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COLUMBIA BRACHYURA**

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THE LARVAL DEVELOPMENT OF BRITISH COLUMBIA BRACHYURA

I. XANTHIDAE, PINNOTHERIDAE (IN PART) AND GRAPSIDAE¹

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Abstract

The larval stages of four species of crabs inhabiting British Columbia are described from series obtained by hatching eggs in the laboratory. In the development of *Lophopanopeus bellus* (Stimpson) there are found to be four zoeal stages, of *Pinnotheres taylori* Rathbun two, and of *Hemigrapsus nudus* (Dana) and *H. oregonensis* (Dana) five. There is only one megalopal stage in each of the species.

Knowledge of the life history of Pacific coast decapod Crustacea is very-limited. The free-swimming larvae form an important part of shallow water plankton, and as such are a component of the food of fish and macro-plankton. Although the larvae occur in great numbers near the shore, comparatively little is known of their development, owing perhaps to the fact that it is usually necessary to rear the stages to be at all sure of correct identification, as the larvae are so unlike the adults and in many cases so like one another. They are difficult to rear in artificial conditions, and as far as the writer has been able to determine, complete series of only four species have been recorded to date. In this paper all the larval stages of four more species that have been reared from the egg are described. Various authors have described series, taking the stages from plankton, but this method is obviously less accurate than rearing them from the egg.

Lebour's paper (10) is invaluable for the study of early Brachyuran development. It is a brief monograph of the larval stages of some 35 species of crabs inhabiting the Plymouth area. In America, Hyman (5-7) gives summaries of work done previously by others, and makes original contributions to the knowledge of the larvae of the families Xanthidae, Pinnotheridae and Grapsidae. Aikawa (1, 2) describes some of the zoeal stages of a large number of Japanese crabs, dealing particularly with the determination of characters

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that might be used for classification. There are a number of other papers describing forms found on both sides of the Atlantic ocean, but the works of these three authors have been of most value in the study of crabs found in British Columbia.

Methods of Rearing

The chief difficulty encountered in rearing decapod larvae is the maintenance of a constant supply of suitable living food. Many of the forms eaten in the natural state, when placed under laboratory conditions, soon die and their decomposition products in the water kill the larvae. The life histories of so few forms in this locality have been worked out that there are practically no records of the spawning periods of the invertebrates, and therefore it is difficult, without considerable research, to determine what larvae are available at the different seasons. Lebour (8-10) was successful in rearing three species of crabs in "plunger-jars" on a diet of *Ostrea*, *Teredo*, *Echinus* and *Pomatoceros*. The megalopa and young crabs were fed on small pieces of the mantle of *Mytilus edulis*. The writer has found the larvae of the native oyster, *Ostrea lurida* Carpenter, satisfactory for feeding, as the larvae are retained for some time in the mantle cavity of the adult and therefore can be obtained in quantity, yet are free-swimming when placed in the water. The veliger larvae of Nudibranchs and the trochophore larvae of the Japanese oyster were also used, but did not prove as suitable as those of the native oyster. The megalopa and young crabs ate finely minced muscle of various molluscs.

Berried females were collected and placed in aquarium jars. When the eggs hatch, the larvae swim to the surface of the water and may be removed with a pipette and placed in large beakers of sea water containing food. The water was aerated by stirring with a glass rod. The larvae were examined daily and fresh water and food given if required, and all dead material and sloughed skins removed. Records of pigmentation were kept and specimens of each stage, as well as cast off skins, preserved.

The Developmental Stages

Few records have been obtained of the length of time necessary for the embryonic development of decapods. According to the writer's observations seven weeks is the shortest period during which the eggs were carried attached to the pleopods of the female, and thus protected, kept free from encrustations and debris, and aerated. The length of time seems to be proportional to the size of the adult. The size of the egg mass and the average size of the eggs vary greatly with the different species.

When the egg hatches, the last embryonic stage, the prezoa or protozoa, is set free. This stage may last for some hours, or in exceptional cases, days, but usually is replaced by the first larval stage soon after hatching. The prezoa is enclosed in a thin membranous cuticle covering the entire body and appendages. In many species this membrane is produced, and delicately plumed, beyond the invaginated tips of the antennules, antennae and telson.

The spines of the carapace, which are present in the first zoea, are held flat against the body by the cuticle in the prezoa and the setae and spines are invaginated upon themselves. The prezoa is able to swim by jerky movements of the abdomen, similar to the movements of gnat pupae. In all the Grapsoid crabs that have been observed to hatch from the egg, the prezoa lacked the prolongations of the membrane found in other forms.

When the embryonic cuticle is cast off, the first zoea swims to the surface of the water by the powerful beating of the exopodites of the first two pairs of maxillipedes. The zoea has a well developed carapace, which may be produced into a rostral, a dorsal and paired lateral spines. There usually is a pair of short setae on the dorsal part of the carapace, above the heart. The abdomen of the first stage is composed of five segments and the telson. The sixth segment may become separate from the telson in a later stage. The thoracic appendages consist of a pair of large compound eyes, tubular antennules, antennae, bilobed mandibles, two pairs of lamellar maxillae and the first two pairs of maxillipedes. The exopodites of the maxillipedes are equipped in the first zoea with four two-jointed, long, plumose setae. The remainder of the thoracic appendages appear as small knobs posterior to the maxillipedes and are covered by the carapace. There are no functioning appendages on the abdomen, but paired swellings may be present on the second to the fifth segments—the pleopods of the post-larva. There is always a lateral knob on either side of the second abdominal segment, and there may be similar, usually smaller ones, on the third, fourth or fifth segments. There may be spines on the lateral posterior angles of the second to fifth segments. The telson is typically bicornuate, with three pairs of internal setae and varying numbers of external spines. The number of internal setae often increases in the later stages and the spines may decrease in number.

When the first zoea moults and the second emerges, the number of setae present on the appendages is found to have increased in most cases. Six is the usual number of setae on the exopodites of the swimming maxillipedes in the second zoea, eight in the third, ten in the fourth and twelve in the fifth. In those forms having only two zoeal stages the non-functioning appendages are of the same degree of development as those of the last zoea of the forms with four or five stages.

The last zoea metamorphoses into the post-larva; the megalopa. It resembles the adult crab in shape and the appendages are all functional. The megalopa can swim freely through the water by means of well developed pleopods, bearing long plumose setae. The abdomen may be flexed under the thorax when the pleopods are not in use. There may be large spines on the carapace and hook-like knobs on the coxae of some of the periopods. In all those crabs that have been reared from the egg only one megalopal stage has been found, the first young crab stage appearing after the first moult of the megalopa. The first young crab stage is like the adult in structure, but usually of different shape and proportions. By subsequent moults the specific characters of the adult are gradually assumed.

Decapod larvae are usually very transparent when alive. The amount and color of the pigment varies according to the degree of contraction of the chromatophores. In some forms the chitin itself may be tinged with bright colors. As the color does not preserve well, it is only of value in preliminary sorting of living or recently killed material, especially in those forms that are morphologically similar but differ in coloration.

The length of time spent in each stage seems to depend considerably on the relative abundance of food, the temperature and salinity of the water and other such external conditions. The first zoeal stage, in suitable natural conditions probably lasts for two or three days, and the time spent in each stage increases as the larva grows. Under laboratory conditions, four to five weeks is usually required for development from the egg to the young crab stage.

The larvae vary considerably in size, so that measurements are only relative. That this variation is not entirely due to the food supply is shown by the lack of uniformity in size and color of the brood hatched by one female.

In attempting to find characteristics suitable for classification, it is necessary to use those that do not become greatly modified as the animal develops. The spines of the carapace, the armature of the abdomen and telson, and the form of the antennae are perhaps the most important. Aikawa (2) uses the number of setae on the endopodites of both maxillae and of the second pair of maxillipedes. The form of the rostrum, the spines on the carapace, the presence of sensory setae on the last pair of legs, and the number of setae on the exopodites of the uropods are characteristic of the megalopae.

