercle slightly behind orbital margin; antennal spine below rounded lower orbital angle sharp and slender; anterolateral angle rounded and not produced. Eyes well developed, cornea as broad as short stalk and rounded. Basal article of antennular peduncle broad, stylocerite closely appressed, extending about to midlength of article, distolateral spine strong; second and third articles together half length of first; upper antennular flagellum thick and hairy, indistinctly jointed, fused with longer ramus for half its own length. Antennal scale 3 times as long as broad, far overreaching antennular peduncle; slightly sinuous outer margin ending in strong, laterally divergent tooth exceeding lamella; latter narrowed anteriorly and subrectangular mesiodistally; antennal peduncle not reaching midlength of scale.

First leg slightly overreaching antennal scale,

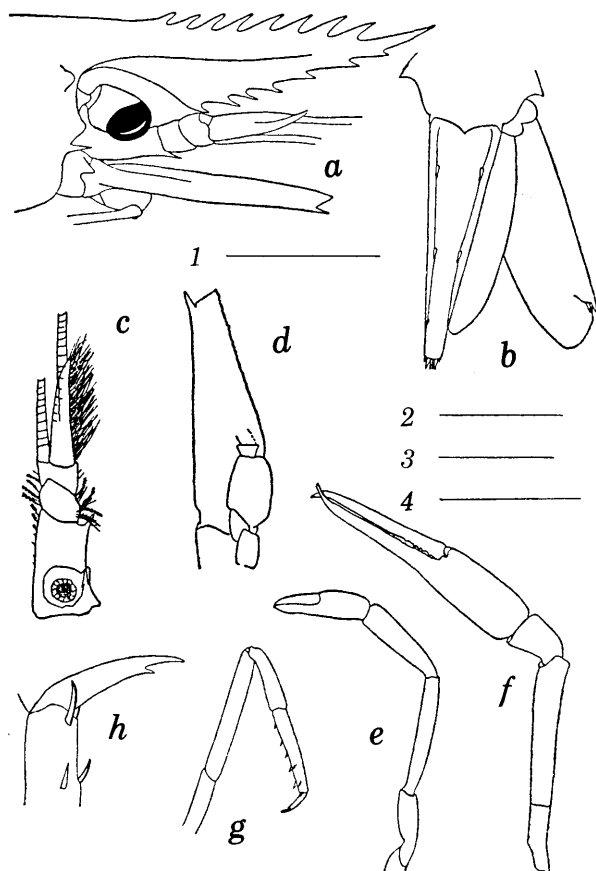


Fig. 52. *Anchistioides antiguensis* (Schmitt). a, Anterior part of body in lateral view; b, telson and right uropod in dorsal view; c, antennule; d, antenna; e, first leg; f, second leg; g, third leg; h, dactyl of third leg. Scales: 1(a-c, e, g) = 2 mm; 2(d) = 2 mm; 3(f) = 2 mm; 4(h) = 1 mm (from Holthuis 1951a).

fingers about as long as palm, carpus slightly longer than chela. Second legs very strong and equal, fingers or part of palm reaching beyond antennal scale; fingers long, slender, tips curved and crossing, cutting edges entire, fitting closely; palm somewhat inflated and cylindrical; carpus somewhat conical, $\frac{1}{2}$ length of palm, $\frac{1}{3}$ length of merus. Third leg not reaching tip of antennal scale, dactyl narrow and indistinctly bifid; fourth and fifth similar but fourth both more slender and shorter than third or fifth.

Abdomen smooth, pleura of first 5 segments broadly rounded, those of sixth pointed. Fifth and sixth segments of about same length, posterior margin of latter with minute median tooth. Telson twice length of sixth segment; 2 pairs of dorsal spines in anterior half; 2 pairs of spines on posterior border, outer pair minute. Uropods elongate oval; outer margin of exopod ending in tooth flanked mesially by movable spine.

Measurements in mm.—Length of body: 25; ovigerous female 18 (Holthuis 1951a).

Habitat.—Coral rock, white rocks and coral, coarse sand and coral, coarse gray sand and broken shells, calcareous algae, fine white sand and black specks, enclosed in cavities in sponges (USNM); surface to 118 m.

Type-locality.—English Harbor, Antigua.

Known range.—Off Charleston, S. C. (Wenner and Read 1982); off west Florida through West Indies to Maranhão, Pernambuco, and Alagoas, Brazil (Coelho and Ramos 1972); Bermuda.

Remarks.—Samples of *A. antiguensis* taken throughout the year at or near the Biological Station in Bermuda in The Reach have shown regular nocturnal periodicity in occurrence at the surface, sometimes of sufficient intensity to indicate swarming (Wheeler and Brown 1936; Wheeler 1937). The peaks of abundance appear to coincide with two phases of the lunar month from last quarter to first quarter of the new cycle. The animals appear to come up from the bottom directly below, not to be drifting in with the tide. Swarming is thought to be inhibited by light. Sex and reproductive period, surface temperature, wind and weather, and stage of tide were shown to have no connection with swarming, but feeding on annelids (identified as epitokes of *Perinereis melanocephala* and *Leptonereis* sp. near *L. glauca*) may account for the behavior; stomachs of the shrimp were filled with setae of these species.

Ovigerous females of the shrimp were observed in June and early July. The double maximum of swarming was thought to represent two stages of growth. The species was less frequent in July-August and again in December-March. The summer reduction is due to dying out of a generation in

July, but the winter scarcity was attributed to seasonal conditions.

Genus *Neopontonides* Holthuis 1951

Holthuis 1951a:189.

***Neopontonides beaufortensis* (Borradaile)**

Fig. 53

Periclimenes beaufortensis Borradaile 1920:132.

Neopontonides beaufortensis.—Holthuis, 1951a:190, pl. 59, figs. g-k; pl. 60, figs. a-k.—Williams 1965:49, fig. 41.—Chace 1972:25.

Recognition characters.—Rostrum slender, straight; a little shorter than antennular peduncle; laterally compressed but broadened at base, covering eyestalks, lateral margin of widened base not merging with orbital margin; upper margin with 0–5 teeth, most proximal teeth, when present, in front of posterior margin of orbit on a crest, crest remaining visible in absence of teeth; lower margin unarmed. Carapace smooth or somewhat areolated; anterior margin of carapace with lower angle of orbit produced in rounded lobe; antennal spine strong, located considerably below orbit; rounded lobe slightly below antennal spine followed by an emargination ending in produced anterolateral angle; hepatic and supraorbital spines absent. Eyes large, reaching almost to end of rostrum. Basal article of antennular peduncle with stylocerite rather broad, ending in slender point reaching almost to middle of article; outer margin of article slightly concave ending in strong anterolateral spine reaching end of second article; upper antennular flagellum with rami fused for 2–4 joints; short ramus with 2–4 free joints. Antennal scale reaching beyond antennular peduncle; concave outer margin ending in strong tooth; lamella exceeding tooth; small lateral tooth at base; antennal peduncle reaching about to middle of scale.

First leg reaching beyond end of antennal scale; fingers slightly shorter than palm, unarmed, slightly agape; carpus about as long as merus. Second legs unequal. Part of palm of larger leg exceeding antennal scale; fingers half or less length of palm, dactyl with 2, fixed finger with 1 tooth on cutting edge; palm slightly swollen; carpus short, conical; merus about twice as long as palm, slender, unarmed; carpus nearly as long as palm. Third leg with heavy, simple dactyl.

Abdomen smooth, all pleura broadly rounded. Sixth segment as long as telson. Telson with 2 pairs of dorsolateral spines; posterior pair midway between anterior pair and tip; 3 pairs of spines on

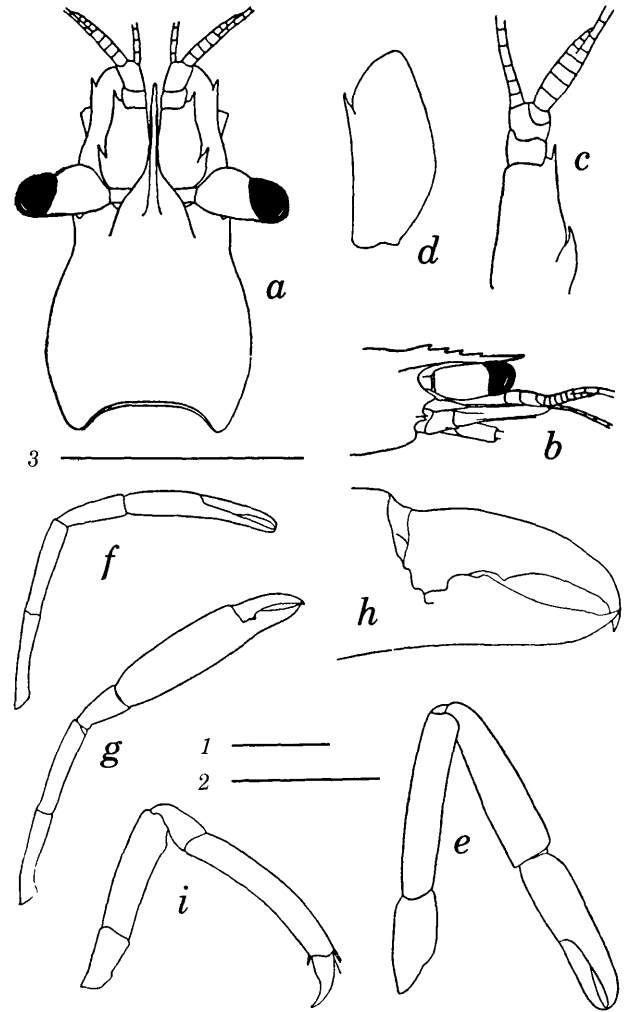


Fig. 53. *Neopontonides beaufortensis* (Borradaile). Anterior part of body in *a*, dorsal view, *b*, lateral view; *c*, antennule; *d*, antennal scale; *e*, first leg; *f*, smaller second leg; *g*, larger second leg; *h*, fingers of larger second leg; *i*, third leg. Scales: 1(*b*)=1 mm, (*c*, *d*, *f*, *g*, *i*)=0.5 mm, (*e*)=0.33 mm; 2(*a*)=1 mm; 3(*h*)=0.5 mm (from Holthuis 1951a).

posterior border, intermediate pair less than twice length of inner pair. Uropods elongate; outer margin of exopod ending in tooth flanked mesially by movable spine.

Measurements in mm.—Length of body: male 9; ovigerous females 7 to 10.

Variation.—In young specimens, the legs are relatively shorter than in adults, and the larger second leg resembles the smaller second leg of adults.

Color.—At Beaufort, N. C., Patton (1972) observed females bearing yellow and red chromatophores located in ventral half of main portion of body; by differential expansion of pigments, animals match yellow or orange color of host *Leptogorgia*. Males basically transparent, although containing some of same pigments.

Habitat.—This species is found in coastal waters

where it lives in association with gorgonian coral, *Leptogorgia virgulata*; surface to a few meters. It also has been noted on the octocoral, *Eunicea tourneforti*, in the Dutch West Indies (Criales 1980).

Type-locality.—Beaufort, N. C.

Known range.—Beaufort, N. C., to Grand Isle, La. (Dawson 1963); Caledonia Bay, Panama; Antigua.

Remarks.—*Neopontonides beaufortensis* is one of the commensals living on *L. virgulata*. The shrimp usually rests motionless on the coral with walking legs wrapped around a branch, the propodus of each leg somewhat bowed outward to facilitate grasp (Patten 1972), but it is capable of rapid movement. Scavengers feeding mainly on material on the surface of the host or from inside extended polyps,

starved individuals placed on a piece of the coral soon fill the stomach with spicules, mucus, and other surface material in a flurry of activity; occasionally they will stretch out to pick at sediment or briefly leave the host to feed. They feed with the first legs, and to some degree with the fourth legs; the large second legs rarely go to mouthparts, and seem to be used mainly in aggressive behavior.

Ovigerous females have been taken in Bogue Sound near Beaufort Inlet, N. C., in August and November; in Panama in April, and in Antigua in May.

Genus *Periclimenaeus* Borradaile 1915

Holthuis 1951a:76.—Hemming 1958b:159.

Key to Species

1. Antennal scale with no terminal tooth *P. schmitti*
 Antennal scale with terminal tooth *P. wilsoni*

Periclimenaeus schmitti Holthuis

Fig. 54

Periclimenaeus schmitti Holthuis 1951a:90, pl. 27, figs. a-m.—Williams 1965:45, fig. 37.—Chace 1972:29.

Recognition characters.—Rostrum short, straight, or somewhat decurved, not reaching to end of basal article of antennular peduncle; upper margin bearing 1 or 2 teeth, exclusive of upturned tip; lower margin convex, unarmed. Carapace smooth; post-orbital ridge paralleling orbit, extending from strong antennal spine dorsally and becoming gradually obsolete; anterolateral angle broadly rounded, produced forward. Eyes well developed, cornea globular, shorter and narrower than eyestalks. Basal article of antennular peduncle with short, broad, blunt-tipped stylocerite reaching about to middle of article; outer margin with blunt angle at level of stylocerite tip, concave beyond angle, anterolateral angle of article with rather large tooth; second and third articles short; upper antennular flagellum with 3 fused joints, free part of short ramus with 1 short joint. Antennal scale broadly ovate; outer margin nearly straight, with no terminal tooth.

First leg with carpus and chela extending beyond antennal scale; chela slender, fingers $\frac{2}{3}$ length of palm, unarmed, carpus about as long as chela, slightly shorter than merus. Second legs unequal, both reaching with chela and part of carpus beyond antennal scale. Larger second leg heavy, fingers slightly less than half as long as palm, inwardly curved; upper margin of dactyl broadly

rounded, cutting edge finely denticulate distally, with large rectangular-shaped tooth fitting into pit on fixed finger when closed; fixed finger with strong, narrow tooth at inner margin of pit; palm

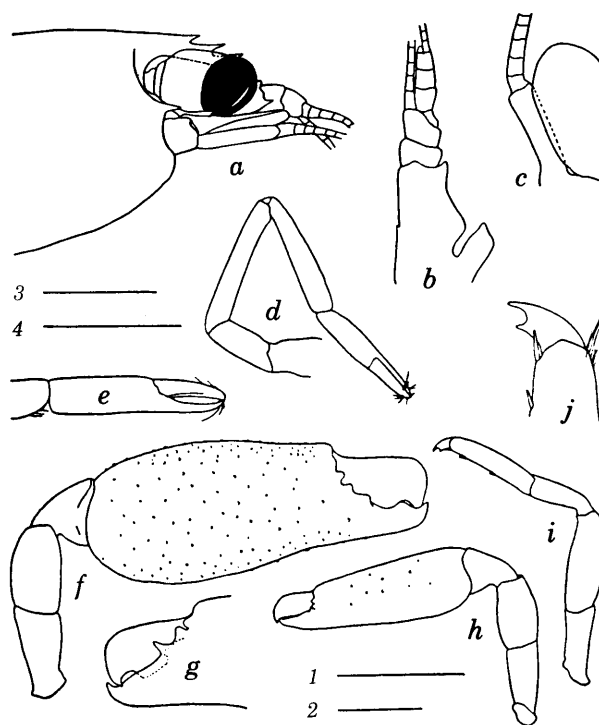


Fig. 54. *Periclimenaeus schmitti* Holthuis. a, Anterior part of body in lateral view; b, antennule; c, antenna; d, first leg; e, chela of first leg; f, larger second leg, outside; g, fingers of larger second leg, inside; h, smaller second leg; i, third leg; j, dactyl of third leg. Scales: 1(a) = 1 mm, (e) = 0.5 mm; 2(b-d) = 0.5 mm; 3(f-i) = 1 mm; 4(j) = 0.33 mm (from Holthuis 1951a).

swollen, covered with number of small scalelike tubercles; carpus conical, about $\frac{1}{4}$ length of palm; merus about $\frac{1}{3}$ length of palm, sometimes with small tubercles at lower edge. Smaller second leg with fingers straight, slightly shorter than $\frac{1}{3}$ length of palm; cutting edge of dactyl denticulate throughout, that of fixed finger straight; tubercles on palm fewer than on opposite member. Third leg with propodus and part of carpus reaching beyond antennal scale, dactyl short, distinctly bifurcate.

Abdomen smooth; pleura of first 5 segments rounded; sixth segment about as long as fifth and about $\frac{2}{3}$ length of telson. Telson with 2 pairs of small dorsal spines somewhat removed from lateral margin, placed at $\frac{1}{3}$ and $\frac{2}{3}$ length; 6 spines on posterior margin placed in row, intermediate spines longest. Uropods broadly ovate, exopod with outer margin ending in tooth flanked mesially by movable spine.

Measurements in mm.—Length of body: ovigerous females 8–10 (erroneously 20 in Williams 1965).

Variation.—Specimens with a single rostral tooth are young.

Color.—Specimens preserved a few days in 10% formalin and one day in 40% isopropanol: scattered small reddish chromatophores on body and limbs, background yellowish white.

Habitat.—Shallow water.

Type-locality.—Tortugas, Fla.

Known range.—Bogue Sound, Black Rocks off New River, and Lockwoods Folly River, N. C.; Tortugas, Fla.

Remarks.—Two specimens from North Carolina were taken August 16, 1957, in a nighttime surface plankton tow on flood tide near Beaufort Inlet. Though these have intermediate spines on the telson longer than the other terminal pairs, they agree well with specimens of *P. schmitti* from Tortugas. A third specimen (color notes above) was taken in nocturnal plankton from Lockwoods Folly River on flood tide in December.

Ovigerous females are known in July and August from North Carolina, and August at Tortugas.

Periclimenaeus wilsoni (Hay)

Fig. 55

Coralliocaris wilsoni Hay 1917:71.—Hay and Shore 1918:394, text-fig. 13; pl. 27, fig. 8.

Periclimenaeus wilsoni.—Holthuis 1951a:103, pl. 31, figs. a-m; pl. 32, figs. b-c.—Williams 1965:46, fig. 38.—Chace 1972:29.

Recognition characters.—Rostrum nearly straight

or somewhat decurved, almost reaching end of antennular peduncle; upper margin somewhat convex, bearing 10–12 regularly spaced teeth, first tooth directly over or immediately behind orbital margin; lower margin straight or concave, unarmed. Carapace smooth with only an antennal spine placed close to acute lower orbital angle; postorbital ridge paralleling orbit indistinct; anterolateral angle somewhat anteriorly produced, broadly rounded. Eyes well developed. Stylocerite of antennular peduncle broad, short, and pointed, almost reaching middle of basal article; outer margin of basal article with blunt angle near tip of stylocerite, concave beyond angle, ending in strong tooth; second and third antennular articles about same size; upper antennular flagellum with 6 to 9 fused joints; free part of short ramus with 2 joints. Antennal scale a little longer than antennal peduncle; outer margin straight, ending in small spine; lamella broadest proximally.

First legs with carpus and chela extending be-

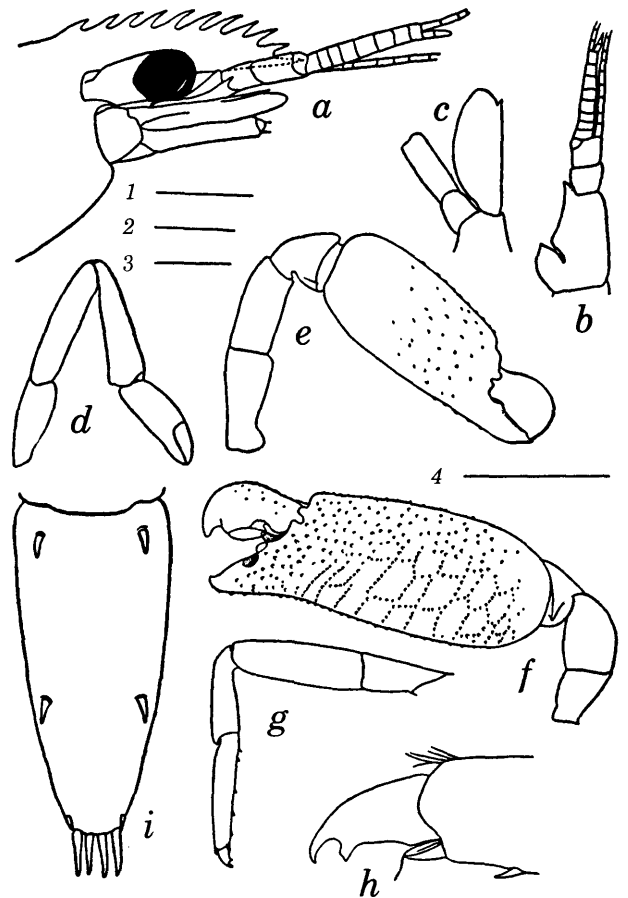


Fig. 55. *Periclimenaeus wilsoni* (Hay). a, Anterior part of body in lateral view; b, antennule; c, antenna; d, first leg; e, smaller second leg; f, larger second leg; g, third leg; h, dactyl of third leg; i, telson in dorsal view. Scales: 1(a) = 1 mm, (h) = 0.2 mm; 2(b-e, g) = 1 mm; 3(f) = 2 mm; 4(i) = 1 mm (from Holthuis 1951a).

yond tip of antennal scale; chela rather thickset; fingers shorter than palm, unarmed; carpus about as long as merus. Second legs strong, unequal, with part of carpus and chela extending beyond tip of antennal scale. Larger second legs with chela almost equal to bulk of body; fingers inwardly curved, somewhat less than half length of palm; dactyl with upper margin convex, cutting edge with large rectangular tooth fitting into pit on fixed finger when closed; fixed finger with distinct tooth at inner margin of pit; palm swollen, tuberculate at base and on base of fingers, tubercles on proximal lower part of palm arranged in rows or honeycomb pattern; carpus smooth, short, cup-shaped; merus about $\frac{1}{3}$ length of palm. Smaller second leg much as larger one in general shape; palm somewhat swollen, with scattered tubercles anteriorly. Third leg with greater part of propodus reaching beyond tip of antennal scale; dactyl short, broad, bifurcate.

Abdomen smooth; pleura of first 5 segments broadly rounded; sixth segment half length of telson. Telson with 2 pairs of dorsal spines somewhat removed from lateral margin; anterior pair close to anterior margin; posterior pair slightly behind midlength; posterior margin with 3 pairs of spines, outer pair short and located in advance of larger intermediate and inner pairs. Uropods broadly ovate, outer margin of exopod ending in tooth flanked mesially by movable spine.

Measurements in mm.—Length of body: male 20;

ovigerous females 16 to 20.

Variation.—Juveniles may have a shorter rostrum with fewer dorsal teeth, and in some specimens the second chelae may be smooth.

Color.—Clear, milky white; integument so transparent that color of internal organs is plainly visible; egg masses light bluish green.

Habitat.—This species is known to live in sponges in coastal waters in company with *Synalpheus longicarpus* and *S. townsendi*; 18 to 73 m.

Type-locality.—Fishing grounds, 20 miles off Beaufort Inlet, N. C.

Known range.—Off Beaufort, N. C.; off Sapelo Island, Ga.; off Loggerhead Key, near Tortugas, and Franklin County, Fla.

Remarks.—Ovigerous females have been reported from Florida in July and North Carolina in August, and are known from Georgia in August. Gurney and Lebour (1941) described the last larval stage of a shrimp doubtfully referred to *P. wilsoni*.

When disturbed, the animals are able to make a snapping sound with the large chela that is quite as loud as that made by one of the true snapping shrimps.

Genus *Periclimenes* Costa 1844

Holthuis 1951a:23.—Hemming 1958b:159.—Chace 1972:29.

Key to Species

(Adapted from Chace 1972)

1. Carapace without antennal spine below suborbital lobe *P. longicaudatus*
Carapace with antennal spine below suborbital lobe 2
2. Pleuron of fifth abdominal segment with posteroventral angle pointed *P. americanus*
Pleuron of fifth abdominal segment with posteroventral angle rounded. 3
3. Third abdominal segment sometimes moderately produced posteromesially but never into laterally compressed hump; rostrum proper with dorsal teeth noticeably raised into an arch *P. iridescens*
Third abdominal segment strongly produced posteromesially into laterally compressed hump; rostrum proper with dorsal teeth not raised into an arch, slender and attenuated in female *P. pedersoni*

Periclimenes americanus (Kingsley)

Fig. 56

Anchistia americana Kingsley 1878b:96.

Periclimenes (Harpilius) americanus.—Holthuis 1951a:60, pl. 18, figs. a-j; pl. 19, figs. a-e.—Williams 1965:43, fig. 36.

Periclimenes americanus.—Chace 1972:31.—Coelho and Ramos 1972:147.—Pequegnat and Ray 1974:253, fig. 65.

Recognition characters.—Rostrum rather high and straight; tip directed upward, reaching about to end of antennular peduncle; upper margin nearly straight, with 7–10 teeth, first 2 behind orbit and

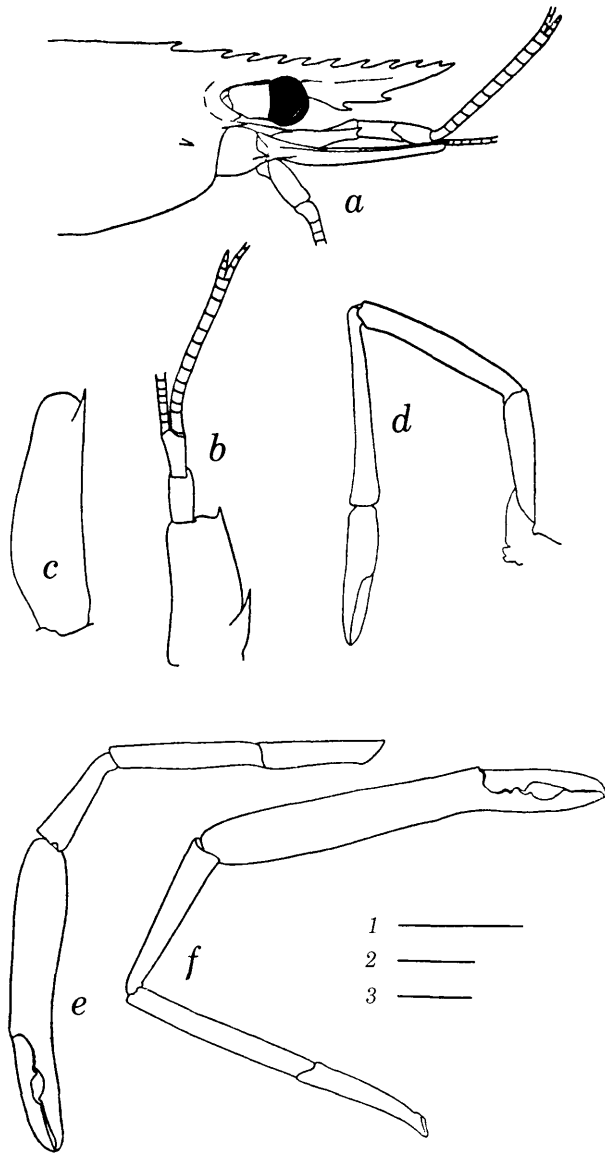


Fig. 56. *Periclimenes americanus* (Kingsley). *a*, Anterior part of body in lateral view; *b*, antennule; *c*, antennal scale; *d*, first leg; *e-f*, second leg (different specimens). Scales: 1(*a*)=1 mm; 2(*b-c*)=1 mm, (*d*)=1.3 mm; 3(*e-f*)=2 mm (from Holthuis 1951a).

considerably separated; lower margin with 2, sometimes 3 teeth, but unarmed stretch before tip. Carapace with only antennal and hepatic spines; lower orbital angle acute; postorbital ridge paralleling orbit; anterolateral angle broadly rounded. Eyes well developed; cornea globular, 2 dark-colored bands visible on cornea in fresh material; ocellus present. Stylocerite rather strong, sharply pointed, almost reaching middle of basal antennular article; outer margin of basal antennular article convex, ending in well-developed anterolateral tooth; second and third articles elongate, second slightly shorter than third; upper antennular fla-

gellum with 2 rami fused for 8–12 joints (often 6 in younger specimens), free part of shorter ramus with 3 or 4 joints, length less than $\frac{1}{4}$ that of fused part. Antennal scale slightly exceeding antennular peduncle, outer margin straight or slightly concave and ending in strong tooth slightly exceeding distally narrowed lamella; scale with distinct spine near base; antennal peduncle not reaching to middle of scale. All maxillipeds with well-developed exopods.

First legs slender; chela and sometimes small portion of carpus extending beyond antennal scale; fingers smooth, as long as palm. Second legs equal in size and shape, very strong and longer than first; adult males with fingers less than half as long as palm, 3 or 4 teeth on cutting edges leaving gape at midlength when closed; second legs shorter and fingers not agape in juveniles and adult females.

Abdomen with pleura of first 4 segments rounded, of fifth ending in small tooth; median posterior margin of third only slightly produced posteriorly. Sixth segment about 1.5 times as long as fifth and about $\frac{3}{4}$ length of telson. Telson with 2 dorsal pairs of spines at $\frac{1}{3}$ and $\frac{2}{3}$ length; posterior margin with 3 pairs of spines, intermediate pair less than twice length of inner spines.

Measurements in mm.—Length of body: male 22; ovigerous females 13 to 20.

Variation.—The carpus of the second pair of legs varies in length as do the dactyls of the last three pairs of legs.

Color.—Ground color translucent grayish white; carapace with three oblique orange-brown lateral lines and pair of dorsal lines running back from base of rostrum; each abdominal segment crossed by narrow brown band and row of small dark spots on posterior margin; tail fan with two larger lateral and median spots and an orange-brown tip (Verrill 1922).

Habitat.—This species lives in coastal waters, preferring sandy or rocky bottom, often between algae or coral, or among turtle grass or debris. Verrill (1922) found large schools near the surface in Bermuda, and Gurney (1943a) found it to swim singly or in small numbers at the surface at night in certain periods of the lunar cycle (see Holthuis 1951a). Shallow water to 73 m.

Type-locality.—Key West, Fla.

Known range.—Beaufort, N. C.; to western Gulf of Mexico (Felder and Chaney 1979), and through West Indies to Aruba; Pará to São Paulo, Brazil (Coelho and Ramos 1972).

Remarks.—Gurney (1943a) listed this species as one of the commonest decapod crustaceans in the littoral region of Bermuda. Females outnumbered males two to one; however, ovigerous females were

never collected there. From plankton, Gurney (1936c, 1943a) described the first and fifth larval, and the first postlarval stages, and gave remarks on allometric growth of the second legs. These legs are stronger and longer in males than in females, with fingers agape in old males. The center of greatest growth is in the palm.

Ovigerous females have been found virtually year round in southwestern Florida (Rouse 1970) where the species endures a temperature range of 12° to 34°C and salinities of 15 to 61‰; a long breeding season is indicated for other parts of the range.

Holthuis (1951a) listed *P. americanus* as common in North Carolina, but it has seldom been taken in surface plankton tows in Bogue Sound that have produced hundreds of *P. longicaudatus*.

Periclimenes iridescens Lebour

Fig. 57

Periclimenes iridescens Lebour 1949:1112, figs. 4–5.—Chace 1972:37.

Periclimenes (Periclimenes) iridescens.—Holthuis 1951a:43, pl. 12; pl. 20, figs. i–j.

Recognition characters.—Rostrum straight, short, rather high, reaching along length of second article of antennular peduncle; upper margin somewhat convex and bearing 5 to 7 teeth, 1 or 2 of these placed behind orbit on carapace and wider apart than others; tip of rostrum often unarmed; lower margin with 0–3 teeth, extremely small if present; lateral carina near lower margin. Carapace lacking postorbital ridge; lower orbital angle produced into blunt lobe somewhat constricted at base; antennal and hepatic spines about same size, no supraorbital spine present; anterolateral angle broadly rounded. Eyes well developed, cornea globular, ocellus present. Stylocerite not reaching to midlength of basal antennular article, slender and sharply pointed; lateral margin of article slightly sinuous, ending in strong tooth extending about as far forward as sinuous distal margin; second and third articles about equal in length; upper flagellum with 2 rami fused for 6 or 7 joints. Antennal scale with outer margin somewhat concave, ending in distal tooth overreached by lamella; antennal peduncle reaching almost to middle of scale, distinct outer spine near base of scale. All maxillipeds with well-developed exopods.

First legs slender, not reaching end of antennal scale; second legs unequal, part of palm reaching beyond antennal scale; fingers of larger chela 0.5 to 0.8 times length of palm and armed with 2 teeth on cutting edge, those of smaller chela slightly

longer or shorter than palm, slender and unarmed. Dactyls of last 3 legs simple or bifid.

Abdomen smooth; all pleura rounded. Third segment slightly produced posteromesially but not forming hump. Sixth segment about twice length of fifth and slightly longer than telson. Telson with 2 pairs of minute dorsal spinules at mid and $\frac{3}{4}$ length; posterior margin with 3 pairs of spines, intermediate pair longer than inner pair.

Measurements in mm.—Length of body: ovigerous females 14–15 (Holthuis 1951b).

Habitat.—Sand and algae; reported on both octocorals and antipatharians in Curaçao and Bonaire (Criales 1980); 3.6 to 183 m.

Type-locality.—Off Castle Roads, Bermuda.

Known range.—Northeast off Cape Hatteras, 35°32.9'N, 75°11.9'W (Herbst, et al. 1979); southern and northwestern Florida; Tobago; Cubagua Island, Venezuela; Bermuda (Chace 1972).

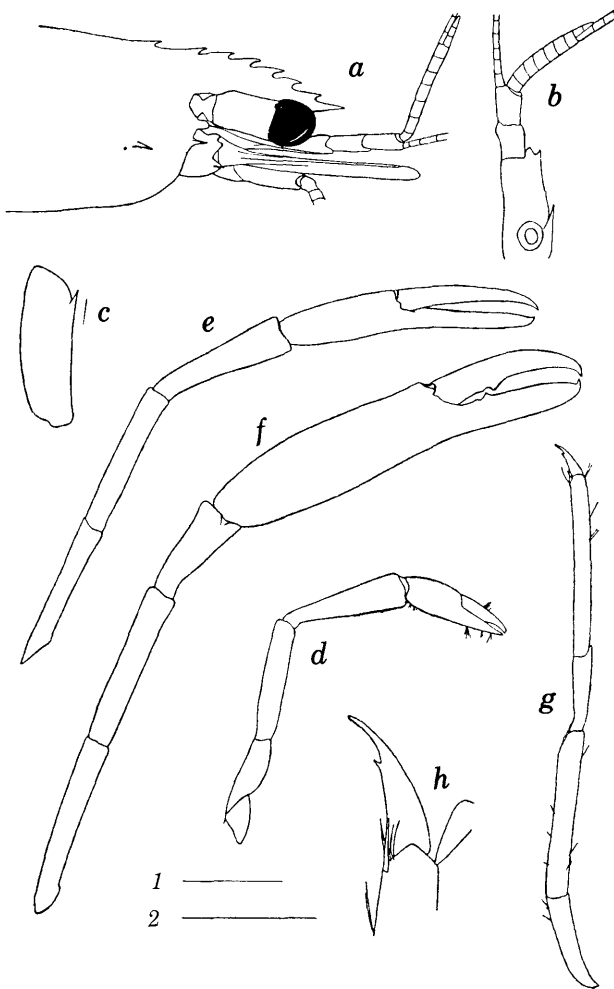


Fig. 57. *Periclimenes iridescens* Lebour. a, Anterior part of body in lateral view; b, antennule; c, antennal scale; d, first leg; e, smaller second leg; f, larger second leg; g, third leg; h, dactyl of third leg. Scales: 1(a) = 1 mm, (b–c) = 1.2 mm, (h) = 0.2 mm; 2(d–g) = 1 mm (from Holthuis 1951a).

Remarks.—The distribution of this tiny shrimp is questionable in some details. Herbst, et al. (1979) cited a record off Panama City, Fla., that was erroneously attributed to Chace (1972), but specimens in two lots from there questionably referred to this species by him are in the USNM along with others from Key West. Some of the Panama City specimens seem to have more slender posterior abdominal segments than the remainder of specimens in four lots, but with such meager material, range of variation cannot be assessed.

From an ovigerous female taken at the type-locality, Lebour (1949) maintained eggs until hatching and described the first larval stage.

Periclimenes longicaudatus (Stimpson)

Fig. 58

Urocaris longicaudata Stimpson 1860:39.—Hay and Shore 1918:394, pl. 27, fig. 7.

Periclimenes (*Periclimenes*) *longicaudatus*.—Holthuis 1951a:26, pl. 6, figs. a-m; pl. 8, fig. m.—Williams 1965:42, fig. 35.

Periclimenes longicaudatus.—Chace 1972:37.—Coelho and Ramos 1972:147.

Recognition characters.—Rostrum straight, short, reaching to end of second or third article of antennular peduncle; upper margin raised into high arcuate crest with 7 to 9 teeth, first 2 teeth behind orbit more widely spaced than distal teeth; lower margin with 1 or 2 small spines near tip. Carapace with lower angle of orbit produced into lobe con-

stricted at base; supraorbital and antennal spines absent; anterolateral angle rounded. Eyes well developed and elongate. Stylocerite well developed but not reaching to middle of basal antennular article; basal antennular article convex and ending in strong spine; upper antennular flagella with 2 rami fused for 4 to 8 joints. Antennal scale with outer margin slightly concave, ending in strong tooth exceeded distally by lamella; antennal peduncle reaching almost to middle of scale, with distinct outer spine near base of scale. All maxillipeds with well-developed exopods.

First legs slender, reaching almost to end of antennal scale; second legs equal in size and shape, stronger and longer than first legs.

Abdomen smooth; all pleura rounded. Third segment somewhat produced in middle of posterior margin. Sixth segment twice length of fifth and longer than telson. Telson with 2 pairs of dorsal spines both lying behind middle; posterior margin with 3 pairs of spinules.

Measurements in mm.—Length of body: male 17; ovigerous females 15 to 22.

Color.—Body transparent in life.

Habitat.—This species is found in abundance on submerged vegetation along with *Hippolyte* species and *Tozeuma carolinense*, on *Leptogorgia*, algae and *Sargassum*, among turtle grass and *Porites* (Chace 1972), or from sponges (Schmitt 1924b); however, it is hard to detect because of its almost perfect transparency. Surface to 27 m.

Type-locality.—Coast of Carolina.

Known range.—Cape Hatteras, N. C., to southwestern Florida; West Indies to São Paulo, Brazil. There are doubtful records from the Indian Ocean and deeper waters of the Gulf of Mexico (Holthuis 1951a).

Remarks.—This species is abundant in the Beaufort, N. C., area, and has been collected there throughout the year. Ovigerous females have been found from May through October. Rouse (1970) found this to be the most common caridean in southwestern Florida, next to *Tozeuma carolinense*; it occurred in a temperature range of 12° to 34°C, and salinities of 15 to 55‰. He found ovigerous females from September to April, but they were never common (see also Tabb and Manning 1961). They occur in Cuba in January and March (Schmitt 1924b) and in Texas in May. Pearse and Williams (1951) found the form on reefs off the North Carolina coast along with an unidentified *Periclimenes*. Last larval, postlarval, and early juvenile stages doubtfully assigned to this species were described by Gurney and Lebour (1941) from Bermuda.

Periclimenes longicaudatus is one of the decapods eaten by the spotted and southern hakes, *Urophycis*

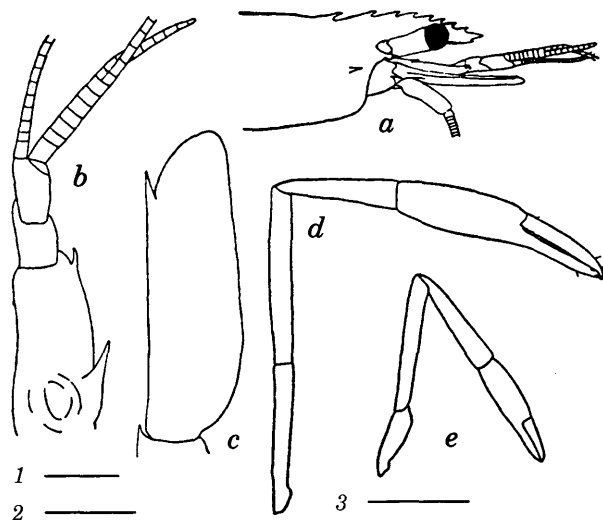


Fig. 58. *Periclimenes longicaudatus* (Stimpson). a, Anterior part of body in lateral view; b, antennule; c, antennal scale; d, first leg; e, second leg. Scales: 1(a) = 2 mm; 2(b-c) = 1 mm; 3(d-e) = 1 mm (from Holthuis 1951a).

regius and *floridanus*, in Georgia estuaries (Sikora, et al. 1972).

***Periclimenes pedersoni* Chace**

Fig. 59

Periclimenes (Periclimenes) pedersoni Chace 1958:125, figs. 1–17.—Limbaugh, Pederson, and Chace 1961:242, figs. 3–4.

Periclimenes pedersoni.—Chace 1972:38.

Recognition characters.—Carapace of male narrowed and bent upward in anterior $\frac{2}{3}$; rostrum directed obliquely upward, scarcely reaching base of cornea in adult; dorsal margin with 3–5 teeth, posterior tooth somewhat anterior to level of hepatic spine, next anterior tooth at about level of orbital margin; unarmed ventrally. Carapace of adult female not bent upward anteriorly; rostrum attenuate, nearly horizontal, reaching to or beyond second article of antennular peduncle; dorsal margin with 5–6 teeth, posterior tooth about at level of hepatic spine, next anterior tooth just behind orbital margin, remainder at decreasing intervals; 2–4 ventral teeth. Antennal spine small; lower antennal angle blunt and strongly produced. Eyes well developed, cornea subglobular. Stylocerite divergent, not reaching beyond middle of eyestalk; basal article of antennular peduncle slightly concave laterally, distolateral tooth not exceeding acutely produced anterior margin (except in juveniles); second article slightly shorter and broader than third; upper antennular flagellum with 2 rami fused for 12–18 joints, free part of shorter ramus $\frac{1}{4}$ – $\frac{1}{3}$ length of fused part. Antennal scale about as long as antennular peduncle; length over 2.5 times width in males, slightly broader in females, outer margin nearly straight and ending in spine far exceeded by variably subtruncate lamella; antennal peduncle reaching to or beyond middle of scale.

First legs slender, reaching beyond antennal scale by length of finger or entire hand in males, and by at least $\frac{1}{3}$ of carpus in females; fingers as long as palm, carpus longer than chela. Second legs unequal, especially in males. Larger overreaching antennal scale by chela and from $\frac{1}{3}$ to more than $\frac{2}{3}$ carpus, fingers about $\frac{2}{3}$ length of palm; dactyl triangular in cross section, cutting edge with 2–5, of fixed finger with 1–4 denticles in proximal half. Smaller overreaching antennal scale by chela or $\frac{1}{3}$ of carpus; fingers more than $\frac{3}{4}$ length of palm, cutting edges with fewer denticles.

Abdomen with pleura rounded; third segment strongly produced posteromesially into laterally compressed hump. Sixth segment of male nearly

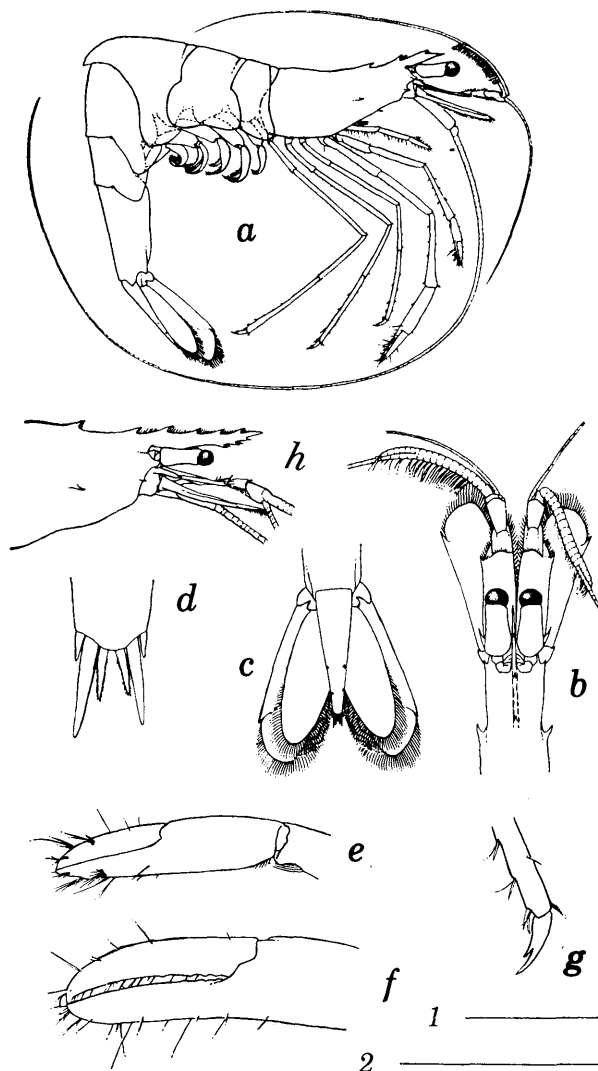


Fig. 59. *Periclimenes pedersoni* Chace. Male: *a*, lateral view; *b*, anterior part of body, dorsal; *c*, tail fan; *d*, tip of telson; *e*, chela of right first leg; *f*, fingers of right second leg; *g*, dactyl of right third leg. Female: *h*, anterior part of body in lateral view. Scales: 1(*a*, *h*)=5 mm, (*d*)=0.5 mm, (*e*–*g*)=1 mm; 2(*b*–*c*)=5 mm (from Chace 1958).

twice length of fifth and longer than telson; that of female usually less than twice length of fifth and shorter than telson. Telson with 2 dorsal and 3 posterior pairs of spinules, both dorsal pairs posterior to midlength.

Measurements in mm.—Length of carapace: male 4.6; female 6.5, may be ovigerous at 3.8 (Chace 1958).

Color.—Variable. Body transparent; longitudinal white line at each side running posteriorly from bases of third maxillipeds to converge dorsally near posterior margin of third abdominal segment. Back of abdomen between lines crowded with irregularly sized violet spots. Outside white lines on each side of posterior half of third segment, two or three

similar small spots of violet followed by large, triangular violet patch edged with white. Fourth and fifth segments each with usually two median spots, others laterally, and about four or five spots diverging posteriorly on either side of midline of sixth. Sometimes a white stripe in dorsal midline of sixth segment as well as near posterior part of preceding two segments. Telson with about three median spots, a transverse bar of violet and a white tip. Uropods tipped with blue violet outlined proximally and laterally with white, and few violet spots near bases. White line on ventral surface of body from base of walking legs to telson. Eyestalks transparent with purple and sometimes a white line below. Two small white dots on either side of rostrum. Outer antennular flagella white from base, inner transparent; antennal flagella mostly opaque white, transparent basally. Third maxillipeds and first and second legs banded with purple and white, brown saddle on inner surface at base of palm and on basal half of carpus. Walking legs translucent pale violet. A color variety off west Florida differs somewhat from Caribbean and Bahamian specimens. (Paraphrased from Chace 1958; Limbaugh, et al. 1961.)

Habitat.—Usually associated with the sea anemone *Bartholomea annulata*; North Carolina specimens taken in a trawl were entangled in an algal mat; seen walking about on coral reef, away from anemones in Belize (B. Kensley, personal communication); 1.5 to 35 m.

Type-locality.—Simms (Lyford) Cay, New Providence Island, Bahamas.

Known range.—East of Cape Lookout, N. C., 34°35.5'N, 75°05.5'W (Herbst, et al. 1979); off northwest Florida (?), Bahamas, through West Indies to Bonaire; Belize.

Remarks.—Limbaugh, et al. (1961) found this

species to be usually hanging from or occupying the same hole as the anemone *Bartholomea annulata*, frequently occurring singly, in pairs, or groups of up to five. The associations may last for a period of weeks. The Pederson shrimp is one of the cleaner shrimps, attracting its fish hosts by whipping its antennae and swaying back and forth. Limbaugh, et al. (1961) observed cleaning of 10 species of fishes. The shrimp crawls onto a fish as soon as it comes near and becomes quiet, picking at parasites, removing tissue around parasites, and picking at injured flesh around wounds; it enters the fish's gill cavity as well as the mouth, probably feeding there on bits of food clinging to the gills, but when it reaches satiety it ceases feeding and retires from the fish even though other fishes may remain to be cleaned. Juvenile arrow crabs, *Stenorhynchus seticornis*, a snapping shrimp and other commensals also are associated with this anemone.

Periclimenes pedersoni is very similar to *P. anthophilus* from Bermuda (Chace 1972) which is associated with other anemones. The North Carolina specimens seem closer to *P. pedersoni* although as Chace pointed out, the range of variation in the Bermuda species is not known. Limbaugh, et al. (1961) found *P. pedersoni* off west Florida that were not associated with anemones and that did not clean fishes; these were morphologically similar to West Indian material but slightly different in color.

Ovigerous females of the species are known in March-April from the Virgin Islands, May in Bonaire, and July to September off northwestern Florida.

Genus *Pontonia* Latreille 1829

Holthuis, 1951a:115.—Hemming 1958b:124.

Key to Species

1. Dorsal spines of telson small and rather inconspicuous *P. domestica*
Dorsal spines of telson well developed *P. margarita*

Pontonia domestica Gibbes

Fig. 60

Pontonia domestica Gibbes 1850:196.—Holthuis 1951a:122, pl. 38, figs. a-j.—Williams 1965:47, fig. 39.—Chace 1972:39.

Recognition characters.—Rostrum depressed, rather narrowly triangular, decurved; reaching to second article of antennular peduncle; tip acute in dorsal and lateral view, flat dorsally; inconspicuous lon-

gitudinal carina ventrally; inconspicuous dorsal and ventral tooth near tip with tuft of long hairs between upper tooth and apex. Carapace with lower orbital angle bluntly triangular, strong antennal spine below angle; anterolateral angle broadly rounded and anteriorly produced. Eyes well developed, not reaching laterally to antennal spine. Antennular peduncle with stylocerite broad, bluntly pointed; anterolateral angle of basal article produced forward, rounded; third article longer than second; upper antennular flagellum with 7–10 fused

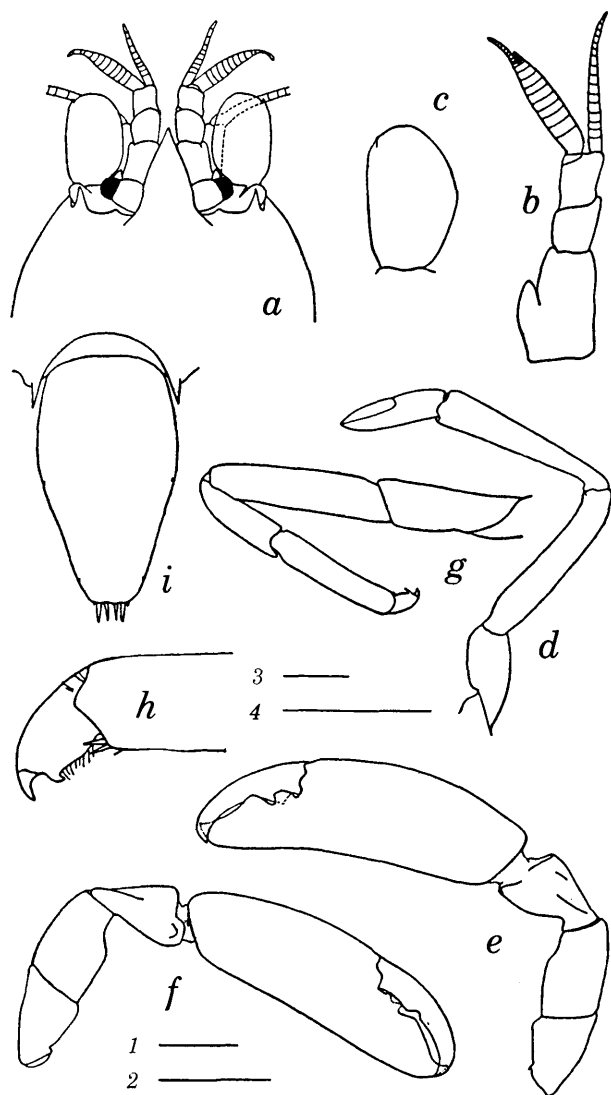


Fig. 60. *Pontonia domestica* Gibbes. a, Anterior part of body in dorsal view; b, antennule; c, antennal scale; d, first leg; e, larger second leg; f, smaller second leg; g, third leg; h, dactyl of third leg; i, telson in dorsal view. Scales: 1(a, d, g)=2 mm, (e-f)=4 mm; 2(b-c)=2 mm; 3(i)=1 mm; 4(h)=1 mm (from Holthuis 1951a).

joints; short ramus with 2-3 joints. Antennal scale broadly oval, outer margin a little convex, terminal tooth small, exceeded by lamella; antennal peduncle reaching beyond middle of scale.

First leg with carpus and chela reaching beyond antennal scale; fingers of chela somewhat longer than palm; carpus as long as merus. Second legs strong, unequal in size and shape; carpus and chela reaching beyond antennal scale. On one leg, fingers about half length of palm; fixed finger somewhat higher than dactyl and bearing 2 large teeth on cutting edge, posterior tooth truncate with crenulate margin; dactyl with 1 tooth, palm with upper and lower margin somewhat compressed,

surface appearing minutely roughened under magnification; carpus short, conical, with depression above and knob below; merus a little longer than carpus. Other second leg much as above but with relatively longer fingers; fixed finger higher in comparison to dactyl; teeth smaller and carpus more slender. Remaining legs with bifurcate dactyls.

Abdomen with first 5 pleura broadly rounded. Sixth segment with pleura and posterolateral angle ending in slender, sharp spines; slightly longer than fifth segment. Telson half again as long as fifth segment; 2 dorsal pairs of spines on lateral margin of telson small, almost invisible; anterior pair about in middle; posterior pair closer to posterior border than to anterior pair; posterior border with 3 pairs of spines in row; inner 2 pairs equal in length, outer pair smaller; uropods broadly ovate, outer margin of exopod ending in blunt angle with small movable spine at tip.

Measurements in mm.—Length of body: male 32; female 33.

Color.—Translucent white.

Habitat.—The species lives commensally in lamellibranch molluscs in coastal waters and has been recorded from *Atrina seminuda*, *A. serrata*, and *Pecten* sp. (Holthuis 1951a), and on 12 April 1971 was taken from the giant Atlantic cockle, *Dinocardium robustum*, off Carteret County, N. C.; shallow water to 42 m.

Type-locality.—South Carolina.

Known range.—Atlantic Beach near Beaufort Inlet, N. C., to Gulf of Mexico S of Houma, Terrebonne Parish, La. (USNM); Bahamas; Madeira.

Remarks.—Brooks and Herrick (1892) illustrated a section through the segmenting egg of *Pontonia domestica* on plate 28.

Pontonia margarita Smith

Fig. 61

Pontonia margarita Smith 1869c:245.—Holthuis 1951a:137, pl. 43, figs. a-i; pl. 44, figs. a-h.—Williams 1965:48, fig. 40.—Chace 1972:39.

Recognition characters—Rostrum depressed and decurved, dorsally flat and triangular; tip reaching to end of basal article of antennular peduncle or slightly beyond; inconspicuous dorsal and ventral tooth near tip with small tuft of hairs between upper tooth and apex; longitudinal median carina ventrally. Carapace smooth; with strong antennal spine located well below narrowly rounded lower orbital angle; anterolateral angle broadly rounded and anteriorly produced. Eyes somewhat larger than in *P. domestica*, reaching laterally beyond antennal

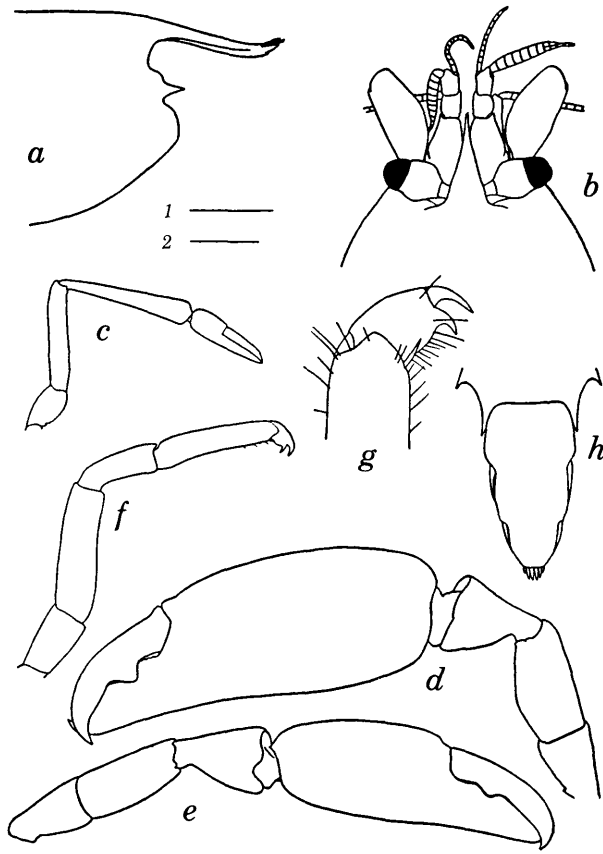


Fig. 61. *Pontonia margarita* Smith. a, Anterior part of carapace in lateral view; b, anterior part of body in dorsal view; c, first leg; d, larger second leg; e, smaller second leg; f, third leg; g, dactyl of third leg; h, telson in dorsal view. Scales: 1(a-b, h) = 1 mm, (c-e) = 2 mm, (g) = 0.17 mm; 2(f) = 1 mm (from Holthuis 1951a).

spine. Basal article of antennular peduncle with blunt-pointed stylocerite more or less pressed against outer border; anterolateral angle of article produced forward, rounded; upper antennular flagellum short, thick, curved backward; fused part with 6-7 joints; short ramus with 2 joints. Antennal scale with convex outer margin ending in small inwardly curved distal tooth, lamella far exceeding tooth.

First leg with half or more than half of carpus reaching beyond antennal scale; fingers longer than palm, unarmed carpus longer than merus. Second legs unequal in size but similar in shape. Larger leg with fingers a little over half length of palm; palm twice as long as deep, somewhat inflated; dactyl narrower than fixed finger and bearing large tooth slightly behind middle; cutting edge of fixed finger with 2 large teeth fitting on each side of opposed dactylar tooth and separated by hole on inner side of edge, posterior tooth with denticles at apex; carpus shorter than merus, conical. Smaller second leg resembling larger except for relatively

longer fingers. Dactyls of last 3 walking legs bifurcate.

Abdomen with pleura of first 5 segments broadly rounded, of sixth ending in strong spine overlapping base of uropods. Sixth segment a little more than half length of telson. Telson with pair of large dorsal spines placed laterally at $\frac{1}{3}$ and $\frac{2}{3}$ of length; posterior border with 3 pairs of spines in row, inner 2 pairs equal, outer pair smaller. Uropods broadly ovate, exopods ending in minute movable spine on outer margin.

Measurements in mm.—Length of body: male 19; ovigerous females 17 to 27.

Color.—Glassy, translucent; internal organs clearly visible; ovigerous females with two colors of eggs, one with light, muddy green eggs and ovarian ova of same color, another with pale orange eggs (from specimens taken in *Argopecten gibbus* and *Pteria colymbus* in North Carolina), and in the pearl oyster *Pinctada fimbriata* on the west American coast; tidal flats to 60 m.

Type-locality.—Bay of Panama.

Known range.—Atlantic coast: Drum Inlet to Beaufort Inlet, N. C.; east and west Florida. Pacific coast: Gulf of California to Colombia; Galapagos Islands.

Remarks.—Ovigerous females have been taken in North Carolina in January and April.

Family Gnathophyllidae

Caridea with first 2 pairs of legs chelate, first pair smaller than second; carpus of second pair not subdivided. Rostrum short and toothed. Third article of third maxillipeds very broad. Mandibles simple. Second maxillipeds with short seventh article.

Genus *Gnathophyllum* Latreille 1819

Armstrong 1940:6.—Hemming 1958b:156.

Gnathophyllum modestum Hay

Fig. 62

Gnathophyllum modestum Hay 1917:72.—Hay and Shore 1918:395, pl. 28, fig. 1.—Manning 1963:48, figs. 1-2.—Williams 1965:61, fig. 50.—Chace 1972:53.