Family Xanthidae

The larval development of a number of species of the family Xanthidae has been followed by other workers. Hyman (7) describes some of the stages of forms found at Beaufort, North Carolina, and compares them with European species described by other authors. Lebour (10) gives the characters of the larvae of the family and the description of stages of three species. Connolly (4) gives an account of the larval stages of *Rhithropanopeus harrisi* (Gould) from New Brunswick. On the Pacific, Aikawa (1) studied the first zoeae of two species of *Xantho* found in Japan.

The zoeae and megalopa of *Lophopanopeus bellus* (Stimpson) described below, fit into Lebour's (10) characterization of the larvae of the family Xanthidae, sub-family Xanthinae, with the exception of the number of lateral spines on the telson of the zoeae. The telson resembles that of *Rhithropanopeus harrisi* (Gould), in having only one lateral spine on each fork.

Lophopanopeus bellus (Stimpson)

Eggs carried in April; hatching May to August, changing in color from deep purple to light brown, and increasing in size from 0.33 to 0.41 mm. in diameter.

Typical prezoëa, four zoeæ and one megalopa. First young crab stage obtained in laboratory five weeks after eggs hatched. Second died five weeks later when attempting to cast its skin.

Prezoëa similar in color to first zoea. Spines of carapace flattened against body. Two embryonic spines, of unequal length, enclose antennule. Exopodite of antenna covered by four hairy projections of cuticle. Telson with seven embryonic spines on each side, all but fourth plumose.

First zoea (Fig. 1, *A*) 1.5 mm. (measured from tip of the telson fork to front of head) and 1.5 mm. from tip of dorsal spine to end of rostral. Body tinged with yellow, and rostral spine, antennæ and telson forks with russet. Black chromatophores on bases of antennules, on mandibles and maxillæ, at bases of lateral and dorsal spines, on postero-lateral part of carapace, on distal part of bases of first and second maxillipedes, and around proximal part of intestine. Pair of chromatophores present at junction of all abdominal segments. A red pigment spot on dorsal spine, a pair on first abdominal segment and on telson.

Dorsal and rostral spines long and tapering, laterals short. No setæ on margin of carapace. Abdomen (Fig. 1, *B*) composed of five segments and telson, with knobs on third as well as second segment, and sharp points on postero-lateral margins of third, fourth and fifth. Dorsal part of each fork of telson with one spine and the usual six setæ on internal margin.

Two long aesthetes and one seta on tip of conical antennule (Fig. 1, *C*). Antenna (Fig. 1, *D*) characteristic of family: protopodite swollen and produced into a long tapering process, sub-equal to or slightly longer than rostral spine; exopodite minute, about 0.025 mm. long with a short hair at tip. Mandible (Fig. 1, *E*) bilobed; incisor cut into two teeth and molar with a broad cutting surface. Maxillule (Fig. 1, *F*) rather narrow; endites of protopodite with 8 and 4 bristles, segments of endopodite with 1 and 6. Maxilla (Fig. 1, *G*) has 7 and 9 setæ respectively on coxopodite and basipodite, 8 on endopodite and 5 soft hairs on scaphognathite.

First maxillipede (Fig. 1, *H*) typical, with 8 bristles on basis, 4 natatory hairs on exopodite and 2, 2, 1, 2 and 5 on the five joints of endopodite. Second maxillipede (Fig. 1, *I*) with 4 bristles on basis, 4 on exopodite and 1, 1 and 5 on endopodite. The remaining thoracic appendages are small and there is no indication of pleopods on the abdomen.

SECOND TO FOURTH ZOEÆ

Second zoea (Fig. 1, *J*) about 2 mm. long and 2.1 between tips of spines; third zoea (Fig. 1, *K*) 2.8 and 3.1 mm., and fourth (Fig. 1, *L*) 3.0 and 3.5 mm. As the zoea develops the dark chromatophores become more distinct and branched. Color of dorsal spine and antennæ becomes concentrated in a russet band almost at tip of spines. With live material these brightly colored bands on the transparent spines serve as a distinctive character, which is unfortunately lost on preservation.

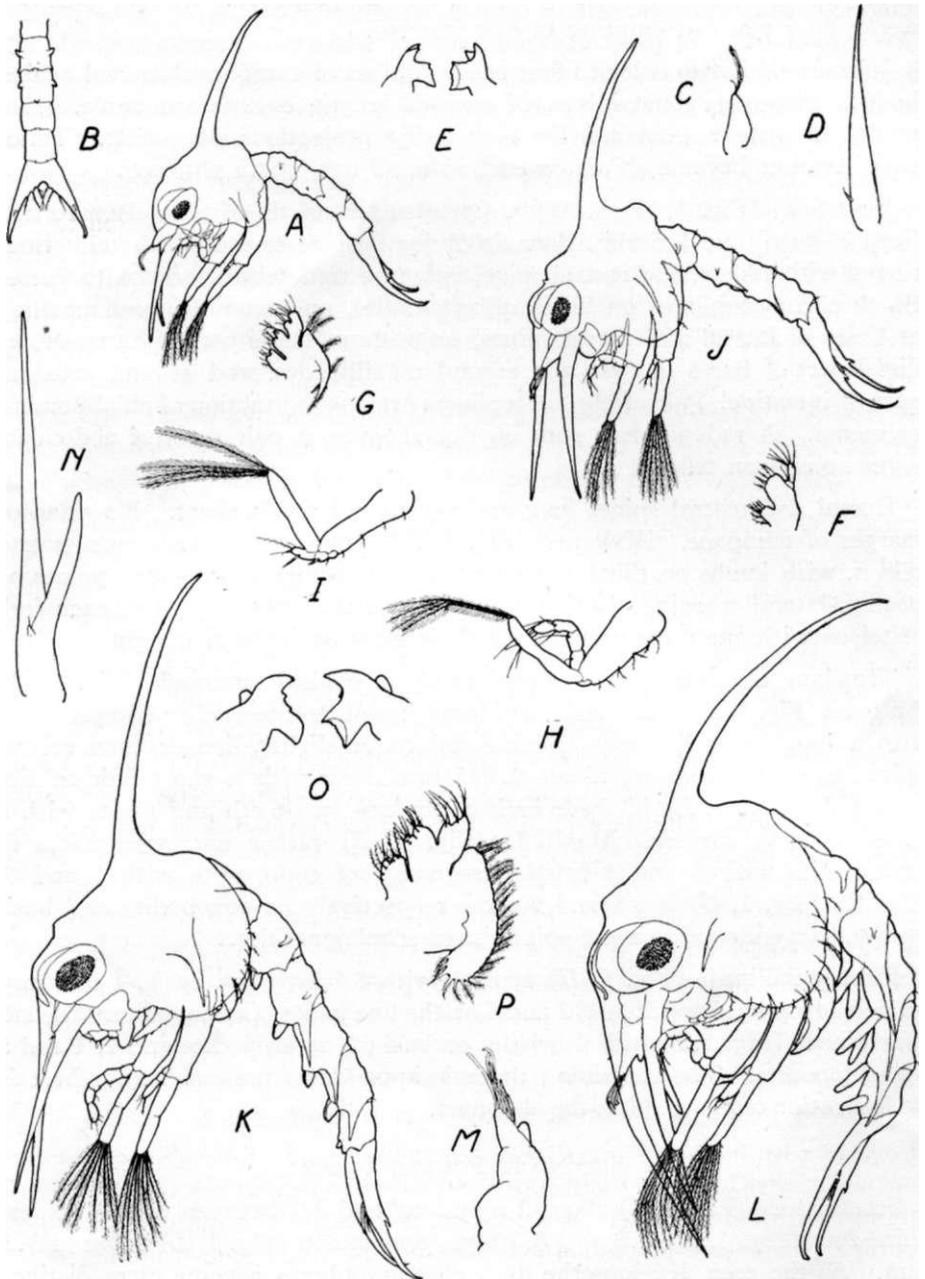


FIG. 1. *Lophopanopeus bellus* (Stimpson). A, first zoea X 30; B, abdomen X 30; C, antennule X 60; D, antenna X 60; E, mandibles X 60; F, maxillule X 60; G, maxilla X 60; H, first maxillipede X 60; I, second maxillipede X 60; J, second zoea X 30; K, third zoea X 30; L, fourth zoea X 30; M, antennule X 60; N, antenna X 60; O, mandibles X 60; P, maxilla X 60.