Recognition characters.—Body short and thick; carapace with moderate carina continuous in front with rostrum and extending about $\frac{2}{3}$ distance to posterior margin. Rostrum obliquely truncate dorsally and armed with 5-6 dorsal teeth; 1-2 small

ventral teeth near tip; tip reaching to distal end of basal article of antennule. Suborbital angle prominent; antennal spine present; anterolateral angle strongly produced. Eyes rather large and with prominent, conical, black protuberance on cornea. Antennular peduncles with basal article large, stylocerite reaching beyond middle of article, spine at anterolateral corner of article; second article with similar but smaller and blunter anterolateral spine; second and third articles of about equal length; outer antennular flagellum bifurcate, upper ramus longer and thinner than lower ramus. Antennal scale reaching beyond antennular peduncles, lateral margin almost straight, terminating in spine; lamella of scale rounded distally, slightly exceeding spine.

Third maxillipeds with merus and carpus broad, closing whole front of buccal region; 2 terminal articles flattened, much more slender, and extended straight forward. Second pair of legs much stronger than first, exceeding rostrum by length of chela; fingers more than half length of palm. Last 3 pairs of legs with dactyls bifurcate.

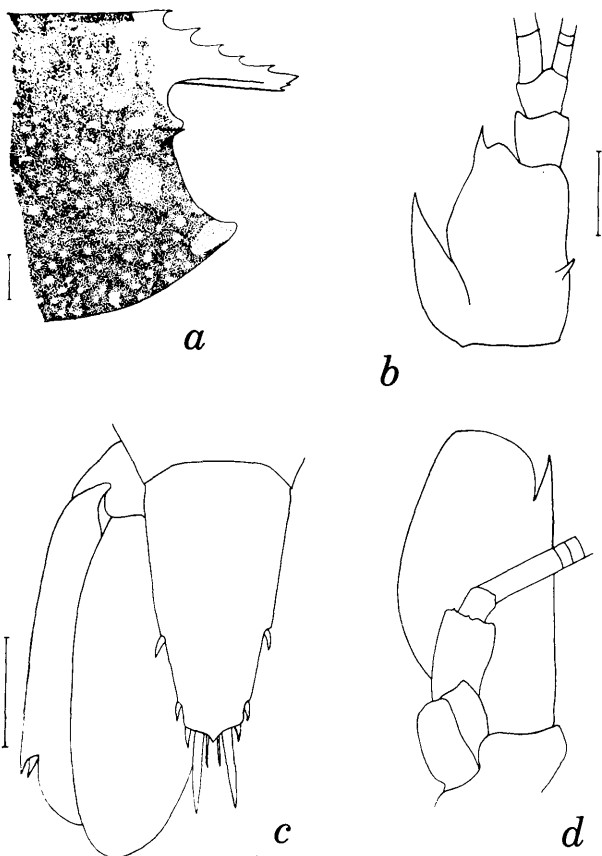


Fig. 62. *Gnathophyllum modestum* Hay. a, Anterior part of carapace in lateral view; b, antennular peduncle in ventral view; c, telson and left uropod; d, antennal scale; 1 mm indicated; b, d to same scale (from Manning 1963).

Abdomen with last 3 segments abruptly smaller than preceding segments and strongly flexed. Telson with pair of marginal spines at about distal third and minute pair near tip, tip with median point and with 3 pairs of spines, intermediate pair longest.

Measurements in mm.—Length of ovigerous holotypic female 21.

Color.—Body deep brown with many scattered small yellow and a few larger orange spots; antennal scale, distal portions of rostrum and tail fan clear; orbital margins and eyestalks white; legs grading from brown proximally through purple to white distally but barred with purple on distal portion of some elements; markings of yellow below and on some articles of appendages (Manning 1963).

Habitat.—Found around clumps of coral and sponges in shallow water; to 27 m.

Type-locality.—20 miles SW Beaufort, N. C.

Known range.—Off Beaufort, N. C.; Biscayne Bay, Fla.

Remarks.—This species, long known only from Hay's ovigerous female type-specimen, was reported from Florida by Manning (1963). Manning reviewed the east American species of *Gnathophyllum*, pointing out the close similarity of *G. modestum* to the eastern Atlantic species *G. elegans*, and giving detail on the importance of color patterns in living material as diagnostic characters in the genus. Excellent figures accompany Manning's discussion.

Ovigerous females are known from Florida in June, and North Carolina in August.

Superfamily Alpheoidea

Family Alpheidae

Carapace smooth, with cardiac grooves; rostrum reduced; antennal and branchiostegal spines always absent; carapace almost always projecting over eyes (*Automate* excepted). Antennular base cylindrical, basal article not longer than sum of other 2 articles. Antennal scale rarely longer than antennal peduncle. Mandible bipartite with palp of 2 points. Chela of first leg predominant, always large (usually asymmetrical); carpus short. Second legs weakly developed; carpus multiarticulate. Third to fifth leg with spinous propodi and simple or bifurcate dactyls; propodus of fifth leg with more or less well-developed brush of bristles in transverse to oblique rows. Abdomen usually with gradual curve, no pronounced bend at third segment; sixth segment short, broad, sexually dimorphic. (Adapted from Banner 1953.)

Key to Genera and One Species

1. Movable plate at posterolateral angle of sixth abdominal segment; carapace extended to cover eyes but rostrum absent *Leptalpheus forceps*
No movable plate at posterolateral angle of sixth abdominal segment 2
2. Eyestalks completely exposed *Automate*
Eyestalks covered by carapace 3
3. Epipods present on at least first 2 pairs of legs *Alpheus*
Legs without epipods *Synalpheus*

Genus *Alpheus* Fabricius 1798

Banner 1953:46.—Hemming 1958b:108.

The status of the name *Alpheus* has been stabilized by the International Commission on Zoolog-

ical Nomenclature (Opinion 334). The suppressed generic names *Alpheus* Weber 1795, and *Crangon* Weber 1795 were placed on the Official Index of Rejected and Invalid Generic Names in Zoology (Hemming 1958a).

Key to Species

1. Orbital hoods of carapace with small supramarginal spine in front *A. formosus*
Orbital hoods of carapace without distinct spine 2
2. Orbital hoods forming anterior toothlike marginal projection; large chela with groove above and below along outer margin, between these grooves a thick tooth *A. normanni*
Orbital hoods rounded anteriorly; large chela broad, notched on both margins 3
3. Base of rostrum passing gradually into dorsolateral surface of carapace; merus of first legs unarmed distoventrally *A. heterochaelis*
Base of rostrum usually with borders sharply defined; merus of first legs armed with distoventral spine *A. armillatus*

***Alpheus armillatus* H. Milne Edwards**

(Banded snapping shrimp)

Fig. 63

Alpheus armillatus H. Milne Edwards 1837:354.—Verrill 1922:73, text-figs. 5a, 6b; pl. 20, fig. 4b; pl. 21, figs. 4, 4a; pl. 26, figs. 1–1d; pl. 23, fig. 4; pl. 27, figs. 1–1s.—Williams 1965:67, fig. 55.—Chace 1972:63.

Crangon armillatus.—Hay and Shore 1918:386, text-fig. 9; pl. 27, fig. 1.—Schmitt 1935a:142.

Recognition characters.—Rostrum in form of narrow raised crest from base to tip, projecting beyond orbital hoods, widening abruptly just behind eyes into triangular area with borders slightly concave and distinctly limiting rostro-orbital depressions, slightly overhanging depressions in adults. Carapace compressed; orbital hoods prominent in front, with slight obtuse anterior lobe but without spine or denticle, and with strong emargination below eyes. Eyes entirely covered by carapace. An-

tennules with stylocerite large, scalelike, not very acute, and not reaching to end of basal antennular article; second article longer than third; inner flagellum filiform; outer flagellum thickened in about proximal half. Antennal scale with strong terminal spine equal to or extending beyond antennal peduncle, scale distinctly curved outward in distal $\frac{2}{3}$; a small spine (basicerite) near base of scale. Third maxilliped covered with long hairs distally, reaching about to end of antennal peduncle.

First legs strongly chelate, hairy, unequal; merus armed distoventrally. Larger chela thick; outer and inner margin deeply notched near base of finger; upper and lower surfaces with irregular shallow grooves; dactyl broad, heavy, curved, with large basal tooth. Small chela slender; cutting edges of fingers closely fitting, dactyl with small tooth at base, dactyl in males lacking setose crests and expanded external surface characteristic of *A. heterochaelis*. Second legs long, slender, weakly chelate, with part of merus reaching beyond rostrum; carpus subdivided with joints diminishing in length as follows (numbered from proximal end): 1, 2, 5, 3–4. Third to fifth legs with simple dactyls, not subspsatulate.

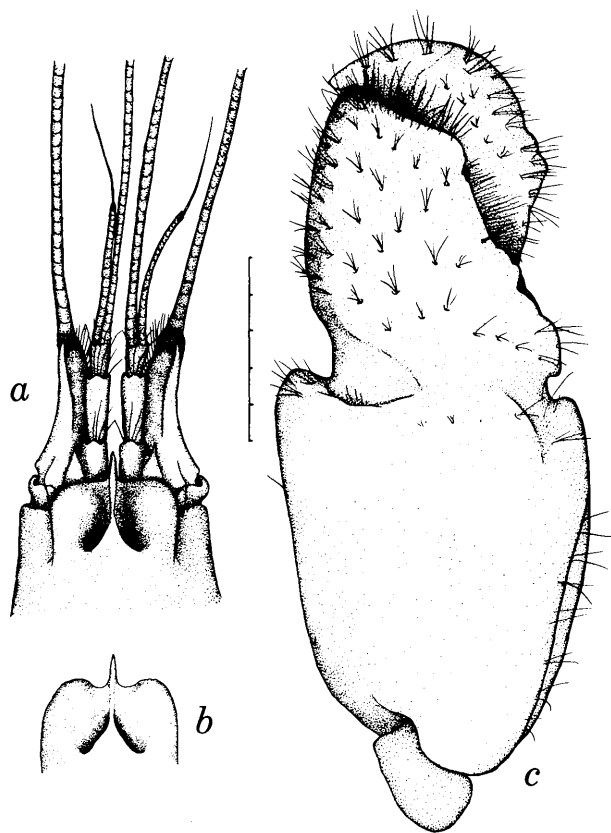


Fig. 63. *Alpheus armillatus* H. Milne Edwards. *a*, Anterior region in dorsal view; *b*, rostral region in dorsal view; *c*, large chela in dorsal view; 5 mm indicated (from Williams 1965).

Abdomen smooth, compressed. Telson with 2 pairs of dorsal spines, first pair at $\frac{1}{3}$, second at $\frac{2}{3}$ length; sides somewhat convergent distally, tip rounded, with pair of spines at each posterolateral corner, mesial spine twice length of outer spine. Uropodal exopod with outer margin ending in small spine flanked mesially by larger spine.

Measurements in mm.—Length of body: male 43; female 45 (Hazlett and Winn 1962).

Color.—Body with dark gray or brown ground color, crossed by 9 conspicuous lunate or elliptical spots or bands of translucent white equal in width to intervening dark bands; carapace with 3 white bands, third one at posterior margin; abdomen with 6 bands, first blending with last on carapace; abdomen often dark green with spots bordered by line of orange; uropods and telson usually with broad crossband and sometimes tipped with orange; chelae thickly speckled with dark gray, whitish bands above, tipped with pale pink or white; antennal peduncles grayish, flagella and walking legs orange yellow banded with white (Verrill 1922).

Hendrix (1971) stated that two other color phases have been recorded from Florida, a blue-gray color similar to that of *A. heterochaelis*, and a straw-yellow

pattern. Male and female pairs in the same burrow are always of matched color, suggesting that sympatric species may be involved.

Habitat.—Under rocks and shells or in holes in rocks; turtle grass; shallow water to 14 m (Felder and Chaney 1979).

Known range.—North Carolina, through Gulf of Mexico and West Indies to Cananéia, São Paulo, Brazil; Bermuda (Holthuis 1956).

Remarks.—This species closely resembles *A. heterochaelis*, its similar-sized and (in the Carolinas) much more abundant congener. *Alpheus armillatus* is named for its conspicuously banded body, but in preserved material it can usually be distinguished from similar species by the distinctive form of the rostrum, and from *A. heterochaelis* males by the lack of a specialized dactyl on the small first chela and by presence of a distoventral spine on the merus of the first legs.

The species is rarely taken in the Beaufort region of North Carolina. Hay and Shore (1918) found males and females living in pairs under rocks at Fort Macon. Ovigerous females are known more or less year round in Florida and Caribbean parts of the range; June in Brazil, and August in Bermuda (USNM).

Coonfield (1940) observed the chromatophore system of this shrimp in one of the early studies of this kind, showing that it reacts to different backgrounds under varying light conditions.

Hess (1940, 1941) demonstrated that *A. armillatus* is sensitive to light in many regions of the body, regardless of the amount of time elapsed since the preceding molt. At Tortugas, he found diurnal molting apparently controlled by daily temperature changes, molting occurring when the temperature rises to or above 29°C. Animals in constant temperature failed to exhibit diurnal molting as did ovigerous females.

Darby (1934) studied regeneration of chelae in *A. armillatus* and *Synalpheus longicarpus*, together with determination of right or left handedness. He found that in development of chelae a stage was reached that permitted determination of which side would have a large chela. Equal chelae were produced experimentally and were of three varieties: (1) both small (pinch claws); (2) both large (snap claws); and (3) both intermediate.

Darby offered a hypothesis, involving two substances and a metabolic condition, which could explain the regenerative phenomena in these and allied crustaceans. In such animals, a substance A is produced which controls production of pinch claws; but at certain stages in the intermolt cycle a substance B is produced, for a limited time, and concentrated in whichever claw is regenerating or al-

ready modified as a snap claw. This circumstance will produce or reinforce production of a snap claw. Chance alone is responsible for whether a snap claw will be on one side or the other, or whether the animal will be symmetrical. Also, time at which regeneration occurs depends on chance.

Identity of the experimental animals reported by Darby is open to some question because Armstrong (1949) ascribed some of Darby's specimens to his newly described *A. viridari*. Presently, there are four lots of Darby's material in the USNM collection identified as *A. armillatus*; two contain adults (28 in all); one lot of larvae is unidentifiable; and one lot of three specimens could not be found in 1980. Therefore, at least some of Darby's material was correctly identified. *Alpheus armillatus* and *A. viridari* occur together in hollowed decayed roots among old mangroves in Belize (B. Kensley, personal communication).

Hazlett and Winn (1962) found that no single part of the major chela fingers is involved in sound production. Whole fingers produced loud sound, but ablation of various parts weakened sound. They considered sound to be used in territorial behavior, as have students of behavior in other alpheids. Actual fighting occurred only when the home of a shrimp was invaded. A male 35 mm long took possession of a glass tube from a 30-mm male after a short fight. Then a 43-mm female was introduced and after some movement and snaps, the two occupied the glass tube together. When a second female 45 mm long was introduced, the first female came out of the tube and after an intense fight retained possession of the tube. The male took no part in this combat and showed no behavior when the 43-mm female returned to the tube. When a *Synalpheus* was introduced to an *Alpheus*, aggression-retreat behavior resulted in *Synalpheus* often backing down the *Alpheus* which was larger.

Sikora, et al. (1972) recorded *A. armillatus* as food of two species of hake in Georgia estuaries.

Pearse (1932b) reported encysted larvae of *Rhyncobothrius* in viscera of *A. armillatus*.

Alpheus formosus Gibbes

(Striped snapping shrimp)

Fig. 64

Alpheus formosus Gibbes 1850:196.—Verrill 1922:84, text-figs. 5d, 6a; pl. 20, fig. 3; pl. 23, figs. 5a, b; pl. 29, figs. 4, a-u; pl. 25, figs. 6-6a.—Williams 1965:64, fig. 52.—Chace 1972:67.—Christoffersen 1979:314.

Crangon formosus.—Hay and Shore 1918:384, pl. 26, fig. 5.—Schmitt 1935a:144.

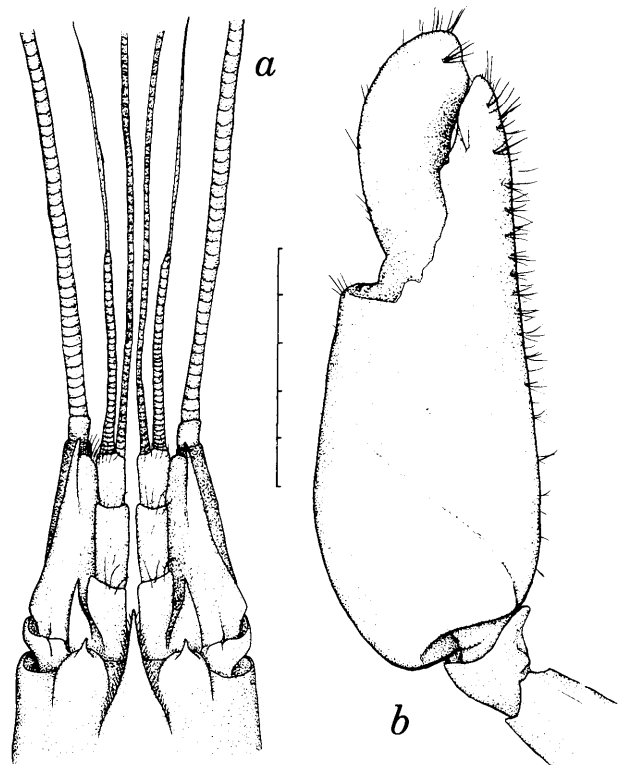


Fig. 64. *Alpheus formosus* Gibbes. a, Anterior region in dorsal view; b, outer surface of large chela; 5 mm indicated (from Williams 1965).

Recognition characters.—Rostrum beginning at posterior line of eyes and reaching about to second article of antennular peduncle; flat above; margins concave at base but regularly convergent anteriorly and with scattered stiff hairs; tip rounded, often bearing 2 or 3 minute spines. Carapace half length of abdomen, compressed, not grooved; orbital hoods each with acute, anteriorly directed spine much shorter than rostrum. Eyes completely covered by carapace. Antennular peduncles with scalelike stylocerite, slender tip reaching slightly beyond basal article; second article twice length of third; inner flagellum filiform, outer flagellum thick proximally, filiform distally. Antenna longer than body; antennal scale with strong apical spine reaching to or beyond tip of antennular peduncle; spine separated from and exceeding lamella; weak spine (basicerite) below near base of scale. Third maxillipeds with terminal article hairy; slightly exceeding antennal peduncle.

First legs strongly chelate, very unequal. Larger leg compressed, smooth above and unnotched along margins; fixed finger acute, incurved at tip, shorter than stout, gradually arched, blunt dactyl; carpus short, convex above, with distal tooth; merus with acute distal spine. Smaller chela much more slender, long and smooth, inner surface with stout spine

overhanging base of dactyl; fixed finger nearly straight, slender, somewhat turned up near tip; dactyl about half length of hand, nearly straight to about middle, then gently arched to tip, hairs arising from nearly straight groove below ridge on both sides; inner surfaces of fingers with slender groove and carina; fingers meeting closely. Second pair of legs slender; weakly chelate; carpus subdivided, with joints diminishing in length as follows (numbered from proximal end): 1, 5, 2, 3-4. Third to fifth legs with simple dactyls.

Telson with 2 pairs of dorsal spines at about $\frac{1}{3}$ and $\frac{2}{3}$ length; posterolateral corners with pair of spines, mesial spine much longer than lateral, distal margin with long hairs. Uropodal exopods with lateral margin ending in black movable spine between 2 fixed spines; black spine remaining amber colored after long preservation.

Measurements in mm.—Length of body: male 40; ovigerous females 17 to 35.

Color.—Color pattern conspicuous and characteristic; ground color yellowish or greenish brown finely speckled with orange; narrow light stripe along middorsal line extending from distal end of antennular peduncle to base of telson, line light orange anteriorly merging into yellowish green and finally gray posteriorly; brown stripe on each side dorsolaterally and below this another stripe of white, or colors similar to dorsal stripe, along each side followed by stripe of light reddish brown and still another stripe of blue bordering abdomen; chelae greenish brown with orange red fingers; antennules, antennae, and walking legs blue; telson and uropods white at base blotched and bordered with yellow.

Habitat.—Chace (1972) recorded the species from "sand, mud flats with and without *Pocillopora* and *Porites*, rock-studded beaches, seawalls, wrecks, and exposed and submerged reefs from above low-tide" to 42 m.

Type-locality.—Key West, Fla.

Known range.—Near Beaufort, N. C., through Gulf of Mexico (Ray 1974; Felder and Chaney 1979) and West Indies to São Paulo, Brazil; Bermuda.

Remarks.—Ovigerous females are documented from January through July in the Bermuda-Venezuela region, and Gore, et al. (1978) stated that the breeding season on sabellariid reefs along east Florida is January-July. They are known from June to January from São Paulo to Bahia, Brazil (Christoffersen 1979), and Bimini in October; Hendrix (1972) stated that they have been collected in all months of the year.

Manter (1933) found metacercariae of *Helicometrina nimia* encysted in muscles of *A. formosus* at Tortugas.

Alpheus heterochaelis Say

(Big-clawed snapping shrimp)

Fig. 65

Alpheus heterochaelis Say 1818:243.—Verrill 1922:76, pl. 22, figs. 1, 2, 4a-c; pl. 24, figs. 7, 7a; pl. 30, figs. 1-1a, lt, 2a-2e; pl. 33, figs. 1, 2.—Holthuis 1959:102.—Williams 1965:66, fig. 54.—Chace 1972:67.—Coelho and Ramos 1972:148.

Crangon heterochaelis.—Hay and Shore 1918:386, text-fig. 8, pl. 26, fig. 6.—Schmitt 1935a:144.

Recognition characters.—Rostrum carinate, extending back about as far as base of eyestalks; tip not reaching to base of second article of antennular peduncle. Carapace more than half length of abdomen, somewhat compressed; without grooves; front produced into rounded ocular hood over each eye; rostro-orbital depressions passing gradually into dorsal surface; emarginate below eye on anterior border. Eyes relatively small, covered by carapace. Antennular peduncles with scalelike stylocerite, minute spine at tip not reaching end of basal article; second article twice length of third; inner flagellum filiform, about half length of antenna; outer flagellum with proximal $\frac{2}{3}$ thickened. Antennae a little longer than body; antennal scale with strong apical spine reaching slightly beyond antennular peduncle, spine separated from and slightly

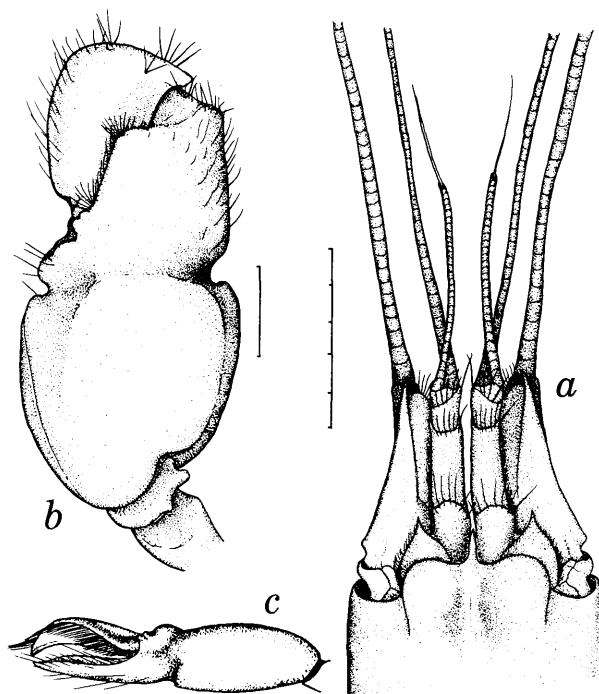


Fig. 65. *Alpheus heterochaelis* Say. a, Anterior region in dorsal view; b, large chela in dorsal view; c, small chela of male (after Verrill 1922); a-b, 5 mm indicated (from Williams 1965).

exceeding lamella; weak spine (basicerite) below near base of scale. Third maxillipeds with terminal article hairy; slightly exceeding antennal peduncle.

First legs strongly chelate, very unequal; merus unarmed distoventrally. Larger chela thick; outer and inner margins deeply notched near base of fingers; upper and lower surfaces with irregular shallow grooves; dactyl broad, heavy, strongly curved, with large basal tooth. Small chela sexually dimorphic; in male broad, elongate; proximal dorsal area of palm bounded by an impressed line, upper margin notched distally; dactyl flattened and expanded on outer surface; opposed edges of fingers keeled, closely fitting, fringed by dense hairs. Fingers of small chela in both sexes weaker, less curved, and more hairy than in large chela; carpus short; merus smooth. Second legs slender, weakly chelate; carpus subdivided with joints diminishing in length as follows (numbered from proximal end): 1, 2, 5, 4, 3. Third to fifth legs with lateral movable spine on ischium, dactyls usually subspatulate.

Abdomen compressed, smooth, tapering. Telson with subparallel sides and rounded tip; dorsal surface with 2 pairs of movable spines, first pair at about midlength, second at a little less than $\frac{3}{4}$ length; pair of spines at each posterolateral corner, mesial spine longest; distal margin heavily setose; pair of anal tubercles beneath with accompanying cups on uropods forming locking devices. Uropodal exopods with lateral border ending in fixed spine flanked mesially by longer movable spine.

Measurements in mm.—Length of body: male 40; ovigerous female 54.

Color.—Dark translucent green, slightly flushed with purple on sides of carapace; white markings on chelipeds; walking legs pale red; tips of uropods blue with narrow border of orange on distal margin; outer blade with patch of red just above blue, and a narrow white border; articular surfaces and joints of abdominal segments, and a small streak along cervical groove, white.

Habitat.—Lives among broken shells and stones or in burrows in mud, often among shells; water's edge to 30 m; common in lakes and canals of Everglades National Park, Fla., in salinity of 2‰ (Hendrix 1971).

Type-locality.—Amelia Island, Nassau County, Fla.

Known range.—Lower Chesapeake Bay (Van Engel and Sandifer 1972) to Aransas County, Tex.; Cuba; Curaçao; Surinam (Chace 1972); Bermuda. Other authors have listed the range as extending to São Paulo, Brazil.

Remarks.—This is the largest snapping shrimp found in the Carolinas. It is nearly as abundant as *A. normanni*. Brooks and Herrick (1892) gave a good

colored figure of *A. heterochaelis* (plate 2), as well as a series of figures of segmenting eggs and developing larval stages, but the latter are confusing because the authors skipped or overlooked larval stages and confused these with early postlarvae (Knowlton 1973b).

Ovigerous females have been taken through much of the annual cycle in various localities: February and April in Surinam (Holthuis 1959); March to October in the Gulf of Mexico; at least June to November in North Carolina; October to January in Cuba, Puerto Rico, and Bonaire; also March, July and August, if Brazilian specimens are included (Ramos 1971).

Knowlton reared the larvae of *A. heterochaelis* in laboratory cultures maintained at 24.6°–27.6°C in salinities of 31–36‰, describing an abbreviated development through three stages, postlarvae, and juveniles. Eggs of females from near Beaufort, N. C., hatched in 27 days at 25°C, usually between 8:00 p. m. and 2:00 a. m. Larvae passed through Stage I usually within 6 h, but sometimes skipped this stage, hatching at Stage II. Stage II was almost always completed in a day, and Stage III lasted 2.5–3 days at 25°C. Postlarvae usually molted to juveniles 3–3.5 days following metamorphosis, usually between 5:00 and 9:00 a. m. Two-week-old young are 5 mm long; Brooks (1892) illustrated this stage (pl. 17, fig. 3). At one month the first walking legs are stouter than the second pair, and asymmetry of the first legs is first noticeable at two months (~7 mm length). Sandifer (1973d) found Stage II and III larvae attributed to this species in lower Chesapeake Bay rarely during July and August.

Larvae swim dorsal side down, horizontally or at an angle, and are positively phototropic. Postlarvae and juveniles are nearly always benthonic. The larvae apparently feed somewhat on detritus despite their containing an amount of yolk sufficient to sustain them through metamorphosis. Postlarvae and juveniles fed actively on *Artemia* in experiments (Knowlton 1973b).

The full geographic range of this species is in doubt because identity has not been fixed with certainty (Chace 1972). Knowlton, in his comprehensive review, pointed out that specimens from North Carolina with large eggs produce larvae with abbreviated development (rare in the Alpheidae), whereas some specimens from Florida identified as *A. heterochaelis* had smaller eggs and normal extended larval development. He noted that there were minute differences between these forms in adult morphology, indicating that two or more species were being treated as one.

Abundant in a Florida mangrove-*Juncus* system (salinities 1–27.5‰) (Odum and Heald 1972), *A.*

heterochaelis is preyed upon by several species of fishes (see also Heard 1970, white catfish; Sikora, et al. 1972, hakes). Shrimp stomachs contained particles ranging up to 400 μm in diameter; contents of vascular plant detritus, inorganic particles, harpacticoid copepods, amphipods, and unrecognizable material, indicating omnivorous feeding which was observed mainly at night.

Snapping sounds produced by the large chela in shrimps of the genera *Alpheus* and *Synalpheus* have been the subject of a number of papers reviewed by Knowlton and Moulton (1963). Snap audibility is positively correlated with body size (Schein 1975), and is relatively louder in *Alpheus* than in *Synalpheus*; moreover, a large population of snapping shrimp in water 1–6 m deep can produce a continuous crackling sound resembling the fine sizzle of sparks drawn from an electrostatic generator, a sound clearly audible through the bottom of an anchored skiff (see also Knowlton and Moulton 1963:311). Each snap is caused by the sudden impact of the hardened major finger tips coming rapidly together. Structural detail of fingers differs among alpheid genera. Cocking devices that hold the dactyl open until overcome by great muscular contraction of its adductor would seem to increase the sound produced, and Ritzmann (1973) showed by experiment with *A. californiensis* that a pair of smooth discs at the base of the dactyl and adjacent distal margin of palm are temporarily held together by cohesive forces of water until overcome by this contraction. Matched protuberances on propodus and dactyl of *Synalpheus* may serve the same function (Knowlton and Moulton 1963).

Male *A. heterochaelis* collected near Beaufort, N. C., have proportionately larger major chelae than females, although females tend to have longer bodies than males (Schein 1975). In Y-maze tests, males tend to seek females by chemical clues. Stimulus intensity offers potential clues to size of another individual. The snaps signal presence of an alpheid, identify the genus, and indicate size and location of the snapping animal (Schein 1977). Initial contacts between wandering males and unpaired females in burrows elicit snap-threats and possibly other behavior related to "fight winability"; in the case of heterosexual contact, the encounter leads to suppressed aggression with possibility of burrow sharing and mating. Schein discussed other behavioral aspects as did Nolan and Salmon (1970) in great detail.

Laboratory experiments show that after removal of the large chela or immobilization of its dactyl, *A. heterochelis* can not compete successfully with normal shrimp in acquiring or holding a shelter (Conover and Miller 1978); evidently action of the

dactyl plays a primary role in successful defense of a shelter. Shrimp lacking the large chela often were allowed to encroach beneath shelters by their like-sexed competitors, suggesting that structure of the chela itself and not its movements elicit aggressive behavior by competitors.

Alpheus normanni Kingsley

(Green snapping shrimp)

Fig. 66

Alpheus affinis Kingsley 1878a:195 (not *A. affinis* Guise 1854: 275–280).

Alpheus normanni Kingsley 1878b:93.—Williams 1965:65, fig. 53.—Chace 1972:68.—Christoffersen 1979:322.

Alpheus packardii Kingsley 1880:417.—Verrill 1922:80, pl. 20, figs. 2, 5; pl. 21, fig. 5; pl. 22, fig. 7; pl. 23, figs. 6, c-d; pl. 25, figs. 4, 4a; pl. 31, figs. 1, b-l, 2, b-u, 3, u, t.

Crangon packardii.—Hay and Shore 1918:385, pl. 26, fig. 4.—Schmitt 1935a:144.

Crangon normanni.—Chace 1937:122.

Recognition characters.—Rostrum with carina extending as far back as base of eyestalks, spiniform tip not reaching to base of second peduncular article of antennule. Carapace about $\frac{2}{3}$ length of abdomen, somewhat compressed; cervical groove hardly evident; front with ocular hoods produced into blunt angle above each eye; anterior border emarginate below ocular hoods. Covered eyes well developed. Antennules with third article of peduncle much shorter than second; stylocerite scalelike with spiniform tip reaching about to end of basal article; inner flagellum slender, outer one shorter with proximal $\frac{1}{2}$ enlarged. Antennae a little longer than body, slender; antennal scale reaching a little beyond end of antennular peduncle, lateral margin slightly sinuous with strong terminal spine separated from and exceeding lamella; strong ventral spine (basicerite) near base of scale. Third maxillipeds slender, not reaching tip of antennal scale; terminal article with long hairs.

First legs strongly developed with chelae unequal. Larger leg broad and flattened; slightly sinuate along inner margin; outer margin with longitudinal groove above and below, ridge between grooves ending in strong tooth behind base of dactyl; dactyl heavy, curved, toothed at base. Smaller chela about half as wide and $\frac{3}{4}$ as long as larger one; similarly formed but with sharp spine above (and small one below in males) at base of dactyl; no basal tooth on dactyl; sexually dimorphic fingers in males broad externally but with keeled, closely fit-

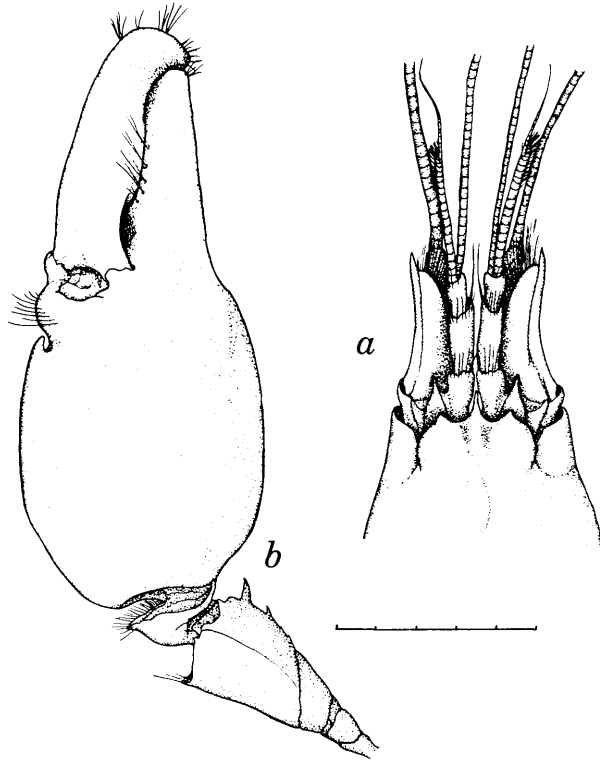


Fig. 66. *Alpheus normanni* Kingsley. *a*, Anterior region in dorsal view; *b*, large chela in ventrolateral view; 5 mm indicated (from Williams 1965).

ting opposed edges fringed by dense hairs; females with hand a bit hairy but fingers unornamented; carpus of both legs short, broad, irregularly cup shaped, merus with spiniform tooth near distal end and 1 or 2 spines below, distal end cupped to receive carpus with leg extended. Second legs very slender, weakly chelate; with carpus subdivided, joints diminishing in length as follows (numbered from proximal end): 2, 1, 5, 3–4. Third to fifth legs with dactyls simple.

Abdomen somewhat compressed. Telson with sides slightly convergent distally; 2 pairs of dorsal spines, first pair at $\frac{1}{3}$, second at $\frac{2}{3}$ length; tip broadly rounded, pair of spines at each posterolateral corner, distal margin heavily setose; pair of anal tubercles beneath with accompanying cups on uropods forming locking devices. Uropods oval; exopod with lateral margin ending in small spine flanked mesially by strong movable tooth.

Measurements in mm.—Length of body: male 26; ovigerous female 30; carapace length ovigerous females 4.5–10 (Hendrix 1971; Christoffersen 1979).

Color.—Gray or dull green, sometimes with median and lateral stripe of whitish often clouded or mottled with dark green or brown, a paler spot behind each eye; large chela dark green usually banded with yellowish brown or yellow on inner

surface; smaller chela and other legs paler, often banded with dull gray or reddish; occasionally body banded with red and pale yellow, large chela with 2 pale bands, fixed finger blackish, dactyl reddish (various authors).

Habitat.—Shelly or rocky bottoms, in burrows in sand or on pilings in shallow water, common in saltier parts of estuaries in Carolinas. Nolan and Salmon (1970) found the species in 10-m water offshore in March near Beaufort, N. C., but mainly in eel grass beds or in small-sized rubble during summer. Van Engel and Sandifer (1972) found the species occasionally in oyster trays on the eastern shore of Virginia. Chace (1972) found it most frequent on sand and mud flats covered with turtle grass and *Porites*, occasionally on mud bottom under rocks and oysters, and among reef corals in the Lesser Antilles. Hendrix (1971) reported it most abundant among blades and rhizomes of *Thalassia testudinum* from spring through late fall, noting that it does not build permanent burrows or shelters but is often found in sabellariid polychaete tubes, on mats of *Halimeda* sp., and in some sponges. Water's edge to 73 m.

Type-locality.—Key West, Fla.

Known range.—Bermuda; around Cape Charles, Va., and lower Chesapeake Bay through Gulf of Mexico (Ray 1974) and West Indies to São Paulo, Brazil (Christoffersen 1979); Gulf of California and Panama (Chace 1972).

Remarks.—This is one of the commonest snapping shrimps in the Carolinian region. As Hay and Shore (1918) pointed out, this was probably the species called *Alpheus minor* in early lists for the area. The epithet *minor* is correctly referred to *Synalpheus minus* (Say) found only in offshore waters, a different habitat from that frequented by *Alpheus normanni*. Brooks and Herrick (1892) followed the older lists adopting the name *Alpheus minor (minus)* and illustrated the adult in color on plate 1 and larval stages on plates 16 and 17. They illustrated the first three larval stages, as well as stages in segmentation of the embryo, but their specific identifications are somewhat unreliable.

Knowlton (1973b) considered *A. normanni* to have an extended larval development, i.e., small eggs and 5 larval stages. Sandifer (1973d) found larvae of the species uncommon in surface samples from lower Chesapeake Bay in a salinity range of 21.35 to 25.77‰ in temperatures of 25.3°–26.9°C during August and September.

Ovigerous females have been recorded throughout the year in various parts of the range, the season being most extended in lower latitudes (Tabb and Manning 1961; Rouse 1970; Hendrix 1971; Christoffersen 1979; USNM). Knowlton (*in* Nolan

and Salmon 1970) found ovigerous females from April 26 to September 20 at Beaufort, N. C.

In a compendious paper, Nolan and Salmon (1970) discussed behavior of *A. heterochaelis* and *normanni*, finding many traits to be similar. Though their discussion cannot be covered completely here, they found that animals in the laboratory tend to hide under or alongside hard objects or the sides of containers. Shelters or burrows may be constructed by digging with legs, pleopods and body, burrow maintenance being a more or less continuous process. If a unisexual pair of a species has a single available shelter, one animal will become dominant by action of a suite of aggressive acts: moving forward, lunging, fanning, spread stance, cocked claw, chela snap, touching or overlapping head and thoraci appendages, prowling and chasing. Retreat and avoidance are submissive acts. Moreover, when individuals from each of these two species are paired, the larger animal, usually *A.*

heterochaelis, almost always dominates. Other behavioral aspects are reviewed in the account for *A. heterochaelis*.

Sikora, et al. (1972) found *A. normanni*, *armillatus*, and *heterochaelis* in stomach contents of hakes, *Urophycis regius* and *U. floridanus*, in Georgia estuaries.

Genus *Automate* de Man 1888

de Man 1888:529.—Rathbun 1901:112.—Banner and Banner 1966b:36.

Carapace compressed. Eyes not covered by carapace, cornea reduced. Antennular peduncles extremely long; stylocerite reduced. Third maxillipeds longer than antennular peduncles. Chelate first legs asymmetrical and sexually dimorphic; surface smooth; fingers without cylinder and plunger as in *Alpheus*.

Key to Species

(Adapted from Chace 1972)

1. Rostrum reduced to acute, short tooth; propodus of legs 3 and 4 setose, not spinulose; dactyl of legs 3 and 4 subspatulate *A. evermanni*
Rostrum broadly rounded or subtriangular; propodus of legs 3 and 4 armed with series of stout, movable spines on flexor margin; dactyl of legs 3 and 4 slender, not subspatulate *A. gardineri*

Automate evermanni Rathbun

Fig. 67

Automate evermanni Rathbun 1901:112, fig. 22.—Holthuis 1951b:115, fig. 24.—Crosnier and Forest 1966:306, fig. 33.—Chace 1972:74.
Automate kingsleyi.—Williams 1965, fig. 51.

Recognition characters.—Carapace compressed, deeply emarginate behind eyestalks, slightly produced over base of antenna, anteroventral corner receding and very broadly rounded, deeper at level of first leg. Rostrum a small acute tooth. Eyestalks exposed and flattened dorsally, contiguous, base broadened, small cornea subterminal. Antennular and antennal peduncles long and nearly equal; stylocerite scalelike, reaching to $\frac{2}{3}$ length of basal antennular article; second article reaching $\frac{1}{2}$ – $\frac{2}{3}$ length of penultimate article, outer margin straight, ending in tooth equal to or exceeded by lamella. Third maxilliped exceeding antennal peduncle by length of terminal article.

First pair of legs chelate, very unequal. Major hand of male granulate along lower side near middle; not so in female; fingers gaping, pointed

tips crossing; fixed finger in line with hand and broad at base, lower edge in female slightly sinuous, cutting edge with complex blunt tooth near base, finely serrate and slightly concave near tip; dactyl tapering, small tooth near base, remainder of cutting edge sinuous. Carpus with lateral tooth on anterior margin projecting distoventrally, smaller tooth on mesiodistal corner. Second legs slender, overreaching antennal peduncle by full length of carpus, weakly chelate, carpus divided into 5 joints with proportions of 1:2.8:1.3:0.9:1.2. Third to fifth legs with dactyls subspatulate, merus of 3 and 4 with setae along flexor margin.

Abdomen well developed, compressed, pleopods strong. Telson tapering, margins laterally constricted near base but convexly curved to converge toward narrow posterior margin bearing 2 pairs of spines, outer stout, inner longer and more slender; dorsally armed with 2 pairs of very small spines, anterior pair distinctly anterior to mid-length.

Measurements in mm.—Length of body: male 14.2 (Rathbun 1901); female 27.4.

Color.—Practically colorless except eggs of ovigerous female color of red lead (W. L. Schmitt notes).

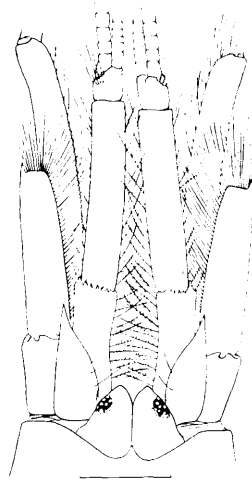


Fig. 67. *Automate evermanni* Rathbun. Anterior region of body in dorsal view, 25 mm indicated (from Crosnier and Forest 1966).

Habitat.—Sand, mud, shells; to 250m (Rathbun 1901).

Known range.—North Carolina (?); Georgia to Texas and Puerto Rico; eastern Atlantic from Cape Verde Islands and Liberia to Nigeria (Chace 1972).

Remarks.—Hay and Shore (1918) confused the description of *A. kingsleyi* by including illustrations of *A. evermanni*, and Williams (1965) continued the error by copying their figure (Chace 1972). Specimens of *Automate* formerly in the UNC-IMS collection were inadvertently discarded, therefore the old collections cannot be redetermined. Several speci-

mens from the S. Gray collection from off Sapelo Island, Ga., now in the USNM, include the largest female measured. The Georgia occurrence suggests that the species ranges into the Carolinas.

Automate gardineri Coutière

Fig. 68

Automate Gardineri Coutière 1902:337.

Automate kingsleyi Hay 1917:72.—Hay and Shore 1918:387, text-fig. 10; pl. 26, fig. 7.—Williams 1965:62.

Automate johnsoni Chace 1955:13, fig. 7.

Automate gardineri.—Banner and Banner 1966a: 150.—1966b:37, fig. 8.—Chace 1972:74, fig. 23.

Recognition characters.—Carapace about half length of abdomen; deeply emarginate dorsally behind eyestalks with rostrum a broadly rounded projection; anterior margin entire, produced farthest forward at base of antennular and antennal peduncles. Eyestalks contiguous, broad at base; cornea well developed with minute point on anterior surface in lateral view. Antennular and antennal peduncles long; stylocerite scalelike, reaching to end of basal antennular article; second antennular article nearly equal in length to first; third very short. Antennal scale extending to middle of penultimate article of antennal peduncle; lateral border ending in small spine; lamella broadly rounded distally, equaling spine. Third maxilliped exceeding anten-

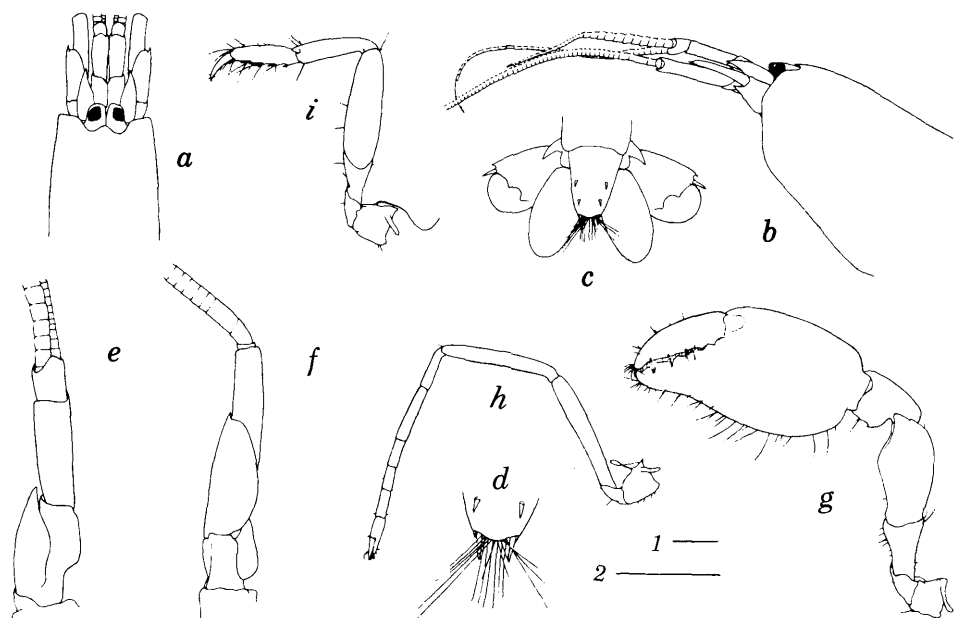


Fig. 68. *Automate gardineri* Coutière. Female: *a*, anterior region in dorsal view; *b*, same, lateral view; *c*, telson and uropods; *d*, end of telson; *e*, left antennule; *f*, left antenna; *g*, left first leg; *h*, left second leg; *i*, left third leg. Scales: 1(*a-c, g, i*), 2(*d-f, h*) = 1 mm (from Chace 1972).

nal peduncle by less than length of terminal article.

First legs chelate, prismatic, unequal; larger appearing somewhat rougher and stouter than smaller; fingers slightly gaping, fixed finger in line with hand and broad at base; dactyl narrower and moderately curved; carpus short; merus nearly as long as dactyl. Second legs nearly as long as first but slender, weakly chelate, and with carpus divided into 5 joints with proportions of 1:1.25:0.80:0.66:0.80. Third to fifth legs with dactyls slender, simple; merus of 3 and 4 with movable spines along flexor margin.

Abdomen well developed; compressed pleopods strong. Telson tapering; truncate terminally, ending in 2 short lateral spines flanked mesially by 2 longer spines and median pair of feathered setae; dorsally armed with 2 pairs of spines, first pair at midlength, second at $\frac{3}{4}$ length. Uropods with oval blades; lateral border of exopod deeply notched distally, border ending in small tooth flanked mesially by strong movable spine.

Measurements in mm.—Length of body: ovigerous females 7 to 16.

Color.—Almost transparent except for a small amount of red pigment on appendages and telson.

Habitat.—Under rocks at low tide; shallow grass flats to 50 m (USNM).

Type-locality.—Maldive and Laccadive Islands.

Known range.—Beaufort Inlet, N. C.; Yucatan; Virgin Islands, Barbados; Indo-Pacific region from Red Sea to Samoa.

Remarks.—Chace (1972) stated that *A. kingsleyi* is a synonym of *A. gardineri*, that the latter is probably a pantropical species, including two other species named from the eastern Atlantic and eastern Pacific, and that all of these may be synonyms of *A. dolichognatha* de Man (1888).

Ovigerous females are known from North Carolina in July and September.

Genus *Leptalpheus* Williams 1965

Williams 1965a:193.

Leptalpheus forceps Williams

Fig. 69

Leptalpheus forceps Williams 1965a:194, figs. 1–2.—
Chace 1972:77.

Recognition characters.—Body compressed. Carapace smooth, produced into hood projecting over eyes, nearly flat dorsally, extremely shallow excavation between eyes, anterior margin bent slightly downward in front of eyes; anterolateral angle obtuse; cardiac notch on posterior border well devel-



Fig. 69. *Leptalpheus forceps* Williams. Female: a, anterior region in lateral view; b, same, dorsal view; c, lateral view of antennular peduncle showing mesioventral keel; d, large cheliped in lateral view; e, part of large cheliped in mesioventral view; f, fingers of large chela; g, ischio-meral articulation of large cheliped; h, tail fan in dorsal view. Scales: a-b, d-e, h, 1 mm; c, f-g, 0.5 mm indicated (from Williams 1965a).

oped. Eyes concealed from dorsal view but visible from anterior, cornea well developed. Antennular peduncle slightly longer than antennal peduncle, a little broadened proximally, first and second articles of about equal length, each with prominent but appressed anterolateral spine, third shorter; stylocerite small, appressed, with thin mesioventral keel terminating in small anterior spine, outer flagellum shorter than inner, fused part with 10 segments. Antennal peduncle slightly convex, ending in spine exceeding lamella.

Chelipeds very asymmetrical, chelae carried folded back completely on merus; major with propodus longer than merus, slender, excavated along flexor surface, finely tuberculate ventrally, fingers thin, not inverted, conspicuously curved,

gaping, with meshing teeth proximally, tips crossing; merus long irregularly triangular in cross section, excavate somewhat internally, twisted and smooth; ischium triangular in cross section, blade-like spine on mesiodistal border. Minor cheliped with propodus somewhat longer than merus, flexor side of each excavated; fingers and palm of nearly equal length, fingers with single tooth at mid-length and thin shearing edge distally, tips crossing. Second legs weak, carpus divided into 3 segments, proximal longest, distal intermediate, middle 3 equally short. Third and fourth legs strong, merus well developed, carpus with distoventral movable spine; fifth legs weaker.

Abdomen smooth; pleura of first 5 segments broadly rounded, of sixth ending in acute, triangular, movable plate. Telson rounded distally, 2 pairs of movable dorsal spines at $\frac{1}{3}$ and $\frac{2}{3}$ length, movable outer short spine and adjacent long spine mesial to it at each corner. Uropods with exopod more or less truncate distally, lateral edge broken by overlapping rectangular cleft armed with strong subterminal spine, mesial margin with overlapping pointed lamina; no well-defined transverse suture present; endopod ovate and longer.

Measurements in mm.—Length of carapace: male 5.2; ovigerous female 7.8.

Variation.—Fingers of the major chela are slightly less gaping in females than in males, and the number of teeth on fingers of the major chela vary as do the fused segments on the outer antennular flagellum.

Color.—Translucent, colorless in life; eggs light green in formalin.

Habitat.—The species is a commensal in *Upogebia affinis* burrows (Williams 1965a; Saloman 1971; Simon and Dauer 1977), and may occur in *Callinassa* burrows as well (Dawson 1967). Specimens have often been taken at night in surface plankton inside inlets and in tidal currents in the sounds of North Carolina.

Type-locality.—Gallants Point, Newport River, Carteret County, N. C.

Known range.—Drum Inlet, Beaufort, Banks Channel near Wrightsville Beach, and Lockwoods Folly Inlet, N. C.; Old Tampa Bay, Fla. (Saloman 1971; Simon and Dauer 1977); Davis Bayou, Miss. (Dawson 1967).

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

Genus *Synalpheus* Bate 1888

Banner 1953:26.—Hemming 1958b:161.

Key to Species

1. Dactyls of third to fifth legs with 2 very unequal hooks, ventral strongest (broadest); an inconspicuous, obtuse supernumerary process proximal to ventral hook *S. fritzmuelleri*
 Dactyls of third to fifth legs with 2 hooks approximately equal in width at base 2
2. Dactyls long and slender, hooks continuing general direction of axis of dactyl; stylocerite longer than basal article of antennular peduncle; lamella of antennal scale present 3
 Dactyls short, hooks strongly curved, ventral one usually bent at considerable angle to axis of dactyl; stylocerite not exceeding first article of antennular peduncle; antennal scale lacking lamella in male, small in female *S. longicarpus*
3. Frontal teeth more or less equilaterally triangular, at times with an inferior vertical prolongation to rostrum; basicerite strongly spinous above *S. minus*
 Frontal teeth always longer than wide, spinous; rostrum armed with ventral prolongation which embraces ocellary beak; basicerite unarmed above *S. townsendi*

Synalpheus fritzmuelleri Coutière

Fig. 70

Synalpheus fritzmuelleri Coutière 1909:35, fig. 18.—Verrill 1922:97; Schmitt, 1935a:148.—Williams

1965:69, fig. 56.—Chace 1972:92.—Coelho and Ramos 1972:150.—Christoffersen 1979:341.

Recognition characters.—Rostrum slender, compressed, acute from dorsal view, a little longer than

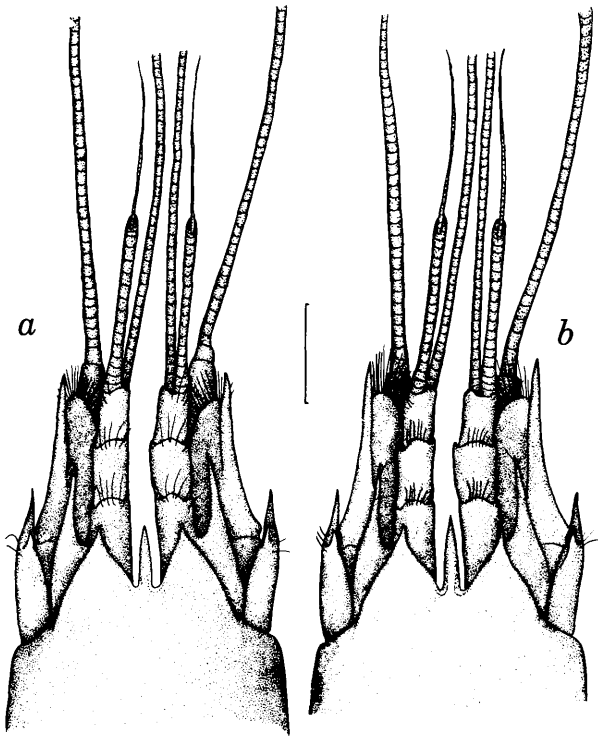


Fig. 70. *a*, *Synalpheus fritzmuelleri* Coutière, anterior region in dorsal view; *b*, *S. f. elongatus* Coutière, anterior region in dorsal view; 1 mm indicated (from Williams 1965).

orbital spines, reaching to midlength of visible portion of basal antennular article. Orbital spines wide at base, acuminate; margins incurved. Eyes completely covered by carapace. Antennular peduncle with stylocerite of basal article reaching to middle of second article; third article slightly shorter than second; inner flagellum filiform, outer bifurcate beyond about eighth joint, thickened proximally. Spine of antennal scale equaling terminal article of antennal peduncle, both reaching a little beyond antennular peduncle, spine separated from and exceeding narrow lamella distally; basal article (basicerite) with short, sharp lateral spine nearly as long as stylocerite; above it a smaller, acute, secondary spine.

First pair of legs chelate, unequal. Large chela ellipsoidal, only a little swollen in middle; small obtuse tubercle on distal dorsal margin; width of palm about $\frac{1}{3}$ total length of chela; dactyl heavy, strongly arched above; fixed finger narrow at tip; carpus short and wide, prolonged downward and inward; merus stout, superior margin ending distally in sharp angular point. Smaller chela similar in form; fingers pointed; carpus short, cup shaped; merus like that of larger chela. Second legs slender, weakly chelate; carpus subdivided, first joint about equal to remaining 4. Third to fifth legs with bifurcate

dactyls, hooks unequal; outer one thinner and a little longer, regularly curved, sharp; inner one wider at base, strongly divergent, curved inward; slight obtuse protuberance or rudimentary spur proximal to inner hook.

Telson broad, tapering, obtusely rounded distally; each posterior angle with pair of unequal spines; 2 pairs of small dorsal spines, first pair at midlength, second at $\frac{3}{4}$ length. Uropodal exopods with lateral margin ending in notch with fixed spine on each side, longer movable spine between them.

Measurements in mm.—Length of body: ovigerous female 22.

Variation.—In the subspecies *S. f. elongatus* Coutière (1909:37, fig. 19) the lateral spine of the antennal scale greatly exceeds the terminal article of the antennal peduncle, and the rostrum is decidedly longer than the ocular spines. In the subspecies *S. f. carolinensis* Verrill (1922:99, pl. 22, fig. 6; pl. 39, figs. 1–1d) and *S. f. caribaea* Verrill (1922:98, text-fig. 8; pl. 39, figs. 3a–3c) the basicerite is shorter than in typical specimens.

Color.—*Synalpheus fritzmuelleri*: chela varying shades of green, darker toward extremities of fingers; body more or less colorless, specked with quite numerous tiny red chromatophores. *Synalpheus fritzmuelleri elongatus*: similar to preceding; chelipeds and second legs blue, except anterior part of chela light green (Schmitt 1930).

Habitat.—Often living in sponges; variety of niches on reefs and jetties such as loose boulders, crevices, fouling mat, and nearby bottom (Gore, et al. 1978; Christoffersen 1979; Felder and Chaney 1979); low tide mark to 51 m.

Type-locality.—*Synalpheus fritzmuelleri*, Marco, Fla.; *S. f. elongatus*, mouth of Bull Creek, S. C.

Known range.—Off Beaufort, N. C., to Santa Catarina, Brazil; Bermuda; St. Helena Island, South Atlantic; Baja California (Chace 1972).

Remarks.—Distribution of the named subspecies and varieties of *Synalpheus fritzmuelleri* shows that local populations parallel each other at widely separated locations. As Banner (1953) pointed out, earlier workers, with only a few specimens from these widely separated localities, naturally tended to name the variants, the range of variation being then unknown. Varietal names, therefore, must be regarded as conditional. Verrill (1922:89) may have concurred for he quoted Stebbing's dim view of naming infinite variations but proceeded to name varieties anyway.

In the Carolinas, this species lives on offshore reefs (Pearse and Williams 1951) in large sponges. Specimens may be found in beach drift after severe storms. Ovigerous females of typical *S. fritzmuelleri* are known from the Carolinas in February,

and June to October, indicating a long breeding season. Gore, et al. (1978) found breeding populations year round along central eastern Florida; they are known from January to April at St. Helena Island (USNM), and year round in Brazil (Christoffersen 1979).

Three recent studies have treated association of *S. fritzmulleri* with reef substrates. McCloskey (1970) found it breeding within the *Oculina arbuscula* community off the Carolinas. Gore, et al. (1976; 1978) found it fourth in abundance among decapod crustaceans associated with subtropical sabelariid worm reefs, *Phragmatopoma lapidosa*, off eastern Florida, and Felder and Chaney (1979) in a reef off south Texas found the species in every month of the year at mean densities $> 100/m^2$.

***Synalpheus longicarpus* (Herrick)**

Fig. 71

Alpheus saulcyi var. *longicarpus* Herrick 1892 (part): 383.

Synalpheus longicarpus, Coutière 1909:53, fig. 31.—Hay and Shore 1918:383, text-fig. 6; pl. 26, fig. 2.—Verrill 1922:113, pl. 25, figs. la–1h.—Williams 1965:73, fig. 59.—Chace 1972:93.—Christoffersen 1979:344, figs. 23–27.

Recognition characters.—Rostrum carinate, slender and slightly longer than triangular, obtuse orbital hoods, reaching about to middle of basal antennular article; space between rostrum and hoods U-shaped, broadest in females. Eyes small, completely covered. Basal article of antennular peduncle with short stylocerite reaching to distal $\frac{1}{3}$ of article; second article $\frac{1}{3}$ longer than third article; inner flagellum filiform, outer branching at seventh joint, thickened proximally. Terminal article of antennal peduncle exceeding antennular peduncle; antennal scale with strong terminal spine separated from and exceeding rudimentary lamella distally; spine variable in length, often exceeding antennular peduncle by $\frac{1}{2}$ length of distal article; lamella of scale rudimentary in males, small and variable in females; basal article (basicerite) slender, acute, with angle but no accessory spine above, tip reaching to end of second article of antennular peduncle.