As the zoea grows the spines on the carapace and abdomen become much elongated. The base of rostral spine is produced laterally to form a shelf curved over bases of eyestalks and there is a distinct median ridge dorsal to this on the carapace. Rostral spine and processes of antennae are sub-equal in second zoea but in later stages rostral spine over-reaches antennae. Dorsal spine more than doubles in length during development but lateral spines become less conspicuous as zoea grows. Plumose hairs on margin of carapace increase from two in second zoea to about 12 in last. Sixth abdominal segment becomes separated from telson in third stage, although indication of the segmentation may be seen in second. Lateral marginal teeth on third, fourth and fifth abdominal segments gradually increase in size until they become longer than the segments against which they lie. An additional pair of small setae appear on internal margin of telson in third zoea.

Aesthetes of antennule increase in number during development; endopodite in fourth zoea (Fig. 1, *M*) can be seen as small knob, and basal part of appendage becomes inflated. The anlage of flagellum of antenna first seen in third stage; in last zoea (Fig. 1, *N*) it is less than half length of protopodite process. A small, unarmed palp present on mandible (Fig. 1, *O*) of last zoeal stage. Setae on inner margin of protopodite of maxillule increased in number, with a densely plumose seta appearing on outer margin in second stage and a bristle in addition in third; endopodite with 1 and 6 setae in all stages. Maxilla (Fig. 1, *P*) large and lamelliform, with increasing numbers of setae on all parts except endopodite, which bears 8 setae throughout. Swimming setae of maxillipedes increase to 6 and 7 in second zoea, 8 and 9 in third, and 9 and 11 in fourth. The slight division into two parts of third maxillipede and chela which can be seen in second zoea, becomes quite distinct in third. All thoracic appendages well developed in fourth zoea although not functional.

MEGALOPA. (FIG. 2, *A*)

Length about 2.8 mm., carapace 1.5 by 1.3 mm. Yellowish in color with brown pigment in liver and around mouth parts; small patches of russet on legs, mainly on carpi and meri, and on fourth and fifth abdominal segments; branching black chromatophores on eyestalks, on mouth parts, on rostrum, around heart, on postero-lateral part of carapace and between segments of abdomen except first and second, and sixth and telson.

Covered with hairs which are especially dense on distal parts of pereopods. Front wide, with a broad tooth near junction of front and sides of carapace; margined with coarse setae. Rostrum blunt, pointing downwards. Surface of carapace depressed in median anterior part; bearing rounded prominences dorsally. Eyestalks elongated. Sixth abdominal segment smaller than others; telson (Fig. 2, *B*) wider than long and usually bearing three plumose setae on posterior margin.

Antennule (Fig. 2, *C*) now composed of peduncle and two flagella: first segment of peduncle swollen to lodge statocyst; third with three long terminal

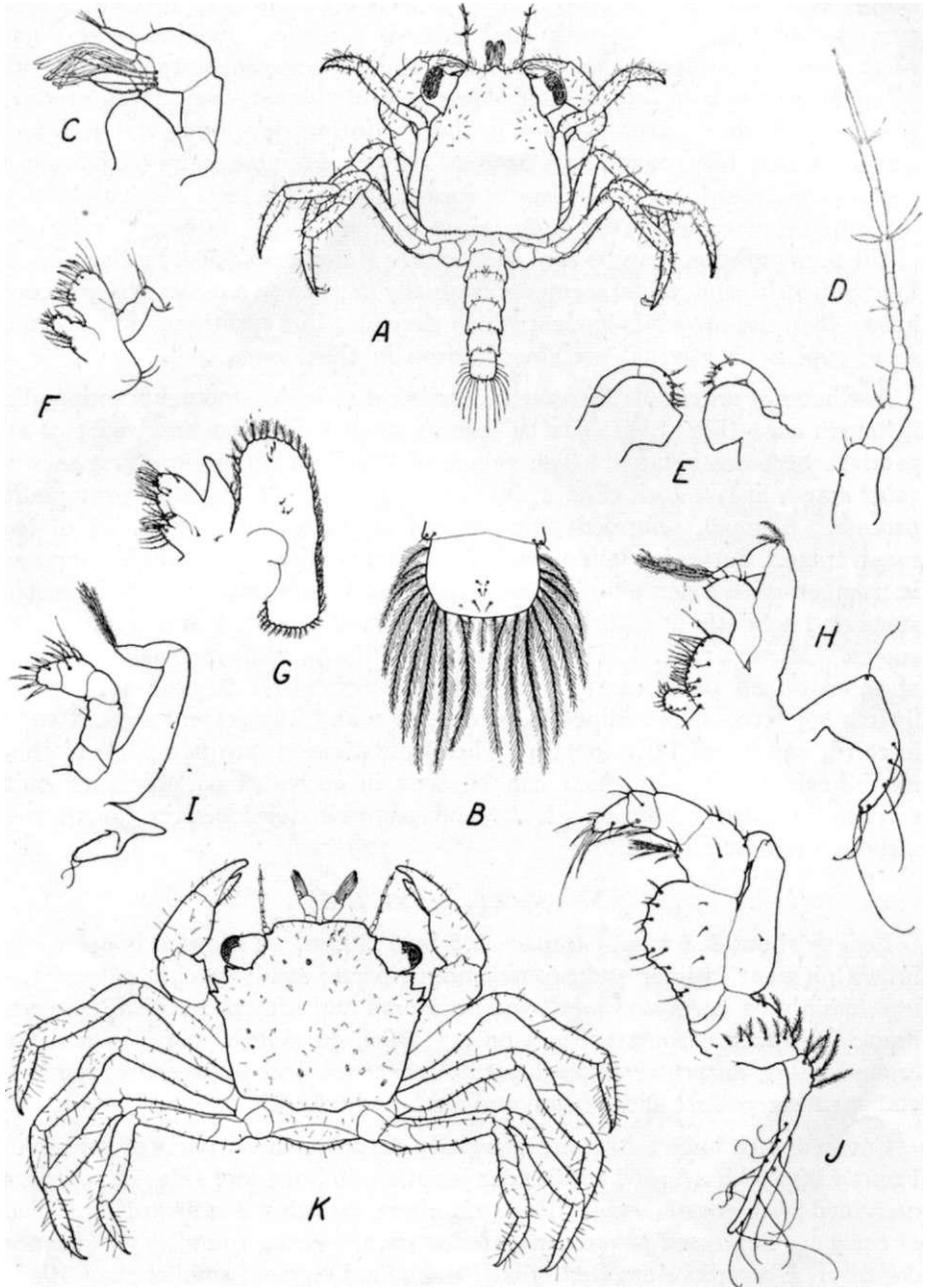


FIG. 2. *Lophopanopeus bellus* (Stimpson). A, megalopa X 15; B, telson X 60; C, antennule X 60; D, antenna X 60; E, mandibles X 60; F, maxillule X 60; G, maxilla X 60; H, first maxillipede X 60; I, second maxillipede X 60; J, third maxillipede X 60; K, first young crab stage X 15.

Plumose setae on inner margin of endopodite of first maxillipede and number increased on distal margin; epipodite larger. More setae on second maxillipede; gill developed. Merus and ischium of third maxillipede flatter, with sharp teeth on medial and distal margins.

Family Pinnotheridae

Hyman states, in reference to the family Pinnotheridae, that the complete history of metamorphosis has not been followed in any species. In his paper (5), he incorporates the work done on the group by authors previous to 1925 and adds descriptions of the early stages of two *Pinnotheres* and a *Dissodactylus* from the Atlantic coast of North America. He found a lack of uniformity in structure and in the number of zoeal stages. When the zoeae described by Aikawa (2) as "*Dissodactylozoea*" and "*Pinnozoea*" are assigned to their correct parental species, some will probably be the larvae of *Pinnotheres*, although superficially the larvae of *P. taylori* Rathbun resemble "*Grapsizoea brevispinosa*".