First legs chelate, very unequal. Larger chela elongate, somewhat ovate, about 2.75 times longer than broad; margins somewhat convex; posterior end swelled and produced backward beyond articulation with small, short carpus inserted below central axis of palm; anterior dorsal margin of palm with small, acute spine near base of dactyl; dactyl somewhat oblique at end, toothed at base, about $\frac{1}{4}$

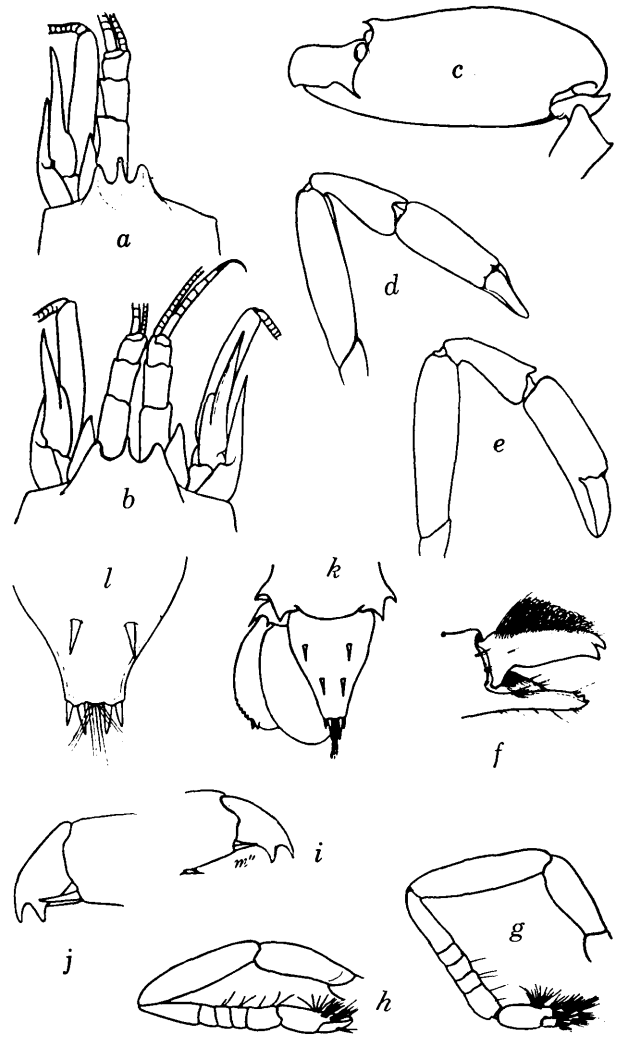


Fig. 71. *Synalpheus longicarpus* (Herrick). Anterior region in dorsal view, a, male, b, female; c, large chela; d, small first cheliped, male; e, same, female; f, fingers of small first cheliped; g, second leg of male showing subdivided carpus; h, same, female; i, dactyl of third leg; j, same in large adult; k, telson and left uropods in dorsal view, female; l, tip of telson (from Coutière 1909).

to $\frac{1}{5}$ length of chela. Small chela elongate, gently arched dorsally, dense tuft of erect hairs on dorsal surface along most of length, cutting edge bearing 2 apical teeth, nearly straight; fixed finger with 3 teeth, apical stronger. Second pair of legs slender, weakly chelate; stronger in male than in female; carpus subdivided, first joint shorter than sum of remaining 4. Third to fifth legs with dactyls bifurcate.

Sixth abdominal segment with strong triangular tooth on each posterior angle. Telson with sinuous sides tapering to subtruncate tip; dorsal spines strong, first at $\frac{1}{3}$, second at $\frac{2}{3}$ length; tip with 2 pairs of strong spines, inner pair slightly longer. Uropodal exopod broadly oval; lateral border spined with 7 or 8 denticles, movable spine at distal end of series.

Measurements in mm.—Length of body: male 18.5 (Christoffersen (1979)); ovigerous females 16 to 22.

Variation.—Length of the carpus of the small cheliped varies with age. The rostrum and projections on the orbital hoods may be entirely lacking or their relative lengths may vary (Wass 1955).

Color.—Translucent white; fingers brown.

Habitat.—To depths of 60 m in and under shells, rubble, coral, rock, or in interior of sponges; especially abundant in *Sphaciospongia* (= *Spirastrella*) (Wells, et al. 1960). Sometimes found in sponges cast on beach during storms at Beaufort, N. C.

Type-locality.—Bahamas [probably Nassau, New Providence Island].

Known range.—Beaufort, N. C., to west Flower Garden Reef, SSE Galveston, Tex.; Yucatan, Mexico, through West Indies to Rio de Janeiro, Brazil.

Remarks.—Christofferson (1979) synonymized *S. pandionis* Coutière and its subspecies with *S. longicarpus*, discussing variations in these groups as well as similarities to still other species that he implied may fall into large and variable species. Presumably, further work needs to be done before the relationships within this complex are understood, but the variability probably poses no obstacle to identification in the Carolinian region.

Synalpheus longicarpus is common in the Carolinas and often occurs in enormous numbers in the canals of large sponges. Infestation by parasitic isopods is common, *Phryxus subcaudalis* occurring on the surface of the abdomen and *Synsynella deformans* in the branchial chambers.

Ovigerous females have been taken off North Carolina in August and December; they are also known from the Windward Islands, West Indies in March and April, in Florida during October-November (USNM), and Rio de Janeiro, Brazil, in February (Christoffersen 1979). Herrick (1892) stated that the species hatches in essentially the adult form, but Coutière (1909) noted that it hatches as a zoea. Coutière (1909) and Wass (1955) remarked that a number of ovigerous females occur among crowded populations in sponges.

Synalpheus minus (Say)

Fig. 72

Alpheus minus Say 1818:245.

Synalpheus minus.—Hay and Shore 1918:382, text-fig. 5; pl. 26, fig. 3.—Verrill 1922:102, pl. 21, fig. 1; pl. 23, fig. 3; pl. 25, fig. 3; pl. 31, fig. 4; pl. 33, figs. 4, 4a; pl. 36, figs 1–1d, 2; pl. 47, figs. 1–1c, 2; pl. 48, figs. 3–3c.—Schmitt 1935a:149.—Williams 1965:70, fig. 57.—Chace 1972:95, figs. 35–36 (not *S. brevicarpus*).—Coelho and Ramos

1972:150.—Christoffersen 1979:350, fig. 28.

Recognition characters.—Front of carapace with 3 teeth each in form of equilateral triangle; rostrum usually a little wider at base, compressed and sometimes slightly longer than orbital teeth. Eyes completely covered by large orbital hoods. Basal article of antennular peduncle with stylocerite reaching to distal 1/3 of second article; third article 1/2 length of second; second of intermediate length; inner flagellum filiform, outer flagellum thickened proximally. Antennal scale narrow, inner edge regularly curved; lateral spine a little longer than antennular peduncle, separated from and exceeding lamella; basal article (basicerite) reaching to distal end of basal antennular article, above it a prominent secondary spine (subject to great variation (Chace 1972)).

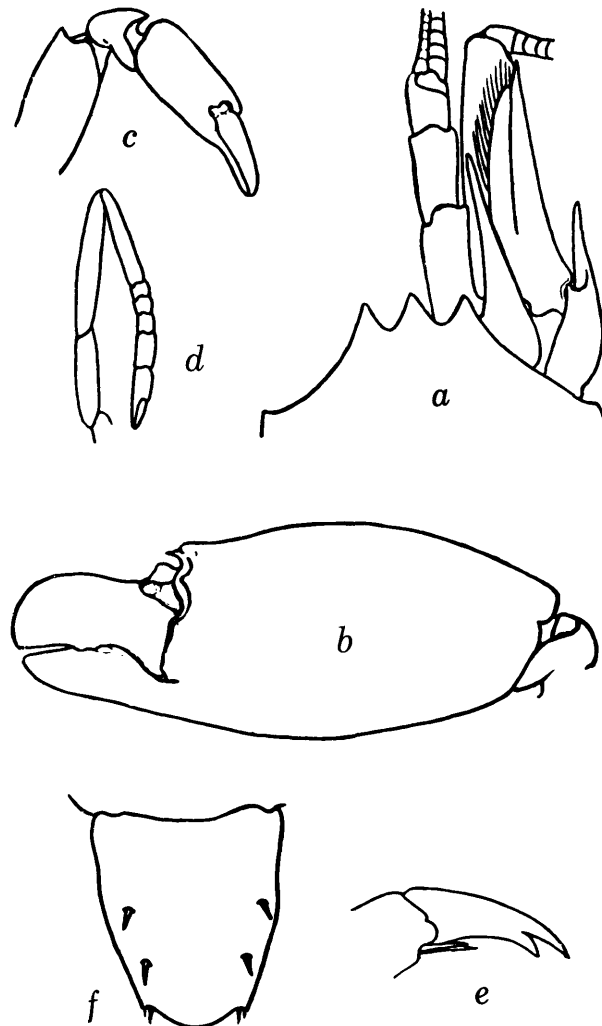


Fig. 72. *Synalpheus minus* (Say). a, Anterior region in dorsal view with right antennule and antenna; b, large chela; c, small first cheliped; d, second leg showing subdivided carpus; e, dactyl of third leg; f, telson in dorsal view (from Coutière 1909).

First legs chelate, unequal, thicker in male than in female. Large chela ovoid; palm about 2.5 times length of fingers, anterior dorsal margin with strong, sharp tooth at inner side and blunter tooth on lateral and ventral side near base of dactyl; dactyl broad, larger than fixed finger, tip obtuse, cutting edge a little sinuous, large tooth at base, dorsal edge curved distally; fixed finger with tip nearly straight, inner edge a little sinuous. Smaller chela elongate, slender, about $\frac{1}{3}$ length of larger; fingers a little shorter than palm, with tufts of hair, acute at tips and curved a little downward; palm narrowly elliptical, surface plain. Second legs slender, weakly chelate; carpus subdivided with joints diminishing as follows (numbered from proximal end): 1, 5, 2-3-4.

Telson with sides slightly sinuous, tip broadly rounded; 2 pairs of dorsal spines, first pair at about midlength, second pair at about $\frac{3}{4}$ length; distal margin with pair of spines at each posterolateral corner. Uropodal exopods with lateral margin ending in notch armed with 2 spines separated by longer movable spine.

Measurements in mm.—Length of body: maximum 38 (Chace 1972).

Color.—Body translucent, yellowish white; large chela white or translucent gray, fingers orange, tips red; banded near base of fingers with white in female, white tipped with green in male. Body sparsely dotted by green chromatophores, tips of third maxillipeds and distal $\frac{1}{3}$ of first pair of chelae bright pink; eggs green (Christoffersen 1979).

Habitat.—Any place that provides hiding; sponges, dead coral, coral rock, abandoned gastropod shells; beneath stones, *Porites*, and *Pocillopora* on grass flats in West Indies (Chace 1972; Christoffersen 1972); intertidal to 85 m.

Type-locality.—“Coasts of the southern states, and off East Florida.”

Known range.—Near Cape Hatteras, N. C., to São Paulo, Brazil (Christoffersen 1979); Bermuda.

Remarks.—A number of authors, among them Hay and Shore (1918) and Verrill (1922), pointed out that Brooks and Herrick (1892) identified *Alpheus normanni* (= *packardii*) as *A. minus*. *Synalpheus minus*, not treated by them, was not available for study in the Beaufort, N. C., harbor area. Christoffersen (1979) gave a detailed synonymy.

A long breeding season is indicated for this species. Ovigerous females have been taken from February to November in various localities from North Carolina to the Gulf Coast; spring in the Windward Islands, West Indies; April in Bermuda; September in Venezuela; January and February in Rio de Janeiro. Adults usually occur in pairs (Wass 1955).

Synalpheus townsendi Coutière

(Small snapping shrimp)

Fig. 73

Synalpheus townsendi Coutière 1909:32, figs. 14-17 (16-17 as subspecies).—Hay and Shore 1918:384, pl. 26, fig. 1.—Verrill 1922:100.—Williams 1965:72, fig. 58.—Chace 1972:104.—Pequegnat and Ray 1974:249, figs. 53d, 55.—Christoffersen 1979:352.

Recognition characters.—Rostrum slender, 1.5 times as long as lateral teeth and reaching usually to end of proximal $\frac{1}{3}$ of second article of antennular pe-



Fig. 73. *Synalpheus townsendi* Coutière. a, Anterior region in dorsal view with left antennule and antenna; b, tip of large chela; c, large cheliped, merus, carpus and proximal end of propodus; d, small first cheliped; e, second leg showing subdivided carpus; f, dactyl of third leg; g, telson in dorsal view (from Coutière 1909).

duncle, armed with ventral prolongation embracing ocellary beak. Teeth on orbital hoods slender; eyes completely covered by hoods. Basal antennular article overreached by stylocerite; third article about $\frac{1}{2}$ length of second; inner flagellum filiform, outer flagellum thickened proximally, bifurcate beyond fourth joint. Antennal scale with strong, slender lateral spine separated from and exceeding lamella distally, spine reaching about to or beyond end of antennal peduncle; basal article (basicerite) well developed, angled above but lacking dorsal spine, extremity reaching to distal $\frac{1}{3}$ of basal antennular article.

First pair of legs chelate, very unequal. Large chela with small, acute dorsal spine at distal margin of palm; upper margin of dactyl elevated into thick crest; carpus small, irregularly shortened; merus with dorsolateral margin convex, ending in hooked spine. Small chela $\frac{1}{3}$ length of large one; no brush of hairs on dactyl. Second pair of legs slender, weakly chelate; carpus subdivided, first joint longer than others combined. Third to fifth legs with bifurcate dactyls, both hooks nearly parallel, ventral one narrower and much shorter than dorsal.

Abdomen compressed. Telson with sides somewhat convergent; posterior angles sharp and each provided with pair of spines, inner spine longer than outer; 2 pairs of strong dorsal spines, first pair at $\frac{1}{3}$, second at $\frac{2}{3}$ length. Uropods ovate, exopod with lateral margin ending in notch with strong fixed spine at its outer and inner angles, between these spines a longer movable spine.

Measurements in mm.—Length of body: ovigerous females 13.

Variation.—The rostrum is variable in length, often shorter than as described above.

Color.—Body and legs translucent pinkish red; large chela pink, changing to green on fingers.

Habitat.—Often found in large sponges or on reefs; low tide mark to 102 m.

Type-locality.—Gulf of Mexico south of Cape San Blas, Fla., 29°14'00"N, 85°29'15"W, 46 m.

Known range.—Off Beaufort, N. C., to Rio de Janeiro, Brazil; Bermuda; Gulf of California.

Remarks.—Ray (1974) discussed variants seen in the western Gulf of Mexico that are similar to the Pacific *S. t. brevispinis*; he concluded, as have other authors, that great variation in *Synalpheus* renders such named subspecies invalid, although Christoffersen (1979) thought that this material might represent a distinct species.

Wass (1955) remarked that the species seems less dependent on sponges than other members of the genus taken in the Alligator Harbor area of Florida. Pearse and Williams (1951) found it on offshore reefs and in sponges off North Carolina at 13–15 and 29–37 m respectively. Gore, et al. (1978) found breeding from January to August on sabel-lariid worm reefs, *Phragmotopoma lapidosa*, along eastern Florida; elsewhere ovigerous females have been found virtually the year round in Florida and in Texas, in February, June, August, and September in the Carolinas, July and August at Obregon, Mexico, September in Venezuela, and November in Brazil (Christoffersen 1979).

Family Ogyrididae

Caridea with first 2 pairs of legs chelate, nearly equal in size and not much if any larger than other legs. Carpus of second legs subdivided. Rostrum small or wanting. Eystalks long, slender, fully exposed but with corneal surface reduced. Telson thick, obtusely pointed. Blades of uropods curved outward. Thelycum present in females (Hay and Shore 1918).

Genus *Ogyrides* Stebbing 1914

Stebbing 1914:31.—Hemming 1958b:158.

Key to Species

1. Single movable spine behind rostrum on middorsal line *O. alphaerostris*
- *O. hayi*
- Postrostral crest with 3 to 14 small, fixed spines *O. hayi*

Ogyrides alphaerostris (Kingsley)

Fig. 74

Ogyris alphaerostris Kingsley 1880:420, pl. 14, fig. 7.

Ogyris occidentalis Ortmann 1893:46, pl. 3, fig. 4.

Ogyrides yaquiensis Armstrong 1949:3, fig. 1.

Ogyrides limicola Williams 1955b:56, fig. 1.—1965:74, fig. 60.

Ogyrides occidentalis.—Christoffersen 1979:356, fig. 31a-i.

Ogyrides alphaerostris.—Williams 1981:144.

Recognition characters.—Rostrum short, depressed, equilaterally triangular. Postrostral carina with 8 to 14 teeth, flanked on each side by row of setae extending to tip of rostrum. Pterygostomian

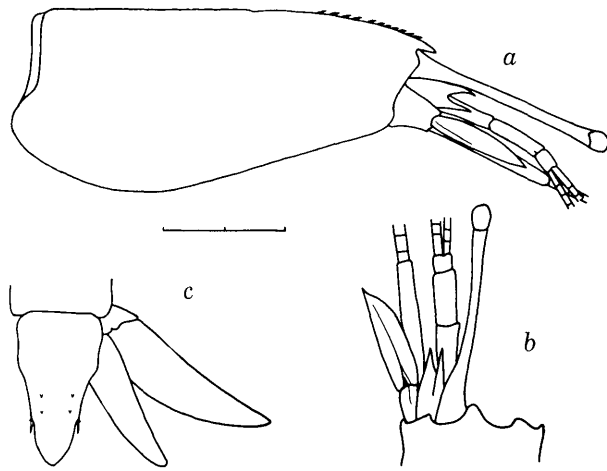


Fig. 74. *Ogyrides alphaerostris* (Kingsley). *a*, Carapace and anterior appendages in lateral view; *b*, anterior region in dorsal view showing left eyestalk, antennule and antenna; *c*, telson and uropods of right side, approximately 2 mm indicated (from Williams 1955c).

area broadly obtuse. Eyestalks long, lightly setiferous dorsally and dorsomesially, narrowest in middle, exceeding antennular peduncles by up to 2.5 times corneal length. Antennal and antennular peduncles nearly equal in length; second antennular article almost 2 times as long as third article; stylocerite of basal article terminating in 2 strong acuminate spines of nearly equal length, never exceeding basal antennular article. Antennal scale and second article of antennular peduncle reaching nearly same level distally; scale evenly rounded mesially, 3 times longer than greatest width, greatest width in basal half; basal article with lateral and ventral spine inconspicuous or absent. Third maxilliped, when extended, exceeding eyestalks.

First legs exceeding midlength of antennal peduncle by full length of chelae; fingers of chelae pointed, agape when closed. Carpus of second legs 4-segmented; third leg with single spine on ischium and merus.

Telson with anterior pair of spines placed well behind lateral prominences. Uropods with exopods slightly falciform, lateral borders nearly straight. Telson with 3 horny ridges at proximolateral corners ventrally, and uropods with an interlocking horny eminence on basal article dorsally.

Measurements in mm.—Length of body: ovigerous holotypic female 16.

Variation.—Individual variations are shown in number of spines on the postrostral crest, in length of eyestalks, and in lengths of spines of the stylocerite.

Color.—Females with general body structure colorless, clear; internal organs visible; gut dark; he-

patopancreas light brown; eyestalks, antennal and antennular peduncles, and distal portions of anterior appendages with red and yellow spots; uropods and sixth segment of abdomen with scattered red spots. Ovigerous females with yellow green (chartreuse) colored eggs on swimmerets (Williams 1955a).

Habitat.—On (or in) the bottom of muddy estuaries, or in plankton; inshore ocean on very fine sand (Frankenberg and Leiper 1977); surface to 52 m. Collections have been made in an observed bottom salinity range of 9 to over 31‰. Felder and Chaney (1979) reported one occurrence in a fish stomach from a nearshore reef off Texas.

Type-locality.—Northampton County, Va., eastern shore, Atlantic side.

Known range.—Eastern shore of Accomack County, and lower James River, Va., through Gulf of Mexico to Rio Grande do Sul, Brazil (Christoffersen 1979).

Remarks.—The systematic confusion surrounding the two species *O. alphaerostris* and *O. hayi* was discussed by Williams (1981). The two species are quite distinct morphologically and differ in total size, *O. alphaerostris* being the smaller. The latter occurs most frequently in collections from estuaries. Young specimens have frequently been taken in plankton tows made at night in Bogue Sound, N. C., but adults are seldom taken by this method of collection. Occurrence of adults in samples taken with a beam trawl suggests burrowing habits similar to those described for *O. hayi*, but in muddier situations or very fine sand (Frankenberg and Leiper 1977), and often in low salinities.

In North Carolina, collections of *O. alphaerostris* have been made in all seasons of the year. Ovigerous females have been taken from May to September there, and in April and October in Florida. From ovigerous females taken July 9 in black mud in a Petersen grab at 6–7 m depth in lower York River, Va., and maintained at 23.9°–28.9°C in 19.6‰ salinity, eggs hatched and developed through 8–9 zoeal stages and a postlarva, molting every two days during the first half of development but less often thereafter (Sandifer 1974b). Lengthened eyestalks and shortened first legs do not assume adult proportions until the postlarval stage. Unlike alpheid larvae which show precocious development of the fifth legs along with the first legs, the legs of *O. alphaerostris* develop in sequence from first to last. In plankton studies, Sandifer (1973d; 1974b) commonly collected larvae of this species in the York River and once in lower Chesapeake Bay, concentrations ranging to 37.5/k. Nearly all were in a salinity range of 15 to 25‰, mostly in temperatures between 23° and 27°C. Eight zoeal stages were re-

covered and these were generally larger than comparable reared stages. Peak occurrences were during July and September, but presence ranged from May to November. All zoeal stages were more abundant in bottom than in surface samples.

Ogyrides hayi Williams

Fig. 75

Ogyris alphaerostris.—Hay and Shore 1918:388, fig. 11, pl. 26, fig. 9.—Pearse, Humm, and Wharton 1942:148, 185, figs. 1, 12.

Ogyrides alphaerostris.—Williams 1955b:56–57.—1965:75, fig. 61.—Van Engel and Sandifer 1972:156.—Chace 1972:106.—Saloman 1979:151.

Ogyrides hayi Williams 1981:145.

Recognition characters.—Rostrum depressed, equilaterally triangular, tipped with setae. A single, postrostral, movable spine. Pterygostomian area obtuse. Eyestalks long, setiferous mesially, narrowest in middle, exceeding antennular peduncle by approximately twice corneal length. Antennal and antennular peduncle nearly equal in length; second article of antennular peduncle about 3 times

as long as third article; stylocerite terminating in 2 acuminate spines; lateral spine longer. Antennal scale and second article of antennular peduncle reaching same level distally; scale evenly rounded mesially, approximately 3 times longer than greatest width near base; basal article with lateral and ventral spine. Third maxilliped, when extended, exceeding eyestalks.

First legs scarcely extending to tip of antennal scale. Second legs exceeding antennal scale by full length of chelae; fingers of chelae pointed, agape when closed. Carpus of second legs 4-segmented; third leg with single spine on ischium and merus.

Telson with anterior pair of spines placed a little behind level of lateral prominences. Uropods with exopods somewhat falciform, curvature greatest distally. Telson with 3 horny ridges at proximolateral corners ventrally, and uropods with an interlocking horny eminence on basal article dorsally.

Measurements in mm.—Length of body: ovigerous female 27.

Color.—Body nearly transparent; red and green spots or flecks on eyestalks, antennules, and antennae; green only on distal joints of third maxillipeds; red only on basal articles of legs on first pleopods, at bases of all pleopods, and on abdominal pleura and sterna; a conspicuous red area on sixth abdominal segment distoventrally and another around mouth.

Habitat.—Often found on firm bars of sand just offshore along open ocean in water 1–3 m deep (Pearse, et al. 1942; Saloman 1979); surface to 9 m.

Type-locality.—Off Bogue Bank W of Ft. Macon, North Carolina, ~3.5 m.

Known range.—Beaufort, N. C., to Sebastian Inlet, Fla.; northwestern Florida to Mississippi; Puerto Rico.

Remarks.—Hay and Shore (1918), lacking comparative material, referred their species with a single postrostral spine to the then only known ogyridid from the western Atlantic, but it remained unrecognized in synonymy until Williams (1981) clarified the taxonomic status of postrostrally multi-spined *O. alphaerostris* and supplied a name for the single spined species.

Ogyrides hayi apparently is more restricted to high-salinity water than *O. alphaerostris*, for it has seldom been collected in the sounds of North Carolina and then only near inlets. Pearse, et al. (1942) described burrowing habits of the species on sandy bars and commented that members of the genus are unusual in that they have long eyestalks like *Uca*, yet are burrowers. *Ogyrides hayi* burrows forward (head first), using the third maxillipeds and legs for digging and propulsion. Sand is pushed upward and over the head, the abdomen often

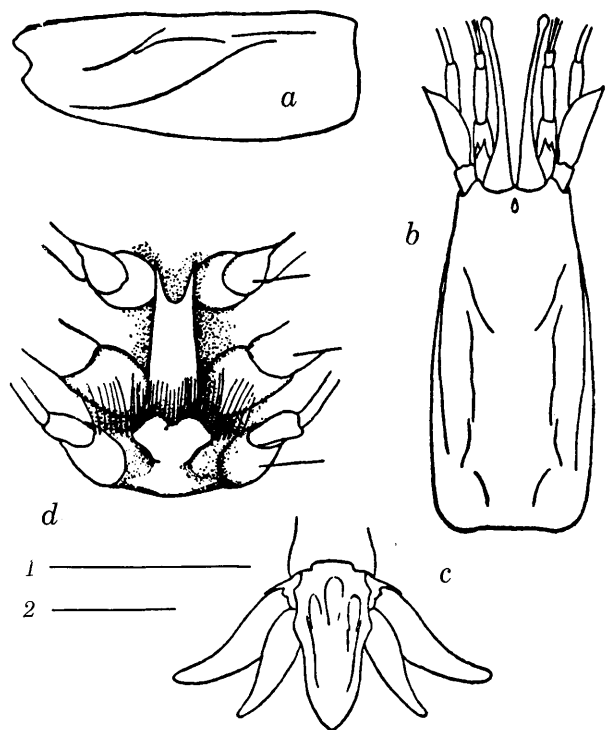


Fig. 75. *Ogyrides hayi* Williams. *a*, Carapace in lateral view; *b*, carapace and anterior appendages in dorsal view; *c*, uropods and telson in dorsal view; *d*, sterna of last three thoracic segments showing thelycum of female. Scales: 1(*a-c*)=5 mm; 2(*d*)=2 mm (from Hay and Shore 1918).

being left above sand for a time, especially in ovigerous females. The fifth leg is held high on the sides and stroked dorsally and posteriorly, legs 1 to 4 are stroked laterally and posteriorly, and the third maxillipeds moved anteriorly and dorsally. The animals scrape food from the antennae with setose mouth parts.

Ovigerous females have been taken in July and August in Florida and North Carolina, July in Puerto Rico, and August in Mississippi (USNM).

Various authors cited imply that the breeding season extends through the summer months.

Family Hippolytidae

Caridea with first 2 pairs of legs chelate, first pair not much stronger than rest; carpus of second pair of legs subdivided. Eyes well developed and not covered by carapace. Mandibles usually deeply cleft.

Key to Genera and One Species

1. Rostrum shorter or longer than carapace, but clearly less than 1.3 times its length 3
Rostrum noticeably longer than carapace, 1.4 times to nearly twice its length 2
2. Rostrum horizontal, lacking basal crest of crowded teeth *Tozeuma*
Rostrum upturned, with basal crest of crowded teeth
. *Exhippolyasmata oplophoroides*
3. Carpus of second leg subdivided into 7 or fewer joints 4
Carpus of second leg subdivided into more than 7 joints, multiarticulate *Lysmata*
4. Carpus of second leg subdivided into 3 or 5 joints 5
Carpus of second leg subdivided into 7 joints 7
5. Carpus of second leg divided into 3 joints 6
Carpus of second leg divided into 5 joints *Thor*
6. Rostrum with deep ventral blade; series of small spines (5- 9) along anterior margin of carapace below eye *Latreutes*
Rostrum lacking deep ventral blade but may be somewhat deepened distally; no small spines on edge of carapace below eye *Hippolyte*
7. Supraorbital spines absent. *Eualus*
Supraorbital spines present 8
8. One supraorbital spine on each side; third maxilliped without exopod *Lebbeus*
Two or more supraorbital spines on each side; third maxilliped with exopod *Spirontocaris*

Genus *Eualus* Thallwitz 1892

Holthuis 1947:10.—1950:46.—1955:100.—China 1966:243.—Noël 1978:22.

Rostrum short or long. Supraorbital spine ab-

sent. Stylocerite long, ending in sharp point. Antennal spine present. Mandible with incisor process and palp of 2 articles. Third maxilliped with exopod. Carpus of second leg divided into 7 joints, third from proximal end longest. Telson with 2-7 pairs of dorsal spines.

Key to Species

(From Williams 1974c; Noël 1978)

1. Tip of rostrum usually not reaching distal edge of eye (rarely exceeding eye). *E. pusiolus*
Tip of rostrum greatly exceeding distal edge of eye 2
2. Rostrum slender, toothed dorsally throughout length; second leg often with epipod *E. gaimardii*
Rostrum noticeably deepened at midlength, lacking dorsal teeth on distal part beyond eye; second leg usually without epipod *E. fabricii*

Eualus fabricii (Krøyer)

Fig. 76

Hippolyte fabricii Krøyer 1841:571.*Spirontocaris fabricii*.—Leim 1921:138, pl. 4, fig. 10.*Eualus fabricii*.—Holthuis 1947:10 (synonymy).—

Couture and Trudel 1968:873, fig. 13.