Lebour (9) describes the only *Pinnotheres* megalopa that has as yet been identified. This megalopa, *P. veterum* Bosc, differs in several respects from that of *P. taylori* described below.

Pinnotheres taylori Rathbun

A berried female, apparently of this little known species, was obtained from a transparent tunicate, March 16, 1933. Straw-colored, with bright orange eggs visible through the abdominal wall. Eggs in early stage of development and did not hatch until the first week in May; mass changing in color gradually to brown, and in size from 0.35 to 0.42 mm. Larvae when hatched covered with a spineless cuticle, shed with appearance of first zoea.

Two zoeal stages and one megalopal. First adolescent stage emerged four weeks after hatching in the laboratory. Zoeae cream-colored, with dark brown chromatophores at base of dorsal spine, around eyestalks, at base of antennules, on mandibles, on carapace postero-laterally, about the centre of basis of first maxillipedes and at junction of all segments of abdomen.

First zoea (Fig. 3, A) about 1.3 mm. long and 1.0 mm. between tips of spines. Rostral and dorsal spines rather short and blunt; laterals missing, but a tooth at postero-lateral margin of carapace, which is large and covers all except tips of swimming maxillipedes. Abdomen (Fig. 3, B) composed of five segments and telson; with sub-equal lateral protuberances on second and third segments; fourth and fifth segments somewhat swollen laterally, sides of telson (Fig. 3, C) parallel to one another, and no lateral spines, but surface covered with minute hairs, grouped in threes and fours, concentrated on telson forks, (which are very sharp pointed) so as to make them appear finely spined; six internal setae.

Antennule (Fig. 3, D) typical. Antenna (Fig. 3, E) small, with a short spinous process of protopodite, a swollen area (endopodite), and no exopodite. Mandibles like *Lophopanopeus bellus* but cutting surface rougher. Maxillule

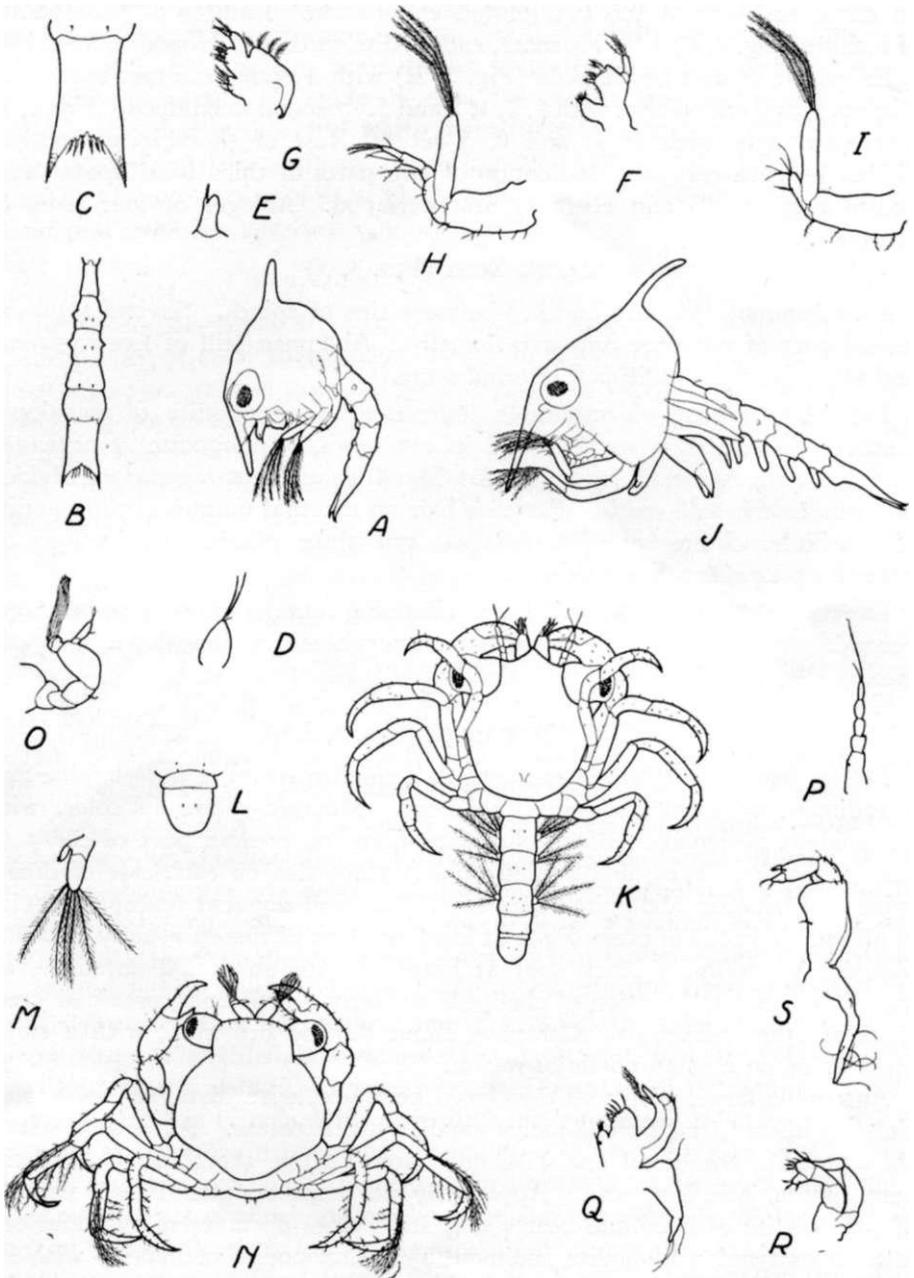


FIG. 3. *Pinnotheres taylori* Rathbun. A, first zoea X 30; B, abdomen X 30; C, telson X 60; D, antennule X 60; E, antenna X 60; F, maxillule X 60; G, maxilla X 60; H, first maxillipede X 60; I, second maxillipede X 60; J, second zoea X 30; K, megalopa X 30; L, telson X 60; M, fourth pleopod X 60; N, first young crab stage X 30; O, antennule X 60; P, antenna X 50; Q, first maxillipede X 60; R, second maxillipede X 60; S, third maxillipede X 60.

(Fig. 3, *F*) usually with five spines on coxopodite and basipodite, and four on distal segment of the two-jointed endopodite. Endites of protopodite of maxilla (Fig. 3, *G*) bear six setae, endopodite three and exopodite four.

Exopodite of first maxillipede (Fig. 3, *H*) with 4 plumose setae; basis with 8 bristles; and endopodite with 1, 2, 1, 2 and 5. Second maxillipede (Fig. 3, *I*) correspondingly with 4; 4; and 0, 5 setae. Rest of thoracic appendages hidden beneath carapace; indication of two parts of third maxillipede (exopodite very small) and chela of first pereopod. Anlages of four pairs of pleopods.

SECOND ZOEAL STAGE (FIG. 3, *J*)

Length about 1.6 mm. and 1.3 between tips of spines. Several setae on lateral part of carapace and two dorsally. Abdomen still of five segments and telson, and no additional internal setae.

Lateral extension of antennule indicative of endopodite of megalopa; aesthetes increased in number and in two rows. Endopodite of antennae enlarged, so longer than protopodite. Mandible with cutting surface divided into numerous small teeth. Plumose hair on external margin of protopodite of maxillule. More setae on maxilla, and three plumose projections on posterior part of scaphognathite.

Exopodite of maxillipedes with six swimming setae. Thoracic appendages becoming fully developed before zoea metamorphoses into megalopa. Pleopods greatly elongated but only four pairs.