Recognition characters.—Rostrum slender but variable in depth; thicker above but lamellate below distally; horizontal or trending slightly upward distally to end in acute tip; about twice length of antennular peduncle; dorsal margin without teeth anterior to distal edge of eye but 1–7 teeth on posterior half (usually 2–3 of these postorbital), and 1–5 ventral teeth. Carapace with strong antennal spine below suborbital lobe and smaller pterygostomian spine at distoventral angle. Eyes well developed. Stylocerite with acutely pointed tip reaching to or beyond distal margin of basal antennular article; second article shorter, with dorsolateral spine; third article about $\frac{1}{2}$ length of second and with dorsal spine on distal margin, slender flagellum extending well beyond antennal scale in male, less far beyond in female. Antennal scale overreaching antennular peduncle by half its length, outer border straight; strong distolateral spine exceeded by lamella. Third maxilliped not reaching to tip of antennal scale; epipod and exopod present.

First leg with epipod; moderately stout, reaching about tip of antennal peduncle; carpus about as long as palm; fingers with darkened and hooked corneous tips. Second leg much longer and more slender, carpus divided into 7 joints, generally without epipod. Legs 3–5 well developed, each with row of spines laterally on merus; dactyls with strong curved spines on flexor surface progressively longer distally, tip biunguiculate.

Abdomen with pleura of first 3 segments broadly rounded; acute posteroventral spine on segments 4 and 5; less prominent on 6, but strong acute spine with ventral shoulder projecting beyond base of telson. Telson with (3)4–8 pairs of dorsal lateral spines.

Measurements in mm.—Length of body: males to 36 (Leim 1921); females to 58.

Color.—White ground spotted with deep bright red: area of fine red dots and larger spots to either side of dorsal carapace spines; larger scattered spots ventrally and posteriorly on cephalothorax; still other spots just posterior to orbit and at end of rostrum. Antennules and antennae with bands near end; edge of each antennal joint with faint red line. Basis and coxa of legs 3–5 purple; merus of first leg with red ring, that of 2–5 with 2; propodus of 3–5 with ring. Abdominal segments with scattered spots, small dots posteriorly on third segment (Leim

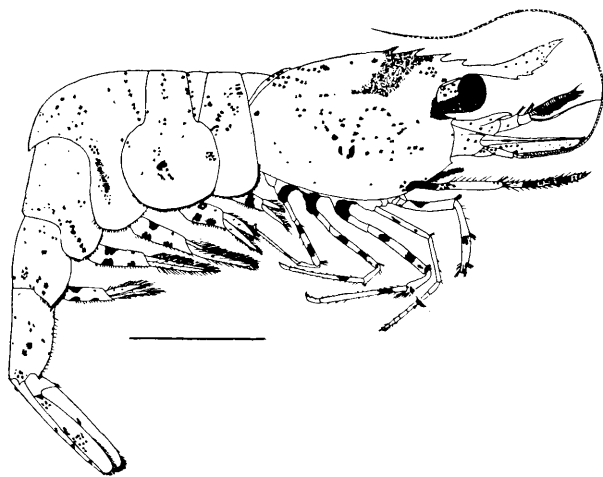


Fig. 76. *Eualus fabricii* (Krøyer). Animal in lateral view, 2 mm indicated (from Leim 1921).

1921). Fairly transparent with reddish orange in hepatic region; ovigerous females translucent white with red markings (MacGinitie 1955).

Habitat.—Variety of bottoms; 4–200 m.

Type-locality.—Greenland.

Known range.—Northwestern Greenland to Cape Cod; arctic Alaska to Cook Inlet; Siberian seacoast; Sea of Japan (Holthuis 1947; Squires 1965a).

Remarks.—Almost all females examined from Newfoundland and Labrador are ovigerous in spring (May–June) and autumn (October–November) (Squires 1965a). In Foxe Basin, Squires (1962) found only 64% of mature females potentially ovigerous in autumn, which may indicate that females in this population spawn only every two years, although those from Hudson Bay may spawn annually (Squires 1967). Ovigerous females in the USNM collection are represented from northwestern Greenland in June and July, Cape Sabine, Alaska, in August, and Point Barrow, Alaska, and Plover Bay, Siberia, in September. MacGinitie (1955) reported them at Point Barrow in mid-October. Stephensen (1916) considered this to be the most widely distributed species of *Eualus* (= *Spirontocaris*) in southern Greenland, and Frost (1936) reported its larvae to be the most common of the genus *Eualus* in plankton; although never numerous, the greatest numbers of larvae were reported off the coast of Labrador in spring and off the southeast coast of Newfoundland in fall. Pike and Williamson (1961) reviewed the work of previous authors on larvae, pointing out that Stephensen described and figured stages III, and V or VI, and that Frost figured the last zoeal stage, probably stage VI or VIII.

Food of the shrimp in the Hudson Bay–Foxe Basin region contains phytoplankton, crustaceans (including ostracods), hydroids, foraminiferans,

polychaete worm fragments, and sponge spicules, in descending order of quantity (Squires 1967). The species is preyed upon by cod, ringed, bearded, and harbor seals (Squires 1965a), and beluga whales (Squires 1967).

***Eualus gaimardii* (H. Milne Edwards)**

Fig. 77

Hippolyte Gaimardii H. Milne Edwards 1837:378.

Eualus gaimardii.—Heegaard 1941:36.—Holthuis 1947:10 (synonymy).—1950:46, fig. 15.

Eualus gaimardi.—Christiansen and Christiansen 1962:18.—Couture and Trudel 1968:875, fig. 14b.

Eualus belcheri.—Couture and Trudel 1968:875, fig. 14a.

Recognition characters.—Rostrum slender, curving slightly upward distally to end in acute tip, slightly carinate laterally, twice length of antennular peduncle; armed usually with 5–7 dorsal teeth (including postrostral crest) progressively more remote distally, and usually 3–5 ventral teeth. Carapace with antennal spine below suborbital lobe and pterygostomial spine at distoventral angle. Eyes well developed. Distal margin of basal antennular article exceeded by acutely pointed stylocerite; second article shorter, with distolateral spine; third article about $\frac{1}{2}$ length of second and with erect dorsal spine on distal margin. Antennal scale overreaching antennular peduncle by half its length, outer border slightly concave; distolateral spine exceeded by lamella. Third maxilliped reaching to or slightly short of tip of antennal scale; epipod and exopod present.

First and second legs with epipods; first leg

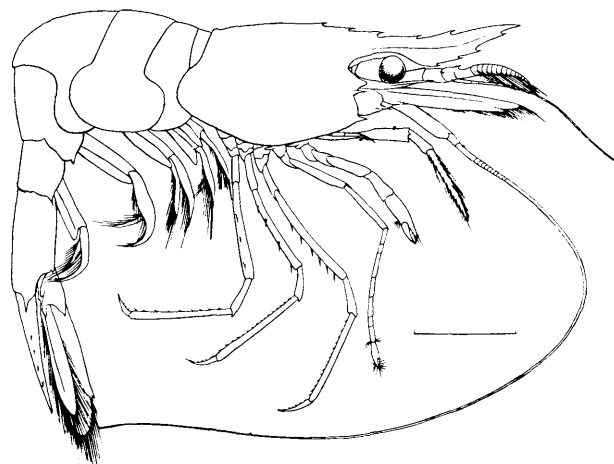


Fig. 77. *Eualus gaimardii* (H. Milne Edwards). Animal in lateral view, 5 mm indicated (from Holthuis 1950).

moderately stout, reaching about to end of antennal peduncle; carpus about as long as palm; fingers with darkened and hooked, corneous tips. Second leg much longer and more slender, carpus divided into 7 joints. Legs 3–5 well developed, dactyls with strong, curved spines on flexor surface progressively longer distally.

Abdomen with pleura of first 3 segments broadly rounded, posterior margin of third segment with mesiodorsal eminence variously developed; acute posteroventral spine on segments 4 and 5, less prominent on 6, but strong, acute spine with ventral shoulder projecting beyond base of telson. Telson with 3–5 pairs of dorsolateral spines.

Measurements in mm.—Length of body: to 100 mm (Smaldon 1979).

Variation.—This species shows great variation over its broad range. The rostrum proper varies considerably in shape and armature (dorsal teeth 3–7, ventral 2–6) (Dons 1915, fig. 5). Holthuis (1947) summarized the status of the named varieties of *E. gaimardii* as viewed by a number of authors. He concurred with the opinion that the species is composed of local forms which cannot be sharply distinguished because they gradually merge over their range: in the southern part of the range, both sexes have the third abdominal segment smooth and rounded (typical *gaimardii*); in the far northern and northwestern Atlantic, Arctic Ocean and North Pacific part of the range, males bear a strong tubercle ending in a curved hook on the posteromedian part of this segment and females have a distinct blunt tubercle (var. *belcheri*); in the area between these range extremes, males have a blunt tubercle on the third abdominal segment and females are smooth (var. *gibba*). Some authors continue to at least mention these varieties, for example, Greve (1963) included them in discussion, and Noël (1978) included them in his key to species of the genus; Couture and Trudel (1968) accorded var. *belcheri* full species rank, and Squires (1965a) recognized it as a subspecies, although in his other papers he did not always make a distinction and in one instance (1968) considered representatives of all these variants from the far northern Queen Elizabeth Islands area as *E. gaimardii*. I follow Holthuis here.

Color.—Translucent, “slightly tinged with greenish brown” (Smith 1879); transparent pale green with markings of red, eggs green (MacGinitie 1955); “pale translucent, with brownish-red markings on carapace on pleon” (Smaldon 1979).

Habitat.—On variety of bottoms such as stones, gravel, sand and shells, or mud bottom with algae, often off glaciers in North, -1.67° to 5.46°C , scarce above 3°C (Christiansen and Christiansen 1962); usually 20 to 150 m, but intertidal (Smith 1879) to 900 m (Smaldon 1979).

Type-locality.—"Habits les mers d'Islande" (off Iceland).

Known range.—Circumarctic southward to Cape Cod; North Sea (Kiel and Yarmouth); White Sea; Sitka, Alaska; Siberia (Holthuis 1947; Squires 1965a). Heegaard (1941) mapped the distribution.

Remarks.—Stomach content of this species in Hudson Bay was found to consist of phytobenthos, ostracods, amphipods, foraminiferans, hydroids, polychaetes, pelecypod shells, and sponge spicules, in descending order (Squires 1967).

Information on occurrence and life history is spotty and undoubtedly reflects discontinuous and seasonal collecting, especially in higher latitudes. For example, Squires (1967) found a few specimens in 33% of hauls taken in Hudson Bay, mostly in Richmond Gulf (east of Belcher Islands). The species was also present in stomachs of beluga whales taken along the northwestern coast of the Bay. Males were judged to be mature at a carapace length of 6 mm, females at 9 mm, but only 41% of females in this bay were assessed as potentially ovigerous per year. Squires postulated biennial spawning in these females (also in Foxe Basin, Squires 1965a), which perhaps are a stressed population. The USNM collection contains ovigerous females from Bering Strait in June to Point Barrow, Alaska, in September, as well as off Newfoundland, Labrador, and northeastern Greenland in July-August. MacGinitie (1955) reported eggs on females in August, September and October in progressive states of development. Smaldon (1979), referring to British coastal species, reported ovigerous females from January to April. Christiansen and Christiansen (1962) found ovigerous females in Spitsbergen during July-August.

From *E. gaimardii* eggs hatched in March at Millport, Scotland, Pike and Williamson (1961) reared and described five zoeal stages and a megalopa. Only stages I and II were found there in plankton. These authors reviewed published accounts of the larvae of this species, remarking on difference in size of eggs and larvae over the geographic range which they thought were most likely features of the named varieties.

Hansen (1897) reported the parasitic copepods *Choniostoma hansenii* and *C. mirabile* from the branchial cavity of *E. gaimardii*, and MacGinitie (1955) added the isopod *Phryxus abdominalis*.

Eualus pusiolus Krøyer

Fig. 78

Hippolyte pusiola Krøyer 1841:576.

Spirontocaris pusiola.—Kemp 1910:107, pl. 15, figs. 6–8.

Eualus pusiolus.—Holthuis 1947:11 (synonymy).—Couture and Trudel 1968:877, fig. 16.

Recognition characters.—Body small. Rostrum small, not exceeding eye; directed slightly downward; dorsal margin with 1-4, rarely 5, teeth, 1-2 of these behind orbital margin; tip acute, rarely 1 ventral tooth near tip making it bidentate. Carapace with antennal spine below suborbital lobe and small pterygostomian spine at distoventral angle. Eyes well developed. Stylocerite broad and not widely separated from basal antennular article for most of its length but narrowed abruptly to acute distolateral tip reaching from $\frac{2}{3}$ length to distal margin of basal antennular article; basal article with strong dorsolateral, distal spine, and mesioventral spine; second article shorter, with prominent, analogous distolateral spine; third article somewhat shorter than second and with small dorsal spine on distal margin. Antennal scale exceeding antennular peduncle by $\frac{1}{3}$ – $\frac{1}{2}$ its length, outer border straight, distolateral spine about equal to lamella; basal article of peduncle bearing distal acute ventrolateral spine and obtuse dorsolateral projection. Third maxilliped reaching to or beyond tip of antennal scale; epipod and exopod present.

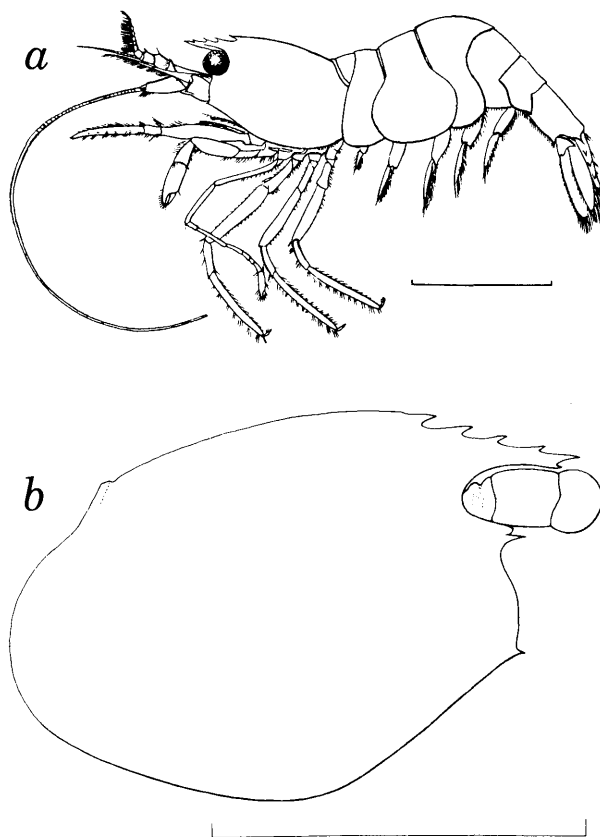


Fig. 78. *Eualus pusiolus* (Krøyer). a, Animal in lateral view, 5 mm indicated (from Kemp 1910); b, carapace in lateral view, 5 mm indicated (from Williams 1974c).

Legs 1–3 with epipods. First leg stout, reaching about as far as tip of antennular peduncle or length of fingers beyond it; carpus as long as palm; fingers with darkened and hooked, corneous tips. Second leg much longer and more slender, carpus divided into 7 joints. Legs 3–5 well developed, dactyls with a few spines on flexor surface, penultimate one stronger and more curved, forming with terminal spine, a biunguiculate tip.

Abdomen with pleura of first 3 segments broadly rounded; acute posteroventral spine on segments 4 and 5; less prominent on 6, but broad, acute spine with slight ventral shoulder projecting beyond base of telson. Telson with 4 or 5 pairs of dorsal spines.

Measurements in mm.—Length of body: to 30 mm (Couture and Trudel 1968).

Variation.—There is some variation in strength of spines on the antennular and antennal peduncles and in separation of the stylocerite from the basal antennal article. Dons (1915) figured some rostral variants; dorsal teeth on the rostrum tend to increase with age (Greve 1963).

Color.—Few deep red to orange-red spots scattered over whitish translucent background; spots evenly spread over cephalothorax and first two abdominal segments, 5 or 6 spots on third abdominal segment, and fourth to sixth segments with 2 or 3 ventral spots and posteroventral edges defined by red line; edges of uropods red. Scattered spots on peduncles of antennules and antennae, third maxillipeds and legs; joints of antennal flagellum and lateral edge of antennal scale red (Leim 1921). Pink, green, and cobalt forms are known (Smaldon 1979). Dark brownish green like color of *Laminaria* among which it occurs; stripes of red brown on body and extremities; eggs green (Greve 1963).

Habitat.—Sandy bottom with algae preferred (Greve 1963); inshore rock and offshore gravel (Allen 1966); intertidal among algae or under rocks low on shore to over 500 m (Smaldon 1979), in a recorded temperature range of -1.3° to 10.5°C (Williams and Wigley 1977).

Type-locality.—Norway's west coast.

Known range.—Gulf of St. Lawrence to off Cape Henry, Va.; Bering Island, Alaska Peninsula, and Aleutian Islands; San Juan Islands, Wash.; Iceland; Murman coast to Channel Islands; southward along Bay of Biscay to Spain (Holthuis 1947; Squires 1965a; Smaldon 1979).

Remarks.—Northeast of the British Isles breeding occurs year round, but is at its greatest intensity from January to September-October (Smaldon 1979). There are two broods of 8–10 weeks each there, a female bearing 100–300 eggs (Allen 1966). In Norway, ovigerous females are present from January to August (Greve 1963). Elsewhere, ovig-

erous females in the USNM collection are known from Massachusetts in July and August, Gulf of Maine in August and September, British Columbia and Bering Sea in June, and San Juan Islands, Wash., in July and August. The latter records are undoubtedly spotty and seasonally biased.

Pike and Williamson (1961) reared stage I larvae from a laboratory hatching at Millport, Scotland, in March, and reported all stages from the Irish Sea and Firth of Clyde from February to August-September. Six zoeal stages and some intermediates were described and figured; the variants probably are attributable to variations in diet. The postlarva was reared from the last larval stage at Millport and Port Erin, Isle of Man. The authors thought "*Spirontocaris C*" of Frost (1936) is almost certainly *E. pusiolus*.

Genus *Exhippolysmata* Stebbing 1915

Stebbing 1915:94.—Chace 1972:110.

Exhippolysmata oplophoroides (Holthuis)

Fig. 79

Hippolysmata (Exhippolysmata) oplophoroides Holthuis 1948:1106.—1959:112, fig. 17.—Williams 1965:85, fig. 69.

Exhippolysmata oplophoroides.—Chace 1972:110.—Christoffersen 1979:360.

Recognition characters.—Rostrum long, slender, directed somewhat upward, reaching beyond antennal scale by nearly half of length; basal portion elevated into crest bearing 9 to 10 closely placed teeth, 1 tooth some distance behind crest, remainder of upper margin with 1 to 6 widely separated teeth; ventral margin with 10 to 14 teeth. Carapace coarsely pitted; anterior margin produced into slight lobe below eye closely followed ventrally by antennal spine; pterygostomian spine at anterolateral angle. Eyes well developed. Basal article of antennular peduncle with stylocerite rather broad and pointed, reaching beyond middle of article; second article somewhat longer than third; upper flagellum simple with about 20 to 25 basal joints thickened, hairy below. Antennal scale almost 3 times as long as broad; outer margin slightly concave, ending in strong tooth; lamella of scale exceeding spine; outer spine near base of scale directed ventrally.

Epipods on first 4 pairs of legs small but distinct. First legs equal, reaching somewhat beyond end of antennal peduncle; fingers short and blunt, fixed finger ending in dark colored, sharp point fitting between 2 dark points on end of dactyl, outer surface of fingers convex, inner surface concave, fin-

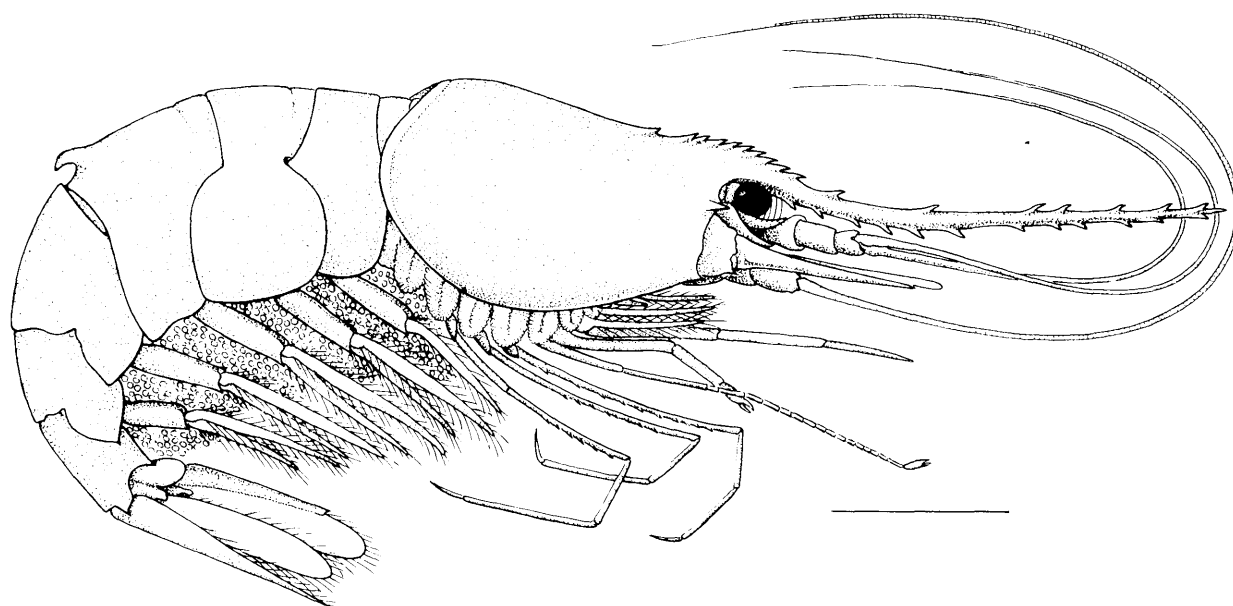


Fig. 79. *Exhippolysmata oplophoroides* (Holthuis). Ovigerous female in lateral view, 1 cm indicated (from Pérez Farfante 1978).

gers about 0.63 length of palm; carpus slightly shorter than chela and $\frac{3}{4}$ length of merus. Second legs slender; slightly unequal in size, reaching almost to end of third maxilliped; chela small and slender; carpus 5 times length of chela and divided into 13 to 15 joints, first and last joints longest. Third to fifth legs slender; dactyls simple.

Abdomen coarsely and shallowly pitted; third segment with dorsal carina ending in strong, posteriorly directed spine; pleura of second to fourth segment produced posteroventrally in narrowly rounded tip, pleura of fifth and sixth ending in distinct sharp tooth; posterolateral angle of sixth spiniform. Telson tapering gradually to slender point; dorsal surface with 2 pairs of spines, anterior pair at $\frac{1}{3}$ length, second pair closer to first pair than to tip. Uropods elongate; outer margin of exopod ending in 2 distinct teeth, between these a slender movable spine.

Measurements in mm.—Length of body: male 77; ovigerous females 47 to 85 (Christoffersen 1979).

Variation.—In the case of a rostrum with one distal tooth dorsally, there were suggestions of three other small, malformed teeth.

Color.—General color pink; rostrum and anterior part of carapace pink, posterior part of carapace white and yellowish; abdomen white with pink most pronounced along posterior margins of first to fourth segments, spine on third segment almost red, fifth and sixth segments entirely pink; tail fan red, pink at base; antennular and antennal flagella pink; legs red, sometimes purplish distally; pleopods red; eggs yellow or greenish (Holthuis 1959).

Habitat.—The species has been taken near shore,

often in estuaries (salinity 15.89‰) over mud bottom (Holthuis 1959); 0-6 to 27 m (Christoffersen 1979).

Type-locality.—Mouth of Suriname River near Resolutie, Surinam.

Known range.—Off Cape Fear River, N. C., to Port Aransas, Tex.; Guyana to the north of Uruguay.

Remarks.—Most information on this species is summarized by Holthuis (1959) and Christoffersen (1979). The species is more abundant than *Xiphopenaeus kroyeri* in Guyana but apparently less abundant to the eastward in nearby countries. Records from the United States are sporadic. Ovigerous females have been reported virtually the year round in Brazil, from Uruguay in April (Christoffersen 1979), April-June in Surinam (Holthuis 1959), and from August to October in the Carolinas.

Genus *Hippolyte* Leach [1814]

Verrill 1922:124.—Holthuis 1947:53.—Barnard 1950:701.—Hemming 1958b:157.

Rostrum long. Supraorbital spine present. Stylocerite acute. Mandible with incisor process and molar, without palp. Third maxilliped with exopod, lacking epipod; epipods present on first and second maxilliped. Chela of first leg rather short and stout. Carpus of second leg 3 jointed. Legs 3–5 subprehensile in male, propodus expanded in middle. Second abdominal segment very large. Telson with 2 pairs of dorsolateral spinules. (Barnard 1950.)

Key to Species

(Adapted from Chace 1972)

1. Lateral (branchiostegal) spine on carapace overreaching anterior margin; tergum of fifth abdominal segment armed with pair of strong posterior spines; antennal scale with blade and distolateral spine about equally advanced. *H. coerulescens*
Lateral (hepatic) spine on carapace not overreaching anterior margin; tergum of fifth abdominal segment unarmed; antennal scale with blade reaching far beyond distolateral spine. 2
2. Rostrum usually with 3 or 4 strong teeth on dorsal margin and distinct lateral carina in proximal 1/3 of length; basal article of antennular peduncle armed with 1–3 distolateral spines. *H. curacaoensis*
Rostrum usually with 2 (rarely 1 or 3) strong teeth in proximal half of dorsal margin and no lateral carina; basal article of antennular peduncle unarmed distally. 3
3. Rostrum not overreaching antennular peduncle in adult females, barely overreaching its basal article in males *H. pleuracanthus*
Rostrum distinctly overreaching antennular peduncle in adult females, extending nearly to distal margin of its second article in males *H. zostericola*

Hippolyte coerulescens (Fabricius)

Fig. 80

Astacus coerulescens Fabricius 1775:414.*Hippolyte acuminata*.—Gurney 1936b:27, 31, pl. 2, figs. 28–31; pl. 3, figs. 32–33; pl. 4, figs. 48–49; pl. 5.*Hippolyte coerulescens*.—Holthuis 1947:15, 53.—1952a:60, fig. 13.—Chace 1972:111, figs. 42–43.

Recognition characters.—As *H. pleuracanthus* except as follows: Rostrum rather stout at base, thinning distally, a little shorter than carapace, slightly decurved, armed with single dorsal and ventral tooth and tapering to acute tip reaching about to tip of antennal scale (somewhat shorter in male). Supraorbital spine strong. Branchiostegal spine overreaching anterior margin. Antennal scale broadest in proximal third, narrowing somewhat distally, lamella rather acutely angled anteromedially and about on level with distolateral spine.

Pleura of abdominal segment 2 very large, bending mesad in female to form broad pouch; segments 5 and 6 with large downturned spinous process on either side. Telson with tip truncate, bearing 3 pairs of small spines; lateral pair tiny; 2 pairs of tiny dorsolateral spines on margins of distal 1/4.

Measurements in mm.—Length of body: male 13; female 12.8 (Gurney 1936b).

Color.—Body “banded with brownish yellow in such a way that it seems to be broken up into two parts [cephalothorax-abdomen], each of which looks very like a vesicle of *Sargassum* (Pl. V)” (Gurney 1936b).

Habitat.—Usually associated with floating *Sargassum* (Chace 1972).

Type-locality.—“Pelago inter Tropicos.”

Known range.—Widespread in tropical and subtropical Atlantic Ocean (Chace 1972).

Remarks.—Chace (1972) thought the distinction between this and other species of *Hippolyte* might eventually warrant reestablishment of the genus *Virbius* Stimpson (1857–60, pars VIII).

Gurney (1936b) described the first larval stage of this species.

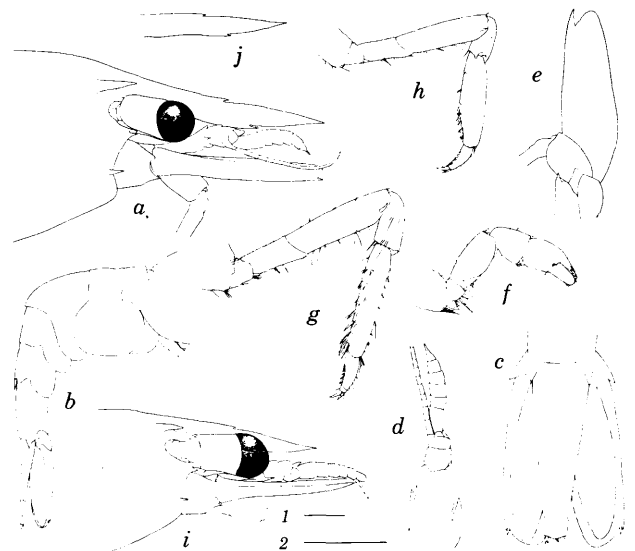


Fig. 80. *Hippolyte coerulescens* (Fabricius). Female: a, anterior region; b, abdomen; c, telson and uropods; d, right antennule; e, right antenna; f, right first leg; g, right third leg. Male: h, right third leg; i, anterior region; j, rostrum. Scales = 1 mm: 1 = b; 2 = all others (from Chace 1972).

Hippolyte curacaoensis Schmitt

Fig. 81

Hippolyte curacaoensis Schmitt 1924c:68, fig. 4.—
Chace 1972:111, figs. 44–45.

Hippolyte zostericola.—Williams 1965:82, fig. 66. [Not
Virbius zostericola Smith 1873c.]

Recognition characters.—Body smooth. Rostrum rather stout at base, thin distally, slightly decurved, armed dorsally with 3–4 and ventrally with 1–3 teeth; tip reaching beyond antennular peduncle in males. Anterior margin of carapace produced into prominent narrow lobe below eye followed ventrally by antennal spine; shallow emargination at base of antenna, anterolateral angle broadly rounded; hepatic spine well developed. Antennular peduncle with basal article long and broad, stylocerite slender, divergent at tip and well separated from article; basal article terminating in 1–3 spines on anterolateral corner; second and third articles much shorter than first; antennular flagella of about equal length, outer ramus stout basally, tapering to slender distal portion, hairy on ventral border. Antennal scale large, slightly exceeding rostrum and reaching nearly to end of antennular flagella, length a little over 3 times width; outer margin slightly concave, terminating in small spine exceeded by lamella; spine near base of scale.