MEGALOPA (FIG. 3, *K*)

Differs from *P. veternm* in presence of a small rostrum, a dorsal spine and a rudimentary sixth abdominal segment. Mustard-yellow in color, with transparent pereopods. Black chromatophores on median part of carapace just posterior to eyes, and behind dorsal spine; also on each side of dorsal spine and between abdominal segments. On each segment (except dactylus of all but cheliped) of every leg is at least one spot of russet, usually medially placed. Ventrally, a black spot at bases of antennules and antennae, on mandibles, and at junction of chelipeds to sternum; russet at proximal junctions of other pereopods. Carapace about 0.7 by 0.5 mm., with a small blunt spine on median posterior region.

Antennule large, with well developed peduncle, with distal segment especially elongated, and flagella rather small, with few setae. Antenna of about six segments; the distal one with one long and one short bristle, and the penultimate, one long seta. Apparently no palps on mandibles. Endites of protopodite of maxillule bear short, stiff spines on inner margin and one seta on external; endopodite rudimentary. Coxopodite of maxilla with six long plumose setae, and basipodite about nine short ones; endopodite quite degenerate, and exopodite with 20 setae around margin.

Setae few on first maxillipedes: four or five on each endite of protopodite, three on shrivelled endopodite, two on exopodite and epipodite. Second maxillipede with poorly developed exopodite, bearing three short setae

terminally; dactylus of endopodite inserted on proximal lateral margin of propodus, instead of terminally. Exopodite of third maxillipede small, with only one distal seta; merus and ischium fused, and dactylus placed in position similar to that of second maxillipede; epipodite small. Chela large and strongly developed. No setae on dactylus of last pair of pereopods as is usual in Brachyrrhyncha, but which seem to be lacking in all the Pinnotheridae. Only four pairs of pleopods, as none on small sixth abdominal segment (Fig. 3, *L*): endopodite of each pleopod (Fig. 3, *M*) bears two short curved setae, and exopodite, six very long plumose hairs.

FIRST YOUNG CRAB STAGE (FIG. 3, *N*)

Small, carapace about 0.75 by 0.7 mm. Straw-colored, with pereopods a shade deeper in color than body. Front broad, and fringed with about 10 short setae; no trace of dorsal spine of megalopa. Young crab able to swim freely—as does adult—by means of long plumose setae on distal segments of third and fourth pairs of legs.

Antennule (Fig. 3, *O*) large, with distal segment of peduncle swollen and elongated. Antenna (Fig. 3, *P*) of about five segments, with two bristles at tip. Maxillule and maxilla like megalopa. First maxillipede (Fig. 3, *Q*) has a few more setae than megalopa and is quite large. Second maxillipede (Fig. 3, *R*) little changed. Merus-ischium of third maxillipede (Fig. 3, *S*) swollen and flattened distally and dactylus inserted more distally than in megalopa; setae on distal part of epipodite. Chela large and sparsely covered with setae, as are all pereopods. Swimming setae present on distal part of carpus and propodus of third and fourth legs.

Family Grapsidae

Hyman (6) found the larvae of the family Grapsidae quite uniform in structure. Aikawa (1), however, observed that the larvae of some of the Japanese forms did not agree with the earlier described types, either in the absence of lateral spines on the carapace, or in the length of the antennae. The development of the two Grapsoid species in British Columbia is similar to that of related forms in Japan. The megalopae that have been described, (with the exception of the first one attributed by Cano to *Pachygrapsus marmoratus* (Fabricius), and which has a large rostrum), are very like those obtained by the writer. There are no sensory setae on the last pereopods of the megalopae in Cano's drawings, which is perhaps an oversight, as they are present in most Brachyrrhyncha. Rathbun (11) gives figures of megalopae, which are designated as "Grapsoid", *Pachygrapsus crassipes* (?) and *Sesarma magdalenensis*, all of which are of the same type as those of *Ilemigrapsus* described below.

The first zoea of *Ilemigrapsus longitarsis* (Miers), as described by Aikawa (1), is similar to the larvae of *H. nudus* (Dana) and *I. oregonensis* (Dana). It is slightly smaller and there are two extra setae on the endopodite of the first maxillipede. The distribution of the setae differs on the joints of the second maxillipede.

***Hemigrapsus nudus* (Dana)**

Berried females found commonly in April and May at Departure Bay, British Columbia; rarely in June, but reported by Bovard and Osterid (3) to be carrying eggs in June and July at Friday Harbour, Washington. Freshly laid egg mass purplish-black, changing to gray when ready to hatch. Increase in size from 0.38 to 0.45 mm. in diameter.

Five zoeal stages and one megalopal; prezoal almost disappeared; embryonic cuticle, shed on hatching, has no embryonic spines on antennae or telson, but spines and setae invaginated upon themselves typically.

First zoea (Fig. 4, A) about 1.65 mm. in length and 1.2 mm. between tips of spines. Very transparent, with a yellow tinge to body and dark chromatophores: pigment spots around eyestalks, one on carapace between eyes, on labrum, on bases of antennules and antennae, on mandibles, on distal part of bases of first maxillipedes, and at bases of dorsal and lateral spines; some pigmentation at joints of each segment of abdomen and around proximal part of intestine. On dorsal spine and also on fourth abdominal segment, red chromatophores. Rostral spine and forks of telson tinged with violet and lateral spines with russet.

First zoea (Fig. 4, A) stout, with all carapacial spines well developed. Postero-lateral margin of carapace bears fine teeth and setae. Abdomen (Fig. 4, B) of five segments and telson; large knobs on second abdominal segment and smaller ones on third. External spines lacking on telson, but tips of fork cut internally into fine teeth and a row of minute spines on dorsal surface of each cornua; six internal setae.

Antennule (Fig. 4, C) tubular-conical, usually with two long aesthetes and one short seta. Process of protopodite of antenna (Fig. 4, D) bears two rows of spines distally, is longer than exopodite, and reaches to about distal third of rostral spine; exopodite with three setae about one-third from tip, which is very minutely spined. Mandibles (Fig. 4, E) bilobed, each with a broad denticulated incisor process, and a smaller, more sharply divided molar: left mandible with additional tooth on ventral side. Endite of coxopodite of maxillule (Fig. 4, F) usually with five plumose setae, basipodite six, endopodite one and five. Endite of coxopodite of maxilla (Fig. 4, G) bilobed with six plumose setae, basipodite with seven; endopodite four and narrow exopodite five, soft, densely plumose setae.

Nine bristles on basis of first maxillipede (Fig. 4, H), 4 swimming setae on exopodite, and 2, 2, 1, 2 and 5 setae on joints of endopodite. Second maxillipede (Fig. 4, I) with 4 setae on basis, 4 natatory on exopodite and 0, 1 and 6 on endopodite. Rudimentary thoracic appendages present as small lobes under carapace.

SECOND TO FIFTH ZOEAE

All zoeal stages similar in coloration; chromatophores enlarge and branch, and spines become almost colorless as zoea develops. Second zoea (Fig. 4, J) about 1.9 mm. long and 1.6 mm. between tips of spines; third (Fig. 4, K)