First legs short, nearly equal, reaching base of distal article of antennal peduncle; chelae lightly setose, palm inflated, fingers about half length of palm, cutting edges finely serrate; carpus irregularly conical in shape, about $\frac{3}{4}$ length of chela, lower outer border with spiniform setae. Second legs slender, reaching to distal end of basal article of antennular peduncle; carpus longer than merus, divided into 3 joints; fingers about $\frac{2}{5}$ length of chelae, tips of cutting edges with spines; chelae hairy. Third to fifth legs long; third reaching to tip of antennal scale; dactyls with series of spines in comblike arrangement on inner border; propodi spined on flexor margin.

Abdomen strongly bent at third segment; posterior portion of third segment raised with hook-like projection overhanging fourth segment. Telson tip truncate, bearing 3 pairs of spines, inner 2 pairs about equal, outer pair much shorter. Uropodal exopods with lateral border ending in small spine flanked mesially by movable spine.

Measurements in mm.—Length of body: male about 7.5 (Schmitt 1924c); ovigerous females 10 to 12.

Habitat.—Sand and mud flats; associated with marine grasses.

Type-locality.—West Punt, Curaçao.

Known range.—Beaufort and Sneads Ferry, N. C.; West Indies from Cuba to Curaçao.

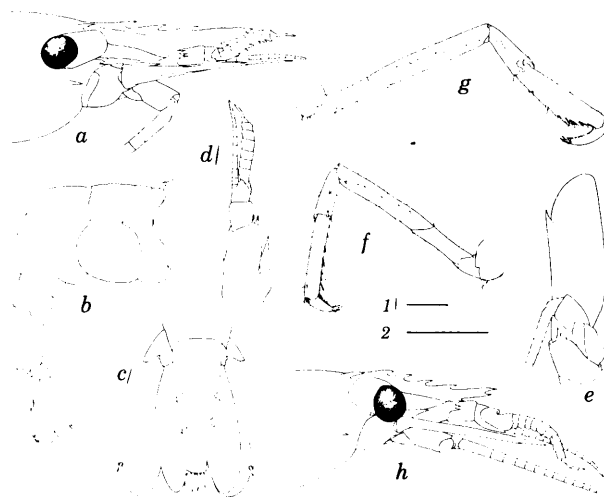


Fig. 81. *Hippolyte curacaoensis* Schmitt. Female: a, anterior region; b, abdomen; c, telson and uropods; d, right antennule; e, right antenna; f, left third leg. Male: g, right third leg; h, anterior region. Scales = 1 mm: 1 = b; 2 = all others (from Chace 1972).

Remarks.—This species, confused with *H. zostericola* by Williams (1965), is the only species of *Hippolyte* in the region possessing a lateral carina on the basal region of the rostrum and terminal spines on the first peduncular article of the antennule (Chace 1972).

Ovigerous females are known from July to September in North Carolina, and November to April in the West Indies (USNM).

Hippolyte pleuracanthus Stimpson

Fig. 82

Virbius pleuracanthus Stimpson 1871b:127.

Hippolyte pleuracantha.—Williams 1965:80, fig. 65.

Hippolyte pleuracanthus.—Chace 1972:118, fig. 48.

Recognition characters.—Body smooth, with tufts of plumose hairs on dorsal surface of carapace and abdomen, tips of abdominal pleura, and distal portion of eyestalks. Rostrum rather stout at base, thin distally, slightly decurved, armed dorsally with 2 (rarely 1 or 3) teeth and ventrally with 1–3 teeth; tip in adult female reaching about to end of antennular peduncle, barely overreaching basal article in male. Anterior margin of carapace produced into lobe below eye followed ventrally by antennal spine, an emargination at base of antenna followed by slightly produced, broadly rounded anterolateral angle; hepatic spine strong. Eyes well developed. Antennular peduncle with basal article long and broad, stylocerite slender, lanceolate, reaching about to middle of article and separated from lateral border of article by about width of stylocerite, article ending in short, broad, elevated, bladelike projec-

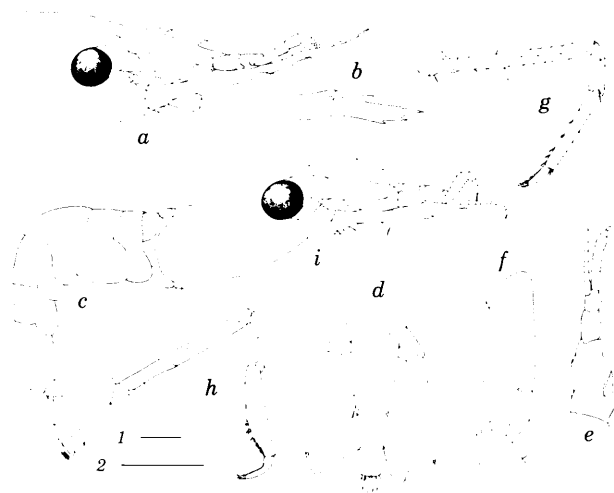


Fig. 82. *Hippolyte pleuracanthus* (Stimpson). Female: *a*, anterior region; *b*, rostrum; *c*, abdomen; *d*, telson and uropods; *e*, right antennule; *f*, right antenna; *g*, right third leg. Male: *h*, right third leg; *i*, anterior region. Scales = 1 mm; 1 = *c*, 2 = all others (from Chace 1972).

tion, a short spine at anterolateral corner under blade; second and third articles much shorter than first; antennular flagella of about equal length; outer ramus stout, broadest in middle; tapering to slender distal portion, hairy on ventral border. Antennal scale large, exceeding rostrum and reaching nearly to end of antennular flagella, length a little over three times width; outer margin slightly concave, terminating in small spine exceeded by lamella; spine near base of scale.

First legs short, nearly equal, reaching a little beyond base of distal article of antennular peduncle; chelae setose, palm inflated, fingers about half length of palm, cutting edges finely serrate; carpus irregularly conical in shape, about $\frac{3}{4}$ length of chela, lower outer border with spiniform setae. Second legs slender, reaching to tip of antennular peduncle; carpus longer than merus, divided into 3 joints; fingers $\frac{2}{5}$ length of chelae, tips of cutting edges with spines; chelae hairy. Third to fifth legs long; third reaching to tip of antennal scale; dactyls with series of spines in comblike arrangement on inner border; propodi spined on flexor margin.

Abdomen strongly bent at third segment; posterior portion of third segment raised with hood-like projection overhanging fourth segment. Telson with tip truncate, bearing 3 pairs of spines, inner 2 pairs nearly equal, outer pair much shorter. Uropodal exopods with lateral border ending in small spine flanked mesially by movable spine.

Measurements in mm.—Length of body: ovigerous females 12 to 18; males somewhat smaller.

Variation.—The rostrum of some females exceeds the antennular peduncle, but is shorter than

that of *H. zostericola*; the rostrum of some males exceeds the second peduncular article (Shield 1978).

Color.—Usually mottled brown or red, often a bright green.

Habitat.—Extremely abundant in beds of vegetation (*Zostera* and *Diplanthera*) in sounds and bays. Also found among rocks of jetties.

Type-localities.—Norfolk Harbor, Va., and Somers Point, Great Egg Harbor, N. J.

Known range.—Connecticut to North Carolina.

Remarks.—*Hippolyte pleuracanthus* and *H. zostericola* have been much confused over the years. Chace's (1972) concept of the former removes from active consideration published observations on its biology made outside the recorded geographic range. Little is lost because virtually the only information concerns breeding time. Provenzano and Dobkin (1962) reared larvae attributed to *H. pleuracanthus* (= *zostericola*?), but Shield (1978) gave results of a more complete study. From ovigerous females collected between June and September in Bogue Sound, N. C., eggs were hatched in the laboratory and larvae reared on a diet of *Artemia salina* nauplii in average water temperature and salinity of 25.2°C and 33.9‰. Eight larval stages were described and figured. Stages occurred in regular sequence until the fifth molt, but varied after that, postlarvae appearing after stages VII and VIII, others passing through intermediate stages, and metamorphosis of survivors occurring during the ninth or tenth molt. Shield summarized studies on larvae of the genus showing that, for two western North Atlantic species, Gurney (1936b) had described stage I of *H. coerulescens* and six zoeae and a postlarva of *H. zostericola* from hatched eggs or plankton, and she outlined developmental variation in a number of forms. *Hippolyte coerulescens* larvae are transparent with a few green-brown chromatophores; *H. pleuracanthus* larvae have twice as many red pigmented spots; *H. zostericola* larvae are dark olive-brown with chromatophores.

Hippolyte zostericola (Smith)

Fig. 83

Virbius zostericola Smith 1873c:550, pl. 3, fig. 11.

Hippolyte zostericola.—Chace 1972:118, figs. 49–50.

Recognition characters.—As *H. pleuracanthus* except as follows: Rostrum somewhat upturned distally in females, more nearly straight or slightly decurved in males; armed dorsally with 2 (rarely 1 or 3) teeth and ventrally with 1–4 teeth; tip reaching beyond antennular peduncle in adult females, nearly to distal margin of second article in males.

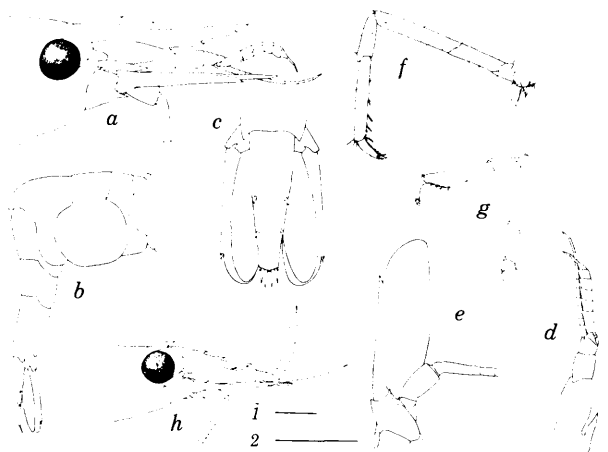


Fig. 83. *Hippolyte zostericola* (Smith). Ovigerous female: a, anterior region; b, abdomen; c, telson and uropods; d, right antennule; e, right antenna; f, third left leg. Male: g, third left leg; h, anterior region. Scales = 1 mm: 1 = b; 2 = all others (from Chace 1972).

Measurements in mm.—Length of body: male 14 (carapace 4.75); female 15.5 (carapace 6).

Variation.—Chace (1972) observed that *H. zostericola* and *H. pleuracanthus* may not prove to be distinct but that the problem may be resolved by study of large series of specimens. His discussion will not be repeated here except to observe that relative

rostral length of the two species overlaps, that of *H. zostericola* females from south of Woods Hole, Mass., to North Carolina being no longer than the antennular peduncle, as in *H. pleuracanthus*, but at Woods Hole many females have the rostrum considerably overreaching the antennular peduncle, as do specimens from east Florida, and especially from the northern and eastern Gulf of Mexico where the tendency is most pronounced.

Color.—Bright green, pale or translucent tinged with green; sometimes specked with reddish brown and with a broad median band of dark brown extending whole length of body (Smith 1873c).

Habitat.—Beds of vegetation such as eelgrass.

Type-locality.—Vineyard Sound, Mass.

Known range.—Southern Massachusetts; North Carolina to Yucatan; Trinidad and Curaçao; Ceará, Brazil (Fausto-Filho (1975); Bermuda.

Remarks.—Ovigerous females are known throughout the year in Florida and the Caribbean region, and from June to October in Massachusetts (USNM). Life history comparisons in which Shield (1978) found differences from *H. pleuracanthus* are given in the account for *H. pleuracanthus*.

Genus *Latreutes* Stimpson 1860

Stimpson 1860:27[96].—Hemming 1958b:157.

Key to Species

1. Carapace and rostrum unarmed dorsally except for single, small, median spine on gastric region; rostrum an elongate blade nearly as long as carapace *L. fucorum*
- Carapace strongly humped and armed dorsally with 5 or 6 spiniform teeth; rostrum a deep ovoid blade, shorter than carapace *L. parvulus*

Latreutes fucorum (Fabricius)

Fig. 84

Palaemon fucorum Fabricius 1798:404.

Latreutes ensiferus.—Hay and Shore 1918:390, pl. 26, fig. 13.

Latreutes fucorum.—Verrill 1922:131, pl. 16, figs. 5–5b; pl. 42, figs. 2–2t; pl. 44, figs. 1–1m, 2a–2n, 3.—Sivertsen and Holthuis 1956:31, pl. 1, figs. 1–2 (color).—Williams 1965:78, fig. 63.—Chace 1972:121.—Pequegnat and Ray 1974:251, fig. 60.

Recognition characters.—Rostrum thin, nearly as long as carapace, smooth edged, broadest at base and deepest near base, slightly concave dorsally and upturned at tip, convex ventrally; tip subtruncate and armed with about 5 to 7 small, acute spinules. Carapace smooth; small middorsal spine on gastric

region; anterior margin produced into acute lobe below eye followed ventrally by wide, nearly rectangular emargination and series of 4 to 9 small denticles at anterolateral angle; spine removed from margin near suborbital lobe. Eyes well developed, with tuberculate swelling anteromesially near cornea. Antennular peduncle with basal article excavate laterally; stylocerite broad, thin, cupped dorsally; distal spine on lateral border of basal article reaching about to base of third article; second and third articles short; distal border of third obscurely denticulate, outer flagellum thick at base. Antennal peduncle stout; antennal scale wide at base, tapering to acute terminal spine, scale about as long as rostrum. Third maxilliped elongated, leglike; distal article long, with 8 or 9 acute marginal spines.

First legs incurved, short, relatively stout, unequal; larger chela thick, proximally broad, ovate,

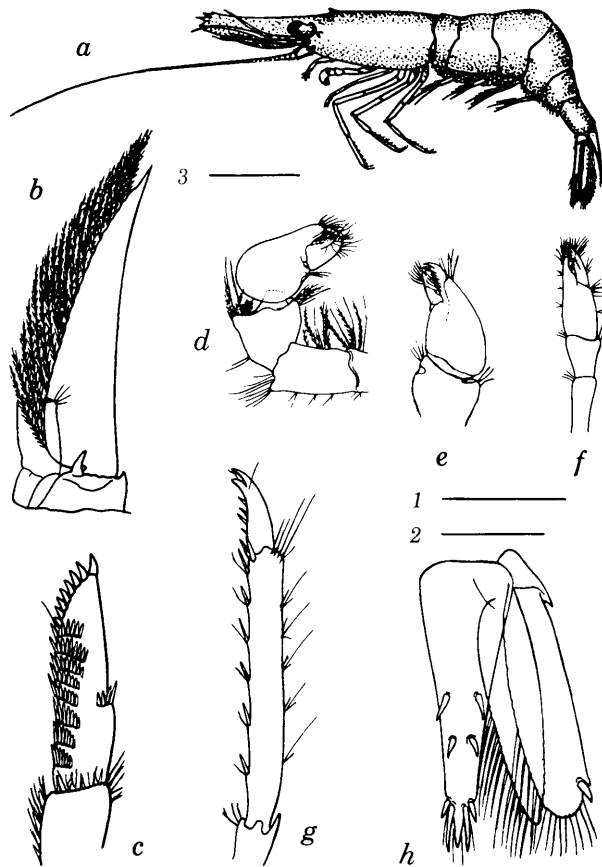


Fig. 84. *Latreutes fucorum* (Fabricius). *a*, Animal in lateral view (from Bate 1888); *b*, antennal scale; *c*, distal article of third maxilliped; *d*, right first cheliped; *e*, left first cheliped; *f*, second cheliped; *g*, distal articles of third leg; *h*, telson and uropods (from Verrill 1922). Scales: 1(*a-b, d, f-h*) = 1 mm; 2(*c*) = 0.3 mm; 3(*e*) = 0.5 mm.

tapering distally; dactyl wide, longer than fixed finger, with broad lateral lobe and about 3 denticles at tip; fixed finger bent slightly inward and arched, tip subacute or slightly bidentate; fingers hairy; carpus large, cup shaped, broader than long; merus and carpus excavate beneath. Second legs slender; chelae slender, somewhat unequal; fingers about as long as palm, hairy at tip; carpus with 3 unequal joints, middle one longest. Third to fifth legs long, slender, subequal; propodi and dactyls with row of spines on lower edge.

Abdomen smooth. Telson long, narrow, tapering to narrow tip with spiniform median process flanked by 2 pairs of unequal spines, inner pair longer than median process; pair of dorsal spines at half and $\frac{3}{4}$ of length. Uropodal exopods with outer edge terminating in small spine flanked mesially by movable spine.

Measurements in mm.—Length of body: adults 12 to 20, males smaller than females.

Variation.—The rostrum varies greatly in length, depth, and number of spines (Wass 1955).

Color.—Often nearly colorless and transparent; sometimes with body pale yellow, yellowish green, greenish brown, brown, red, black, black with white spots and bars; bright blue patches on dorsal and lateral surfaces; often mottled, striped or barred, and corresponding in pattern to irregularly colored bits of weed (various authors).

Habitat.—Common in floating masses of *Sargassum*; surface waters; also common on grass flats in tropical Atlantic (Rouse 1970; Chace 1972).

Known range.—Western North Atlantic between 10° and 50°N; Azores and Cape Verde Islands (Chace 1972).

Remarks.—Ovigerous females have been found virtually year round in various parts of the range. Gurney (1936a) described the first stage larva.

Brown (1939) found four kinds of pigment in this shrimp (white, red, yellow, and blue) similar to pigments found in *Hippolyte*, *Leander*, and *Palaeomonetes* species. The red and yellow pigments respond to white background by concentration into the chromatophore centers and to black background by dispersion into the chromatophore branches. *Latreutes* has a great abundance of white pigment which may vary in color from yellowish white to clear white. Darkness produces concentration of the reflecting white chromatophores. Direct sunlight of a bright sky produces dispersion of white pigment in spite of black background. Blue patches on the animals apparently consists of blue pigment accumulated in particular white chromatophores. Brown concluded that the different color patterns in this species are not solely results of responses to particular situations, but are at least partly genetic patterns repressed or encouraged by light intensity in color of the background. The response is similar to responses in crustaceans having far less ability to change color.

Markham (1977) annotated the description of the bopyrid parasite *Probopyrinella latreuticola*, reviewing its taxonomic status and geographic distribution. This branchial parasite is the only known parasite of *L. fucorum*. It is found equally in right or left gill chambers of the host.

Latreutes parvulus (Stimpson)

Fig. 85

Rhynchocyclus parvulus Stimpson 1866:48.—1871b: 124.

Concordia gibberosus.—Hay and Shore 1918:391, pl. 26, fig. 11.

Latreutes parvulus.—Holthuis 1947:59.—1951b:131, fig. 28.—Williams 1965:79, fig. 64.—Chace 1972:124.—Coelho and Ramos 1972:153.

Recognition characters.—Rostrum laterally compressed, almost circular in outline in female, more elongate in male; upper margin with 6–8 teeth in female, 2–4 in male; few small teeth on tip; lower margin unarmed or with up to 5 shallow teeth; ventral part of rostrum produced somewhat backward. Carapace with middorsal row of 5–7 small, erect teeth, row starting somewhat anterior to middle of carapace, extending to base of rostrum; carapace somewhat swollen in female, making an angle at base of middorsal row of teeth; upper margin nearly straight in males; anterior margin with narrow, anteriorly directed lobe forming lower angle of orbit, slender spine on lobe; anterolateral angle serrate with 2–4 teeth; row of 3 or 4 slender

spines a bit removed from and parallel to margin between anterolateral angle and lower margin of orbit. Eyes well developed; cornea globular; eye-stalks with truncated process at upper inner margin overlapping line separating cornea from stalk. Antennular peduncle with stylocerite broad and rounded, hollowed above and together with basal article of peduncle forming concavity for reception of eye; second article of peduncle much shorter than third; upper flagellum shorter than lower, with 7 or 8 broad and 1 or 2 narrow joints. Antennal scale about twice as long as broad, overreaching end of rostrum; outer margin nearly straight, ending in small tooth reaching about as far as lamella; small spine on outer surface of peduncle near base of scale.

First legs equal, short, thickset, slightly overreaching base of antennal scale; fingers somewhat shorter and narrower than palm, tips of fingers ending in dark-colored nails; palm broadened posteriorly; carpus somewhat conical, about as long as palm. Second legs more slender, reaching about to end of antennal peduncle; chelae with fingers shorter than palm; carpus almost twice length of chela, 3-jointed, median joint longest; merus $\frac{2}{3}$ as long as carpus. Third to fifth legs with dactyls ending in sharp tooth, posterior margin with 4 comb-like teeth progressively smaller proximally.

Abdomen smooth. Telson triangular; with pairs of dorsal spines at $\frac{1}{2}$ and $\frac{3}{4}$ length; tapering to narrow tip with spiniform median process flanked by 2 pairs of spines, inner pair longest; terminal portion with feathered setae. Uropodal exopods with outer margin ending in small spine flanked mesially by movable spine.

Measurements in mm.—Length of body: 7 to 12; males smaller than females.

Variation.—Shape of the rostrum, as well as its spination, is subject to some variation.

Habitat.—Littoral waters from (in?) sponges among shells, dead coral, hydroids, and on sea-grass flats; surface to 44 m.

Type-locality.—St. Joseph Island, Texas.

Known range.—Beaufort, N. C., to Rio de Janeiro, Brazil; West Africa.

Remarks.—*Latreutes parvulus* is not known to be common anywhere in its range. It has been taken throughout the year in the Carolinas. Ovigerous females have been taken throughout the year in various part of the range north of the equator and in February in Brazil.

Genus *Lebbeus* White 1847

Holthuis 1947:9 (synonymy).—China 1966:243.

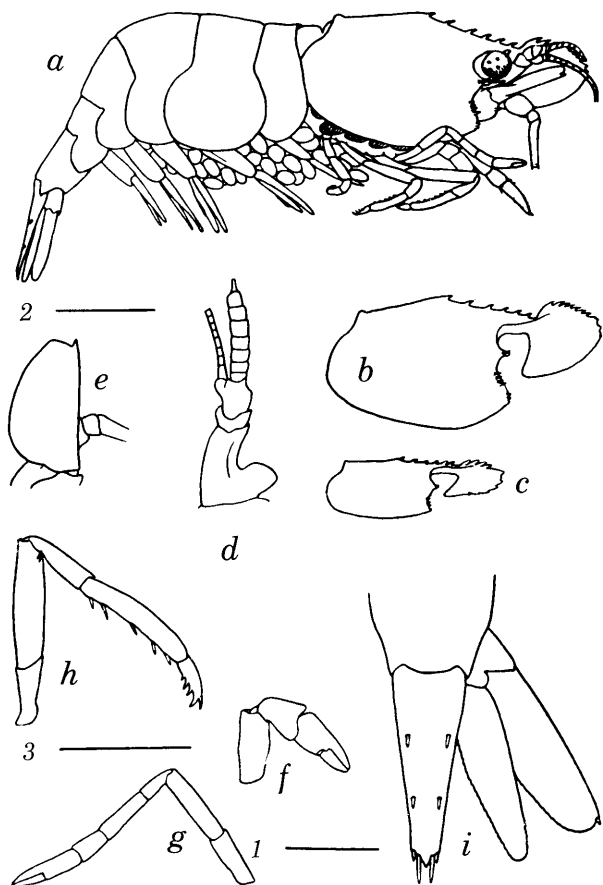


Fig. 85. *Latreutes parvulus* (Stimpson). a, Ovigerous female in lateral view; b, carapace of ovigerous female in lateral view; c, carapace of male in lateral view; d, antennule; e, antennal scale; f, first leg; g, second leg; h, third leg; i, telson and right uropod in dorsal view (from Holthuis 1951b). Scales: 1(a-c)=2 mm; 2(d-e), 3(f-i)=1 mm.

Key to Species

(From Williams 1974c; Couture and Trudel 1968)

1. Four (sometimes 3) prominent spines along middorsal line of carapace; pleura of all abdominal segments toothed ventrally or posteroventrally *L. groenlandicus*
No more than 2 spines along dorsal line of carapace; pleura of first 3 abdominal segments rounded 2
2. Rostrum long, tip exceeding basal antennular article in juveniles and entire peduncle in adults; ventral margin of rostrum variable but not horizontal *L. polaris*
Rostrum short, tip not exceeding basal article of antennular peduncle; ventral margin of rostrum horizontal *L. zebra*

Lebbeus groenlandicus (Fabricius)

Fig. 86

Astacus groenlandicus Fabricius 1775:416.*Lebbeus groenlandicus*.—Holthuis 1947:9 (synonymy).—Couture and Trudel 1968:870, fig. 10.

Recognition characters.—Rostrum rather slender in lateral view, inclined slightly upward to acute tip reaching beyond second article of antennular peduncle in adults; usually 2–3 dorsal spines on rostrum proper, and 2–3 ventral spines near tip, but 0/0 in juveniles and sometimes 2/5 in adults. Carapace surmounted with carina extending from rostrum to posterior margin and bearing usually 4 (sometimes 3) strong, forward pointing spines or teeth; single supraorbital spine very strong and acute; suborbital lobe closely flanked by very long,

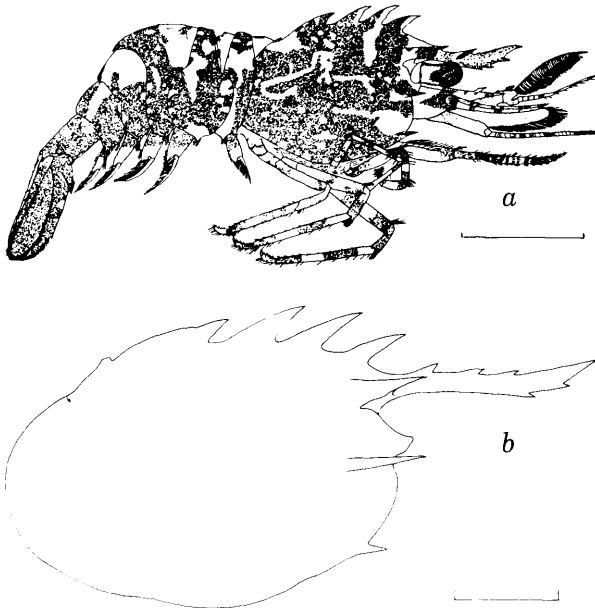


Fig. 86. *Lebbeus groenlandicus* (Fabricius). a, Female in lateral view, 10 mm indicated (from Leim 1921); b, carapace in lateral view, 5 mm indicated (from Williams 1974c).

buttressed, slender, acute antennal spine; concave anteroventral margin ending in smaller pterygostomial spine. Eyes well developed. Antennules with basal article bearing spine on distodorsal margin, strong distolateral spine, and mesioventral spine; stylocerite slender, ending in acute point reaching to beyond third peduncular article; latter with elongate, acute lateral spine; third article about half length of second and bearing slender distal spine directed obliquely dorsad. Antenna with peduncle reaching to about midlength of antennal scale; basal article with acute dorsolateral spine, and longer, stronger ventrolateral spine; antennal scale with lateral margin slightly concave or straight, distolateral spine strong, slightly short of or exceeding convex tipped lamella. Third maxilliped with epipod, extending beyond antennal scale.

First 3 legs with epipods. First legs stout, reaching beyond antennal peduncle; fingers shorter than palm, tips dark, dactyl cleft distally to receive tip of fixed finger; palm a little shorter than merus, latter with lateral spine proximally. Second legs longer and more slender, carpus 7-jointed. Third to fifth legs with stout dactyls bearing curved spines on flexor margin, penultimate spine stout at base, shorter than terminal spine but making tip biunguiculate; meri of third leg with up to 9, fourth with about 5–7 lateral spines, fifth with about 5–7, distalmost of each distinctly strongest.

Abdomen with pleura of all segments toothed or spined ventrally; that of first segment ending in 2 nearly equal points, posterior somewhat stronger; of second ending in single point; of third to fifth each ending in strong posterior point but secondary smaller point anterior to it, both progressively stronger posteriorly; sixth with long posteroventral spine with shoulder at base and above it a posterior spine with variable shoulder overlapping base of telson. Telson broadly sulcate dorsally, median boss proximally; rather obtusely pointed tip bearing 2 pairs of stout spines, outer pair short, mesial

pair long and setae mesial to these; 4–5 pairs of dorsolateral setae, often asymmetrical in number and arrangement.

Measurements in mm.—Length of body: male 74, female 97.

Variation.—The rostrum varies considerably from stout to rather slender, the latter usually in males (Leim 1921). Moreover, its relative length changes with growth, being shorter than the eyes in juveniles; tooth number increases with age. Number of pleural spines is usually two on segments 1, 3, 4, 5, and one on 2 and 6. About 25% of individuals seen by Leim (1921) had only one pleural spine on segment 3, and a few had this number on 4 and 5; conversely, there were sometimes three on 4 and 5, or an asymmetrical number.

Color.—Shades of color and pattern variable; usually brownish red, sometimes brownish green; greater part of animal colored but carapace uncolored in small areas, just posterior to eye, dorsal to pterygostomian spine, running ventrally from second dorsal spine, posterior to fourth dorsal spine, and scattered smaller areas variable in position except for 5 along posterior half of ventral edge. Abdomen with principal non-colored areas across segment 1 dorsolaterally, anterodorsally on segment 4, narrowing and continuing diagonally across 5 and extending slightly onto segment 6. Ventral edges of abdominal segments red. Rostrum, antennules and antennae with scattered dots, flagella banded; distal article of third maxilliped and legs variously banded (Leim 1921).

Habitat.—Rock and gravel bottom (Proctor 1933); 2 to 314 m in a recorded temperature range of -1.3° to 9.4°C (Holthuis 1947; Squires 1965a; Williams and Wigley 1977).

Type-locality.—“Habitat in mari groenlandico.”

Known range.—Greenland southward to Rhode Island; arctic Canada and Alaska; southern Chuckchi Sea through Bering Sea to Puget Sound, and Sea of Okhotsk southward to Vladivostok (Holthuis 1947; Nesis 1963; Squires 1965a). Heegaard (1941) mapped and summarized the distribution, characterizing it as that of a “boreo-arctic-pacific species which on its way eastwards has reached Greenland,” and Nesis (1963) characterized it as “arctic-boreal or lower arctic-boreal.”

Remarks.—Squires (1965a) reported one ovigerous female in May, but many in August and September from which embryonated eggs probably hatch in late autumn or early winter. A single spawning per year was indicated by his samples from southern to middle parts of the northwestern Atlantic range, but farther north in Hudson and Frobisher bays where animals first mature at carapace lengths of 11 (δ), 15 (f), and 10 (δ), 14 (f)

mm respectively, ovigerous females found in August were judged to spawn only every two years. Samples in the USNM collection contain ovigerous females from Kamchatka in June and September, southeastern Alaska and Aleutian Islands in July to November, Murchison Sound, Greenland, in August, and Puget Sound, Washington, in September; these samples are spotty and seasonally biased.