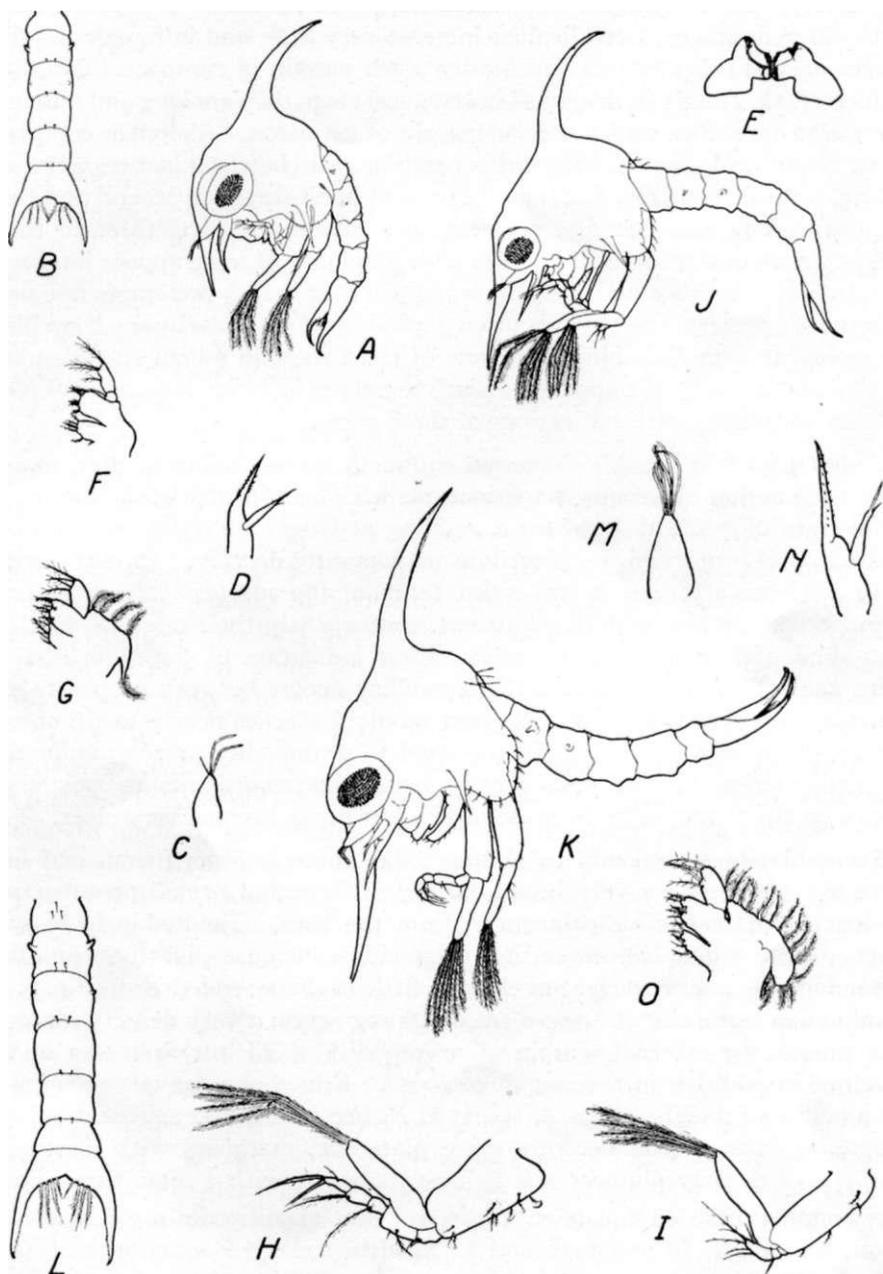


FIG. 4. *Illemigrapsus nudus* (Dana). A, first zoea X 30; B, abdomen X 30; C, antennule X 60; D, antenna X 60; E, mandibles X 60; F, maxillule X 60; G, maxilla X 60; H, first maxillipede X 60; I, second maxillipede X 60; J, second zoea X 30; K, third zoea X 30; L, abdomen X 30; M, antennule X 60; N, antenna X 60; O, maxilla X 60.

2.2 and 2.2 mm.; fourth (Fig. 5, A) 2.6 and 2.8 mm.; and fifth (Fig. 5, B) 3.3 and 3.5 mm. Length of spines as compared to animal as a whole varies with different stages; lateral spines increase very little and in fourth and fifth stages are bent downwards and hardly reach margin of carapace. Marginal hairs increase greatly in size, until in last zoeal stage they are long and plumose; hairs also appear on mid-posterior margin of carapace. Abdomen composed of six segments in second zoea but seventh appears between last segment and telson in third zoea (Fig. 4, L); knobs present in all stages on second and third segments; long setae on first segment: one in second stage, three in third, five in fourth and seven in fifth. An additional pair of setae appear internally in telson of third zoea and again in fourth, so that in last two stages five pairs of setae are present. Slight indication of position of pleopods by small swellings on second to fifth abdominal segments of third zoea; in fourth stage increase in size and a small pair appear on sixth segment; in fifth, these anlagen long, tubular structures with indications of three parts.

Antennules (Fig. 4, M) of second to fourth zoeae similar to first, except that the number of sensory setae increase with age; in fifth zoea (Fig. 5, C) indications of adult shape seen: a swelling at base for lodging of statocyst, and a lateral projection, the flagellum (endopodite) distally. Last two zoeae have aesthetes arranged in two series, terminal and sub-terminal. Antennae increase little in size with development, consequently their relative length as compared with rostral spine varies. First indication of flagellum seen in third zoea (Fig. 4, N) where a slight swelling occurs between exopodite and spinous process of protopodite; at next moult it reaches nearly to tip of exopodite and finally (Fig. 5, D) is sub-equal to protopodite process; indication of segmentation can be seen shortly before metamorphosis to postlarva; spines on tip of exopodite increase in size but never become very clear.

Mandibles of second and third stages like those of first; fourth and fifth have one tooth with a very broad cutting surface; and a small protuberance on fourth zoea mandible enlarges to form the bare, unjointed palp of fifth stage. Setae and spines on endites of maxillule increase slightly in number; appendage becomes stronger but changes little in shape: endopodite (Fig. 5, E) of all stages bears one and five setae on its segments; a very densely plumose seta present on external margin of protopodite of all but first zoea and a bare one in addition in the last three zoeae. Fringe of setae on segments of protopodite of maxilla (Figs. 4, O and 5, F) becomes denser as zoea develops, exopodite enlarges and becomes more plate-like, margined with increasing numbers of densely plumose soft hairs; endopodite with 4 setae throughout.

Swimming setae on tips of exopodites of first maxillipedes are 6 in second stage, 8 in third, 10 in fourth and 12 in fifth; usually 9 setae on basis and 2, 2, 1, 2 and 5 on segments of endopodite, but additional ones found on last three segments of later stages. Setae on exopodites of second maxillipedes correspond in number to those of first; usually 4 setae on basis but these may be reduced to 3 in later zoeae; all have 0, 1 and 6 setae on endopodite. There is an indication of the division into the two rami of the rudimentary third

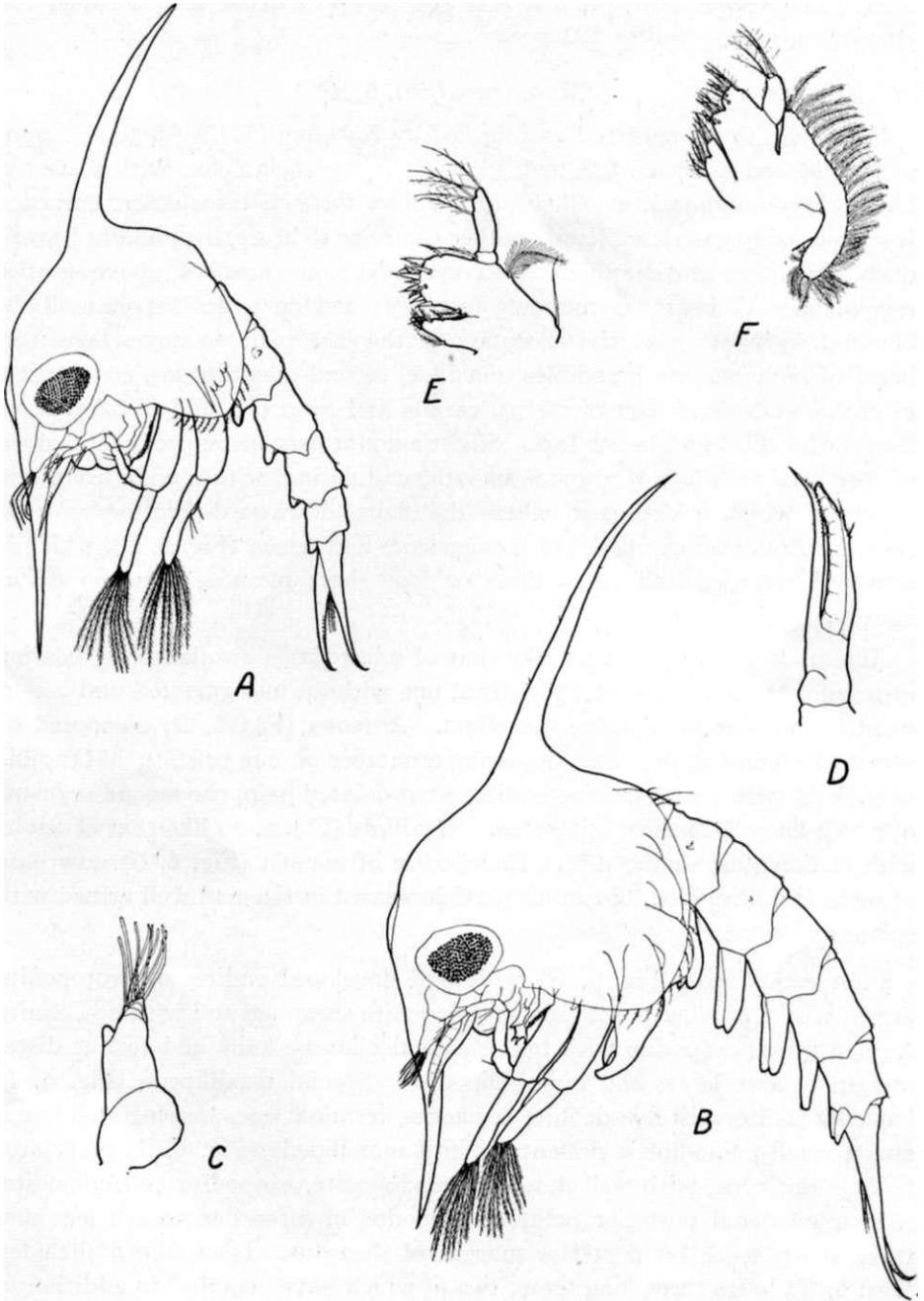


FIG. 5. *Hemigrapsus nudus* (Dana). A, fourth zoea X 30; B, fifth zoea X 30; C, antennule X 60; D, antenna X 60; E, maxillule X 60; F, maxilla X 60.

maxillipede and an indentation at the tip of the first periopod in the third zoea. The segmentation of thoracic appendages can be seen through the enveloping membranes in fifth zoea.

MEGALOPA (FIG. 6, **A**)

Resembles those described and figured by Rathbun (11). About 3.6 mm. in length, and carapace 1.8 to 1.5 mm. Yellowish in color, with scattered black chromatophores: a yellow patch shows through transparent carapace just anterior to gastric mill and another posterior to heart, liver a light brown; dark branching chromatophores on eyestalks, on carapace above gastric region, beneath heart, surrounding intestine, and on joints between all abdominal segments with the exception of the last two; on appendages: on bases of antennae, on mandibles, maxillae, second maxillipedes, coxopodites of chelae and distal part of merus, carpus and propodus and distal part of dactylus of third and fourth legs. Slight amount may be on proximal margin of carpus of fifth leg. Carapace smooth, undulating, with a wide front, the centre of which is depressed where the short, downward-pointing rostrum occurs. Abdomen composed of six segments and telson (Fig. 6, *B*), which is smoothly rounded and bears three or four short plumose setae on distal margin.

Antennule (Fig. 6, *C*) very like that of adult: large swollen base, bearing a peduncle of two segments, the distal one with an unsegmented and a segmented (with sensory hairs) flagellum. Antenna (Fig. 6, *D*) composed of about 11 segments, the distal 3 bearing a number of long bristles. Mandible (Fig. 6, *E*) with strong cutting endite, a two-jointed palp, the second segment of which bears 8-10 short stiff setae. Maxillule (Fig. 6, *F*) like that of adult, with rudimentary endopodite. Endopodite of maxilla (Fig. 6, *G*) now bare of setae and atrophied, but other parts increased in size and well armed with spines and setae.

First maxillipede (Fig. 6, *H*) with well developed endites of protopodite armed with a number of stiff setae; endopodite shrunken and with no definite segmentation; exopodite with four terminal plumose hairs and two at distal margin of first joint; and large epipodite. Second maxillipede (Fig. 6, *I*) has endopodite with five definite segments, terminal ones bearing stiff hairs, and a small epipodite is present. Third maxillipede (Fig. 6, *J*) of typical brachyuran type, with well developed endopodite, exopodite and epipodite. A spur on distal posterior point of propodus of second to fourth legs and three sharp teeth on posterior margin of dactylus. Dactylus of fifth leg (Fig. 6, *K*) bears three long setae, two of which have "combs" in addition to spinules. No hooks on coxae of periopods. Five pairs of pleopods; endopodites of first four pairs each with two stout curved setae and exopodites with 18-20 long plumose hairs; uropods with 9 or 10 long hairs on exopodites.

FIRST YOUNG CRAB STAGE (FIG. 6, L)

Carapace square, about 2 mm. in length and breadth. Front of two curved lobes, unlike the straight frontal margin of adult. Eyes large and extend

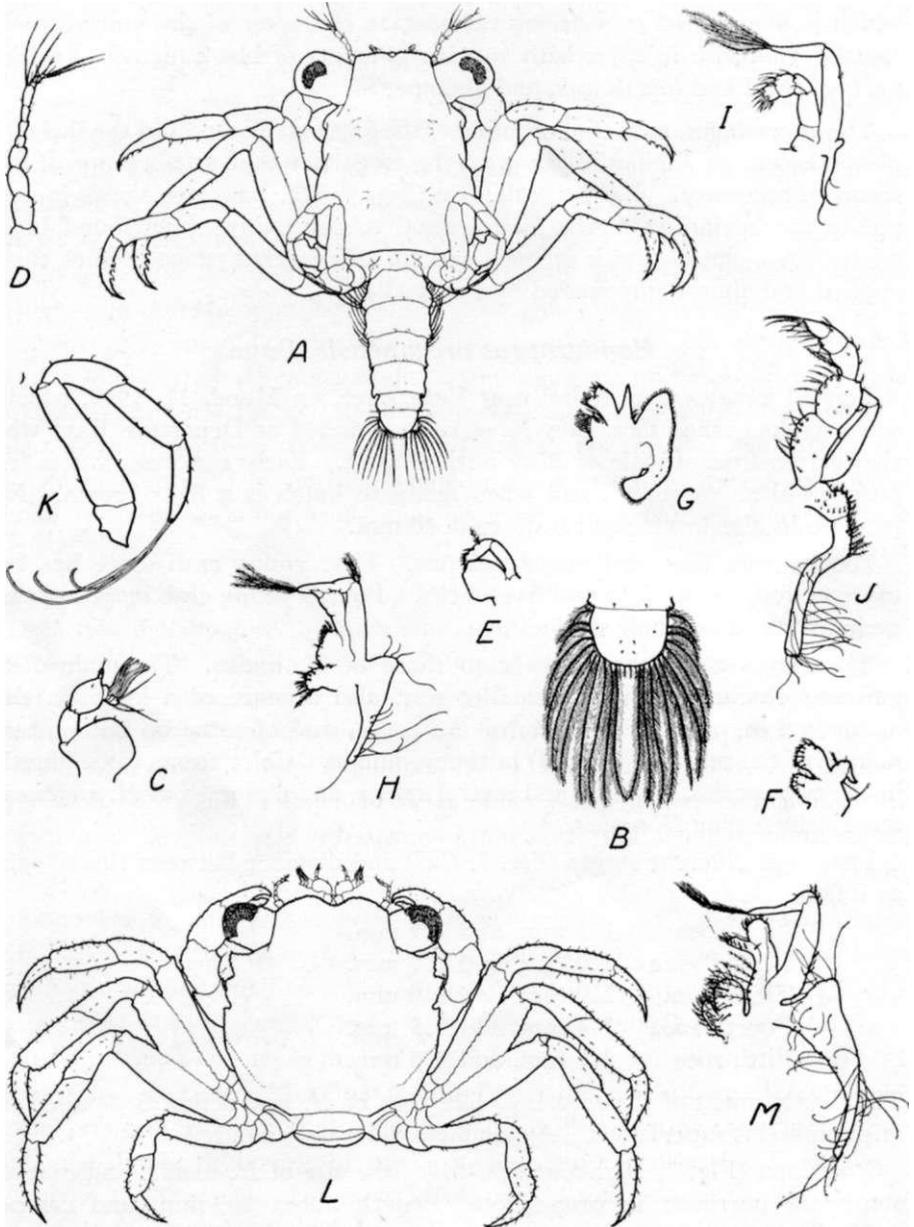


FIG. 6. *Hemigrapsus nudus* (Dana). A, megalopa X 15; B, telson X 30; C, antennule X 30; D, antenna X 30; E, mandible X 30; F, maxillule X 30; G, maxilla X 30; H, first maxillipede X 30; I, second maxillipede X 30; J, third maxillipede X 30; K, fifth pereopod X 30; L, first young crab stage X 15; M, first maxillipede X 30.