From eggs of known parentage held until hatching in a refrigerated recirculating aquarium system maintained between 6° and 8°C at 32–34‰ salinity, Haynes (1978b) reared larval stages of *L. groenlandicus* in flasks suspended at 6-m depths in the sea. Development from the rather large eggs passed through two zoeal stages and a megalopa which were described and illustrated from the reared larvae and plankton. Haynes reviewed the status of larvae previously attributed to this species. Ivanov (1971) also described and illustrated some developmental features of this species from laboratory rearings.

In 35 stomachs examined, phytobenthos, crustacean fragments including euphausiids and ostracods, foraminifera, and hydroids were found in decreasing order (Squires 1967). Cod is a predator on *L. groenlandicus* (Squires 1965a); most specimens taken in the southern part of the northwestern Atlantic were in stomachs of this fish. In Ungava Bay, Squires (1957) found the bearded seal to be a common predator, as is the beluga whale in northwestern Hudson Bay (Squires 1967).

Lebbeus polaris (Sabine)

Fig. 87

Alpheus polaris Sabine 1824:ccxxviii, pl. 2, figs. 5–8.

Lebbeus polaris.—Holthuis 1947:9 (synonymy).—Christiansen and Christiansen 1962:15.—Greve 1963:35, fig. 1E.—Couture and Trudel 1968:871, fig. 11.—Smaldon 1979:62, fig. 23.

Recognition characters.—Rostrum rather long in adults, extending forward to often daggerlike tip reaching beyond antennular peduncle, shorter in juveniles; 0–8 spines in rostral series (2–3 behind orbital margin) and 1–5 ventral spines (see variation); low lateral carina thinning distally toward tip, lamellate portion below it deepest anterior to eye. Carapace with single strong supraorbital spine; suborbital lobe closely flanked by antennal spine; slightly convex anteroventral margin ending in smaller pterygostomian spine (rarely obsolescent). Eyes well developed. Antennules with basal article bearing dorsolateral spine on distal margin, lateral

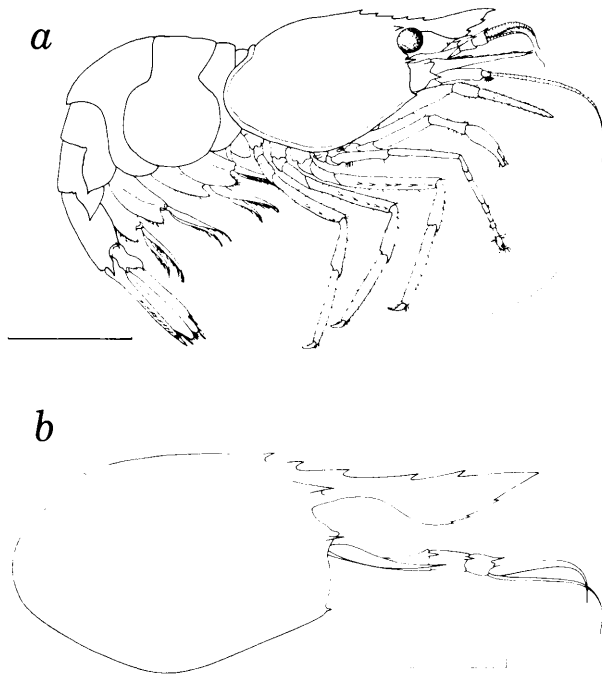


Fig. 87. *Lebbeus polaris* (Sabine). *a*, Animal in lateral view, 10 mm indicated (from Smaldon 1979); *b*, carapace and antennule in lateral view, 5 mm indicated (from Williams 1974c).

spine or lobe below it, and mesioventral spine; stylocerite slender, ending in acute point reaching about to end of basal article or beyond it nearly to distal end of second article bearing lateral spine; third article about $\frac{1}{2}$ length of second and bearing distal spine directed obliquely dorsad; mesial thickened ramus bearing short terminal flagellum, slender lateral ramus longer. Antenna with peduncle reaching about half length of antennal scale; basal article with ventrolateral spine and dorsolateral lobe; antennal scale with lateral margin straight, distolateral spine exceeded by rounded tip of lamella. Third maxilliped with epipod, extending well beyond antennal scale.

First 2 legs with epipods. First legs stout, reaching from about length of fingers to $\frac{1}{2}$ length of chela beyond antennal peduncle; fingers shorter than palm, tips dark, dactyl cleft distally to receive tip of fixed finger; palm about $\frac{1}{3}$ – $\frac{1}{2}$ length of merus, latter with tiny lateral spine proximally. Second legs longer and more slender, carpus 7-jointed. Third to fifth legs with stout dactyls bearing curved spines on flexor margin, penultimate spine stout at base, shorter than terminal spine but making tip biunguiculate; merus of third leg with usually 7–8 (range 5–10) lateral spines, distalmost longest; fourth leg similarly with 6–7 (range 1–9) lateral spines, and fifth with 3–4 (range 1–7) lateral spines.

Abdomen with pleura of first 3 segments

rounded; 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 82, female 90.

Variation.—Sexual dimorphism becomes pronounced with increasing age. Females have both dorsal and ventral rostral spines, but older males lack rostral spines. Younger males (up to 43 mm) have an intermediate spinous pattern on the rostrum (Greve 1963; Squires 1965a). Dons (1915) illustrated several tooth patterns. Variations in number of spines on legs 3–5 (as above) were recorded by Leim (1921).

Color.—Scattered orange red areas of minute dots over carapace and abdomen, mainly dorsally; larger dots behind and below posterior carapace spine and below these some small areas of dots with sulfur yellow tinge. Rostrum orange spotted, ventral edge bright red. Head appendages and first 2 legs with scattered spots; legs 3–5 dark orange. Posterior border of abdominal segments 5 and 6 red (Leim 1921). Butler (1964) found two specimens in British Columbia to have body milkish white with 6 main red and yellow transverse bands extending over dorsal and lateral carapace and abdomen, with 15 lighter bands of blue and yellow between these; most appendages yellow.

Habitat.—Variety of soft to hard bottoms; < 1 to 930 m (Holthuis 1947; Greve 1963; Christiansen and Christiansen 1962; Squires 1965a).

Type-locality.—Coast of Melville Island, 50 fm (91.45 m).

Known range.—Circumarctic southward to off Chesapeake Bay; Bering Sea; British Columbia; Sea of Okhotsk; Skagerrak and Hebrides (Holthuis 1947; Butler 1964; Squires 1965a). Heegaard (1941) mapped the distribution.

Remarks.—Ovigerous females in the USNM collection are from eastern Georges Bank in January, off Woods Hole, Nantucket, Cape Cod, Nova Scotia, Newfoundland and Labrador from July to September, and off Delaware in October; Foxe Basin in August; off northern Greenland in July and August; Aleutian Islands in July and in September, along with Pribilof Islands and Point Barrow; and Franz Joseph Land in July. Heegaard (1941) reported ovigerous females from Greenland throughout the year, and Christiansen and Christiansen (1962) found them during July–August in Spitsbergen. MacGinitie (1955) found females with

new eggs at Point Barrow in September. Greve (1963), in a review, reported ovigerous females from western Norway in November, March, May and July, and northern Norway in summer. She thought that females either carry eggs all year or that there is a difference in time of spawning between southern and northern Norway. Squires (1965a; 1967) found larvae hatched in autumn as well as spring in the northern Atlantic, suggesting that a majority of females reach maturity at an early age and spawn annually more than once, although in the far northern Queen Elizabeth Islands (1968) spawning may be biennial. He presented evidence that there are three age groups representing at least that number of years. Several authors have commented on variation in size in different areas.

Pike and Williamson (1961) commented on knowledge of the larvae, the only described examples being one which Krøyer (1842) dissected from a ripe egg, and specimens described by Stephensen (1916; 1935), some of which probably belong to another species.

Observed stomach contents (Squires 1967) consisted of phytobenthos, detritus, crustacean fragments of shrimps, mysids, amphipods and ostracods, hydroids, sponge spicules, polychaete worms, foraminiferans, and gastropod and pelecypod shells in decreasing order of abundance. Predators are cod, seals, and murre (Squires 1965a).

Hansen (1897) found the parasitic copepod, *Choniostoma hansenii*, in the branchial cavity of *L. polaris* from the Kara Sea and west coast of Greenland.

Lebbeus zebra (Leim)

Fig. 88

Spirontocaris zebra Leim 1921:133, pls. 2–3.

Lebbeus zebra.—Holthuis 1947:10 (synonymy).—

Couture and Trudel 1968:873, fig. 12.

Recognition characters.—Rostrum short, inclined slightly downward; with 2–5 spines in dorsal series, 1 (–2?) behind orbital margin; small acute tip not exceeding basal article of antennular peduncle, slightly overhanging small subterminal spine at end of horizontal ventral margin. Carapace highest at level of posterior spine in rostral series; single supraorbital spine strong, acute; suborbital lobe closely flanked by strong antennal spine; somewhat angled anteroventral margin ending in smaller pterygostomial spine. Eyes well developed. Antennules with basal article bearing 2–4 spines on distodorsal margin (sometimes asymmetrical in number), and appressed mesioventral spine; sty-

locerite ending in acute, slightly divergent point falling slightly short of prominent distolateral spine on short second article; third article much shorter than second, with strong and less acute distodorsal spine; lateral ramus with slender distal whip about as long as thickened proximal portion, mesial ramus slender and longer. Antenna with peduncle reaching beyond distal margin of basal article of antennular peduncle; basal article with acute ventrolateral spine and dorsal lobe; antennal scale exceeding antennular peduncle, lateral margin straight, distolateral spine equaling lamella with convex tip. Third maxilliped with epipod but no exopod, extending well beyond antennal scale.

First 3 legs with epipods. First legs rather stout, reaching about length of fingers beyond antennal peduncle; fingers shorter than palm, tips dark, dactyl cleft distally to receive tip of fixed finger; palm $\frac{3}{4}$ length of merus, carpus $\frac{2}{5}$ length of merus; merus with proximolateral spine. Second legs longer and more slender, carpus 7-jointed. Third to fifth legs with stout dactyls bearing curved spines on flexor margin, penultimate spine stout at base, shorter than terminal spine but making tip biunguiculate; merus of third leg with 3–5 lateral spines, distalmost longest; fourth leg with 2–6 lateral spines; fifth leg with 0–2 lateral spines.

Abdomen with pleura of first 3 segments rounded; fourth segment with small posteroventral spine; fifth similar though with spine directed more posteriorly; sixth with even less prominent

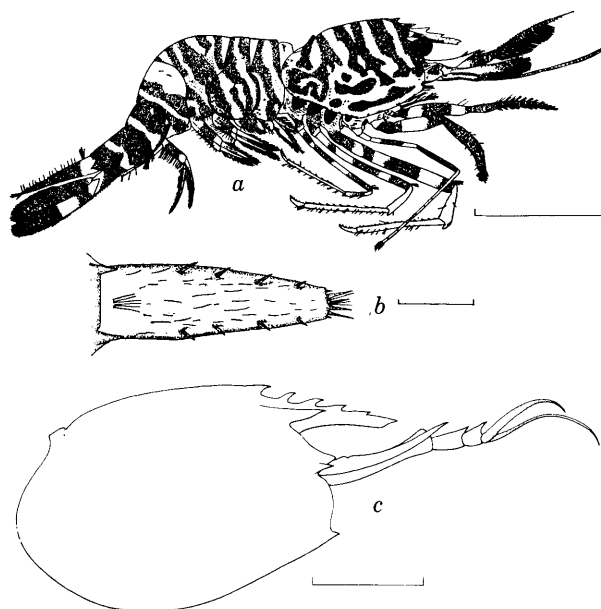


Fig. 88. *Lebbeus zebra* (Leim). a, Female in lateral view; b, telson; a, approx. 10 mm; b, approx. 2 mm indicated (from Leim 1921); c, carapace and antennule in lateral view, 5 mm indicated (from Williams 1974c).

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: female 49 (Leim 1921).

Color.—Banded with bright brownish red to orange stripes generally running dorsoventrally, those of cephalothorax and 3 anterior abdominal segments somewhat oblique; areas between stripes bluish on cephalothorax, white elsewhere. Appendages alternately banded white and orange, but bands purplish on coxa, basis and ischium of legs. Sharp red line defining edges of all abdominal segments (except anterior edge of second), lateral edge of stylocerite, antennal scale, and antennal peduncle (Leim 1921).

Habitat.—On rock (Proctor 1933); 10 to 91 m in a temperature range of 8.2° to 9.7°C (Williams and Wigley 1977).

Type-localities.—Head Harbor, Campobello Island, N. B. (ROM 5143); Passamoquoddy Bay, Joe's Point, St. Andrews, N. B. (ROM 5144); Stn. 4, Passamoquoddy Bay, 30 m (ROM 5145).

Known range.—Port Burwell, Ungava; Gulf of St. Lawrence to southeast of Isles of Shoals, 42°52'N, 70°20'W (Proctor 1933; Holthuis 1947; Squires 1965a; Couture and Trudel 1968); Checleset Bay, Vancouver Island (Butler 1964).

Remarks.—Holthuis (1947) pointed out that in 1935 Makarov described *Hetairus zebra* from the Bering Sea and Kamchatka which may be the same as Leim's species, having similar color and general body structure but differing in shape of rostrum (longer, more dorsal and ventral teeth, and deeper distal to eyes). Butler (1964) compared a female from Vancouver Island with paratypes of *L. zebra*, deciding that they agreed closely in color pattern and morphology, but he thought that Makarov's species differed, as pointed out above. Couture and Trudel (1968) noted the great resemblance of *L. zebra* to *L. microceros* (Krøyer 1841), which may be synonymous, but rarity of specimens has prevented an evaluation of differences or similarities between them.

Genus *Lysmata* Risso 1816

Chace 1972:124.

Key to Species

(Adapted from Chace 1972)

1. Rostrum usually reaching as far as, or beyond, end of antennular peduncle; antennal scale 5 times as long as wide *L. rathbunae*
- Rostrum reaching not much, if at all, beyond second article of antennular peduncle; antennal scale less than 4 times as long as wide
- *L. wurdemanni*

Lysmata rathbunae Chace

Fig. 89

Lysmata rathbunae Chace 1970:59, figs. 1–4.

Recognition characters.—Rostrum straight or slightly concave dorsally, reaching as far as or beyond antennular peduncle; armed dorsally with 5 or 6 teeth, posteriormost widely separated from second tooth, and ventrally with 3–5 teeth. Carapace smooth; not dorsally carinate behind teeth or rostral series; anterior margin with large, sharp antennal spine overlying and concealing bluntly triangular ventral angle of orbit; anterolateral angle rounded. Eyes well developed, short and stout. Basal article of antennular peduncle large, small ventral tooth near midlength of mesial margin; stylocerite tapering to sharp point reaching about to end of proximal 1/3 of article; second and third articles

progressively shorter; each article of peduncle with 2–4 dorsolateral spinules near distal margin; inner flagellum slender; outer flagellum with about 14–35 thickened basal joints. Antennal scale 5 times as long as wide; lateral margin slightly concave, terminating in sharp distal tooth distinctly overreaching subtruncate distal margin of blade.

Epipods on first 4 pairs of legs. First legs stout, reaching to end of antennal scale; fingers slightly more than 1/2 length of palm; carpus slightly shorter than chela. Second legs subequal in length but much longer and more slender than first legs; chela small; carpus nearly twice as long as merus and divided into 30–35 joints, merus into 16–24 joints; ischium with 3–5 joints in distal half. Third to fifth legs not so slender as second, dactyls with few coarse spines on flexor surface.

Abdomen smooth, posterolateral angle of fifth segment acute, sixth with buttressed posteroventral

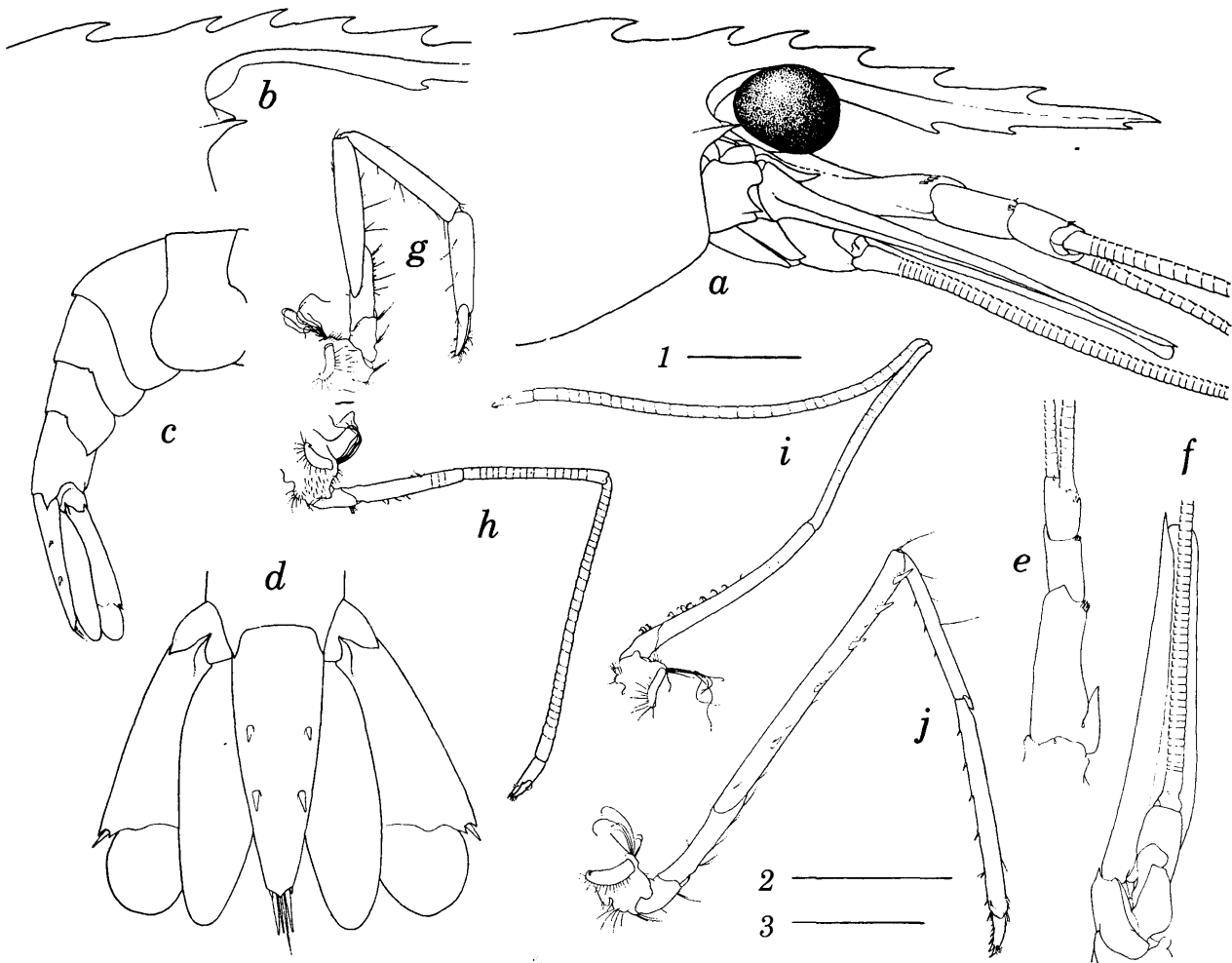


Fig. 89. *Lysmata rathbunae* Chace. Male: a, anterior region in lateral view; b, orbital region; c, abdomen; d, telson and uropods; e, right antennule; f, right antenna; g, right first leg; h, right second leg; i, left second leg; j, right third leg (from Chace 1970). Scales: 1(c); 2(a-b, d); 3(e-j) = 5 mm.

tral tooth. Telson tapering to tip with tiny median projection flanked by 2 long, slender spines, short spine outside these on each side; armed dorsally with pair of prominent spines at $\frac{1}{3}$ and $\frac{2}{3}$ length. Uropodal exopods with outer margin ending in 2 teeth, slender movable spine between these.

Measurements in mm.—Length of carapace: male 6.7; ovigerous females 6.3–9.6 (Chace 1970).

Variation.—Chace (1970) pointed out that there are two varieties of this species, the typical form with the penultimate proximal tooth of the rostral series in line with the rear edge of the orbit, and another form having more numerous rostral teeth with the posterior two teeth of this series placed distinctly posterior to the rear of the orbit, and having 38–43 joints in the carpus of the second leg. The latter may prove to be a distinct species if more material confirms this dichotomy.

Habitat.—Sometimes from sponges; typical form 13 to 119 m; many-spined form 9 m and less.

Type-locality.—Off Boynton Beach, Fla., 26°31'N, 80°01'W, 55–64 m.

Known range.—Typical form: SE Cape Fear, N. C., 33°30'24"N, 77°24'30"W, 25 m; east coast of Florida to Yucatan. Variety with more numerous rostral teeth: Bermuda; Miami, Fla.; Venezuela.

Remarks.—Ovigerous females are reported from Florida in March, and July–September.

Lysmata wurdemanni (Gibbes)

(Red cleaning shrimp)

Fig. 90

Hippolyte Wurdemanni Gibbes 1850:197.

Hippolysmata wurdemanni.—Hay and Shore 1918: 392, pl. 26, fig. 12.

Hippolysmata (Hippolysmata) wurdemanni.—Williams 1965:84, fig. 68.—Coelho and Ramos 1972:153.

Lysmata wurdemanni.—Chace 1972:129.

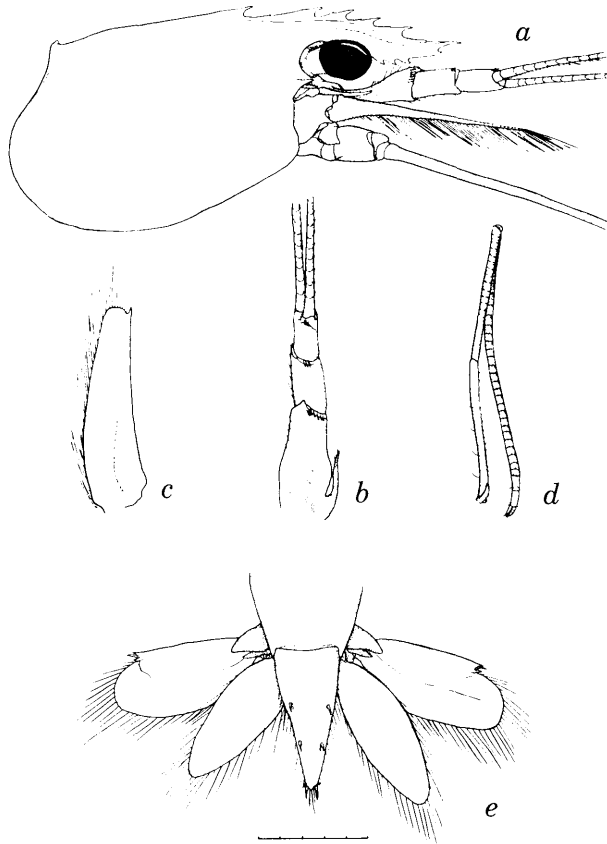


Fig. 90. *Lysmata wurdemanni* (Gibbes). *a*, Anterior portion of body in lateral view; *b*, antennule; *c*, antennal scale; *d*, second leg; *e*, uropods and telson in dorsal view; 5 mm indicated (from Williams 1965).

Recognition characters.—Rostrum reaching distal end of second article of antennular peduncle, slightly decurved, armed dorsally with 4 or 5 teeth and ventrally with 3 to 5 teeth. Carapace smooth; carinate dorsally on anterior half with spine near base of rostrum about midway between rostral tip and posterior border; anterior margin with strong antennal spine somewhat concealing triangular ventral angle of orbit; anterolateral corner rounded. Eyes well developed. Basal article of antennular peduncle large, small ventral tooth near midlength of mesial margin; stylocerite slender, flattened, pointed, reaching a little beyond middle of article; second and third articles progressively shorter; each article with 2–5 dorsolateral spinules near distal margin; inner flagellum slender; outer flagellum with about 20 to 30 thickened basal joints. Antennal scale less than 4 times as long as wide; outer margin slightly concave, terminating in strong spine; lamella of scale subtruncate distally, about equal to spine.

Epipods on first 4 pairs of legs. First legs moderately stout, about equal, reaching to end of antennal scale; fingers about $\frac{1}{3}$ length of palm, spines

at tips of fingers darkened; carpus and hand of nearly equal length. Second legs subequal in length but much longer and more slender than first legs; chela small; carpus small; carpus divided into about 30 joints, last joint longest; merus divided into about 20 joints, and ischium into about 5 in distal half. Third to fifth legs not so slender as second; dactyls with few coarse spines on flexor surface.

Abdomen smooth; posterolateral angle of fifth and sixth segments acute. Telson tapering to tip with minute median projection flanked by 2 long, slender spines, short spine outside these on each side; armed dorsally with 2 pairs of prominent spines at $\frac{1}{3}$ and $\frac{2}{3}$ length. Uropodal exopods with outer margin ending in 2 distinct teeth, slender movable spine between these.

Measurements in mm.—Length of body: males 28 to 54; ovigerous females 38 to 55 (Wass 1955 in part).

Variation.—Individuals from the northern extreme of the range differ in some respects from those in South America (Holthuis 1959). The rostrum in South American specimens has four to seven dorsal teeth, and in specimens from the United States, four or five. Some southern specimens have stylocerites nearly as long as the basal antennular articles. In southern specimens, the tip of the lamella on the antennal scale is more truncate than in northern specimens. The second leg in Guiana material is more slender than in northern material, and the number of articulations in the carpus is higher, 33–37 as opposed to 27–31. Chace (1972) gave further details and remarked on scarcity of the species in the West Indies.

Color.—Translucent white with beautiful longitudinal and transverse markings of red.

Habitat.—Commonly found on stone jetties or among hydroids growing on piles or buoys, or in sponges (Tabb and Manning 1961); surface to 37 m (USNM).

Type-locality.—Key West, Fla.

Known range.—Great Egg Harbor, N. J., to Port Aransas, Tex.; Surinam; French Guiana; Mamanaguape, São Paulo, Brazil.

Remarks.—Ovigerous females are known in January, February, May and June from Florida (Tabb and Manning 1961; Wass 1955; Rouse 1970; USNM), January from South Carolina (USNM), April from Quintana Roo, Mexico (Chace 1972), April and August from North Carolina, May from the Guianas (Holthuis 1959), and August from Louisiana (USNM). Protandry has been observed in two European and Mediterranean species of *Lysmata* (Yaldwyn 1966a). When approached by a spiny boxfish or filefish, this shrimp begins rhythmically rocking to and fro; ascending vertically in

a peculiar walking motion, it mounts its "host" and begins picking off parasites. The shrimp will swarm over the fingers of a person, picking at cuts and dead skin (Anonymous 1975).

Genus *Spirontocaris* Bate 1888

Holthuis 1947:7.—Hayashi 1977:155.

Rostrum well developed, upper margin dentate, lower margin usually so. Carapace with armed dorsal carina and 2–4 supraorbital spines. Eyes well developed, inner basal part of stalk umbonate. Third maxillipeds with exopods. Second leg with carpus subdivided into 7 joints. Epipods on legs 1, 1–2, or 1–3.

Key to Species

(from Williams 1974c; Couture and Trudel 1968)

1. Middorsal teeth extending to or beyond posterior $\frac{1}{3}$ of carapace; spines on rostrum of nearly uniform size *S. phippisii*
Middorsal teeth falling short of posterior $\frac{1}{3}$ of carapace; spines on rostrum definitely unequal in size 2
2. Ventral margin of rostrum with 4–6 teeth; tip ascending to well-defined single point extending beyond antennal scale *S. liljeborgii*
Ventral margin of rostrum with about 2 (occasionally 3) large teeth and variable number of smaller ones (0–many); tip single or often almost equaled or surpassed by prominent ventral tooth; not extending beyond antennal scale *S. spinus*

Spirontocaris liljeborgii (Danielssen)

Fig. 91

Hippolyte Liljeborgii Danielssen 1859:5.

Spirontocaris liljeborgii.—Holthuis 1947:8 (synonymy).—1950:43, fig. 14.—Greve 1963:32, figs. 1B, D.

Spirontocaris liljeborgii.—Couture and Trudel 1968:866, fig. 7.

Spirontocaris liljeborgii.—Smaldon 1979:64, fig. 24A–D.

Recognition characters.—Rostrum deep, convex upper margin ending in acute, horizontal to slightly upturned tip reaching nearly to end of antennal scale; row of many dorsal teeth variable in size and number, smallest anteriorly and extending posteriorly along middorsal carina approximately $\frac{2}{3}$ length of carapace; ventral margin of rostrum convex, bearing 1–5 teeth variable in size, shape, and arrangement. Carapace bearing 2 supraorbital spines on each side, upper one slightly larger; suborbital lobe distinctly flanked by antennal spine; anteroventral margin almost straight; pterygostomian 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 midlength of second article; latter bearing slender lateral spine; third article about half length of second, with slender distolateral

spine; thick 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 extending to about level of distolateral spine. Third maxilliped reaching beyond antennal scale, exopod and epipod present.

First 3 legs with epipods. First leg moderately stout, reaching about length of fingers beyond antennal peduncle; fingers darkened at tips, that of dactyl cleft to accommodate tip of fixed finger; palm about length of carpus; merus with small proximolateral spine. Second leg much longer and more

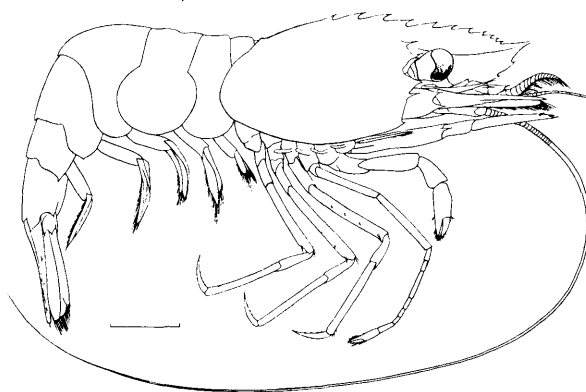


Fig. 91. *Spirontocaris liljeborgii* (Danielssen). Animal in lateral view, 5 mm indicated (from Holthuis 1950).