past sides of carapace, which are parallel for over half their length; three distinct lateral teeth on carapace, the margins cut by minute denticulations. Fine tubercles on carapace and periopods, arranged in definite rows on posterior lateral part of carapace and on chelipeds. All periopods beset with fine hairs, which is unexpected considering the specific character of the mature *nudus*. Usually yellowish in color with varying amounts of black pigment on distal parts of third and fourth legs, and abdomen.

The appendages, with the exception of the first maxillipede and the shrivelled pleopods, are so similar to those of the megalopa that a description of them seems unnecessary. First maxillipede (Fig. 6, *M*), however, shows in endopodite the beginning of the modification to the unique type found in the adult, where endopodite is grooved and tip split so that exopodite lies closely applied and almost surrounded by endopodite.

Hemigrapsus oregonensis (Dana)

Berried females were found near Vancouver, on March 17, 1930, which is some weeks earlier than they have been obtained at Departure Bay, where they hatch from middle of May until August. Early egg mass varies from purplish-black to russet, and when ready to hatch is a light brown. Eggs increase in size from about 0.33 to 0.40 mm.

Zoeal stages five, and megalopal one. First young crab stage has been twice reared, taking four and five weeks. Fourth young crab stage appeared after four and one-half weeks.

The stages correspond closely to those of *H. nudus*. The main distinguishing characters are the smaller size, and absence of a knob on third abdominal segment (Fig. 7, *A*) of the zoeae, and of setae on the posterior margin of the telson (Fig. 7, *B*) in the megalopa. Color seems to be identical in the two species. Dorsal and rostral spines, and abdomen of *H. oregonensis* more slender than // *nudus*.

Length of different stages (Fig. 7, *C-G*) and distance between tips of spines as follows:

First zoea	1.3 mm. and 1.1 mm.
Second zoea	1.6 mm. and 1.6 mm.
Third zoea	2.0 mm. and 2.0 mm.
Fourth zoea	2.4 mm. and 2.5 mm.
Fifth zoea	2.7 mm. and 2.5 mm.

The development of the zoea is so like that of *H. nudus* that a detailed description seems superfluous. Appendages differ only in size.

Megalopa (Fig. 7, *H*) about four-fifths the size of *H. nudus*, and carapace somewhat narrower in proportion. Length about 2.9 mm. and carapace 1.5 by 1.1 mm. No plumose setae on smoothly rounded posterior margin of telson. Appendages naturally somewhat smaller but in form resemble *H. nudus*. First maxillipede differs slightly; endopodite smaller in proportion, and endites of protopodite bear longer setae on a more rounded margin.

First four pairs of pleopods have 14-17 long plumose setae on exopodite; uropods usually have a soft plumose seta on protopodite and eight or nine on exopodite.

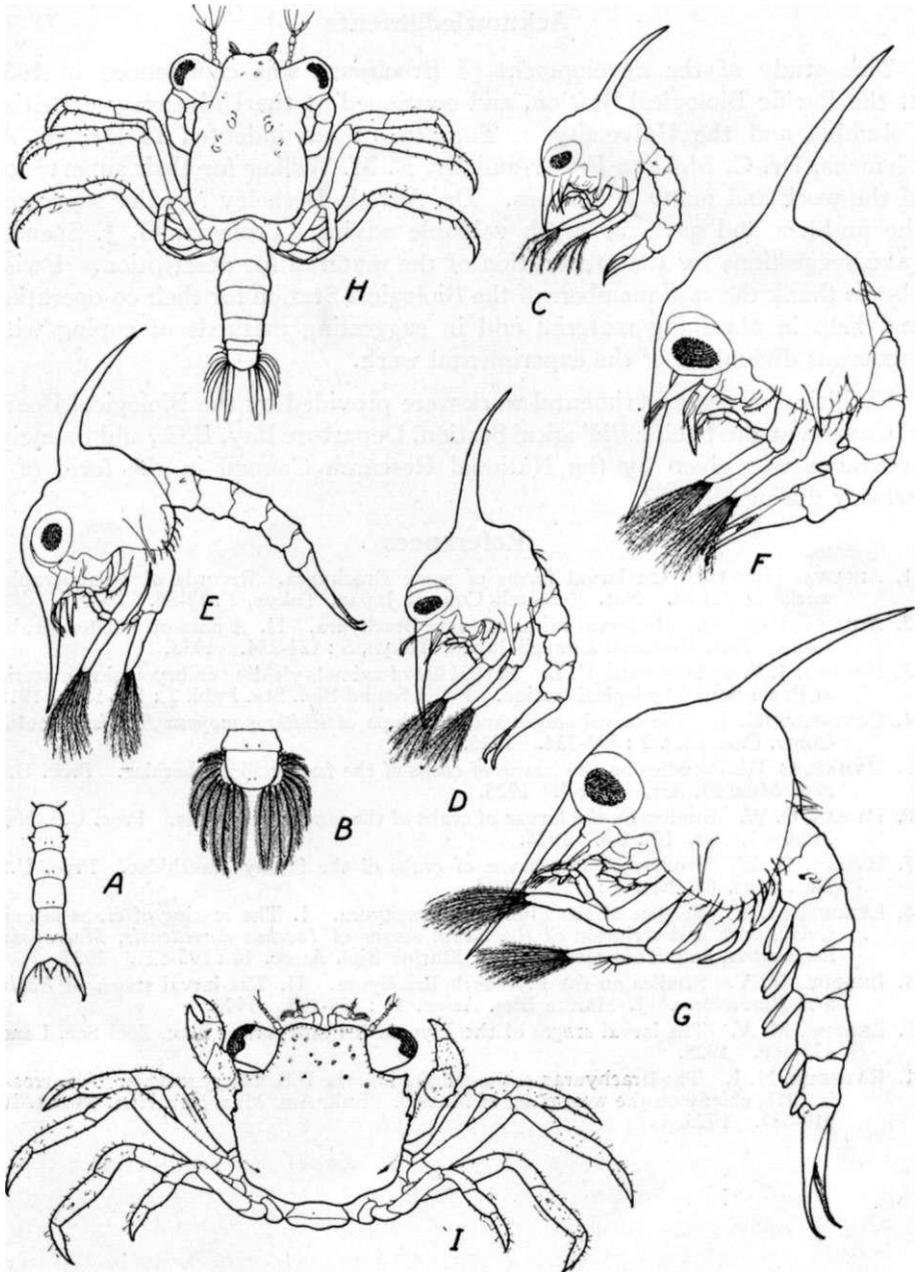


FIG. 7. *Hemigrapsus oregonensis* (Dana). A, abdomen of first zoea X 30; B, telson of megalopa X 30; C, first zoea X 30; D, second zoea X 30; E, third zoea X 30; F, fourth zoea X 30; G, fifth zoea X 30; H, megalopa X 15; I, first young crab stage X 15

First young crab stage (Fig. 7, I) also closely resembles that of *H. nudus*. Carapace 1.6 by 1.6 mm. Chelipeds and walking legs not quite as stout as those of the related species.

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