PHYLOGENETIC STUDIES ON THE LARVAE OF DECAPOD CRUSTACEANS

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by

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To my parents and
in memory of my Auntie and Uncle.

This is to certify that the thesis submitted

by

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Abstract

Detailed descriptions on the prezoeal stage of the following 20 decapod species have been made based on material hatched in the laboratory, and phylogenetic relationships are discussed:
Pandalus montagui Leach, *Pagurus prideauxi* Leach, *Pagurus bernhardus* (Linnaeus), *Hyas araneus* (Linnaeus), *Hyas coarctatus* Leach, *Inachus dorsettensis* (Pennant), *Inachus leptochirus* Leach, *Macropodia tenuirostris* (Leach), *Orithyia sinica* (Linnaeus), *Ebalia tuberosa* (Pennant), *Liocarcinus holsatus* (Fabricius), *Liocarcinus corrugatus* (Pennant), *Liocarcinus marmoreus* (Leach), *Carcinus maenas* (Linnaeus), *Portunus gladiator* Fabricius, *Charybdis bimaculata* (Miers), *Monodaeus couchi* (Couch), *Cancer pagurus* Linnaeus, *Carcinoplax longimana* (De Haan) and *Pinnotheres pinnotheres* (Linnaeus).

The prezoea appears to be derived from a larval form resembling a protozoea, rather than a nauplius as has previously been suggested. The most primitive form of prezoea occurs in the carideans and the most developed form in the Majidae. There has been some suppression of prezoeal characters in some portunids, Grapsidae and Pinnotheridae.

Development of gills were studied in zoea and megalopa stages of the following 17 species of decapods, and the patterns of gill development are discussed in terms of phylogenetic relationships of the larvae:
Pagurus prideauxi Leach, *Pagurus bernhardus* (Linnaeus), *Inachus dorsettensis* (Pennant), *Hyas araneus* (Linnaeus), *Eurynome aspera* (Pennant), *Pisa armata* (Latreille), *Atelecyclus rotundatus* (Olivi), *Carcinus maenas* (Linnaeus), *Liocarcinus corrugatus* (Pennant), *Liocarcinus holsatus* (Fabricius), *Pilumnus hirtellus* (Linnaeus), *Monodaeus couchi* (Couch), *Pinnotheres pinnotheres* (Linnaeus), *Pinnotheres pisum* (Linnaeus), *Pinnaxodes mutuensis* Sakai, *Pinnixa rathbuni* Sakai and *Pinnixa (?)chaetopterana* Stimpson.

The gills of most of the species investigated migrate during development, not only dorsally but, in some cases, also posteriorly. The Pinnotheridae provide the only known example in which rudiments of 'lost' gills appear whithin larval stages only to disappear by the first crab stage.

Complete larval development of *Petalomera japonica* (Henderson), *Eurynome spinosa* Hailstone and *Atelecyclus rotundatus* (Olivi) was described based on laboratory rearing. Detailed comparisons are made with the larvae of related species.

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Contents

CHAPTER 1

GENERAL INTRODUCTION

Since last century, a large body of information has been made of decapod larvae in various aspects. Of these, taxonomy and phylogeny of the larvae is one of the main themes.

For decapod larval study, larval characters have been focused on the morphological features of zoea and megalopa stages, particularly relative sizes, segmentation and setation of appendages. Gurney (1942) made a comprehensive review on the various features of decapod larvae, but since then there have been only scattered descriptions of the prezoeal stages of various species and scarcely any work on the development of gills in the larval stages. The prezoea is the first phase of the larval development in most of decapod species, and it is assumed that this stage may have some phylogenetic information on the developmental stages before zoeal phase apart from characters of the zoea and megalopa. Gills are adult organs which first appear in the zoeal stage.

Williamson (1976, 1982) and Rice (1980, 1983) reviewed some major problems on phylogeny of decapod larvae. Some of them include: taxonomic position of Dromiidae; relationship of Atelecyclidae to Corystidae and Cancridae; taxonomic position of Pinnotheridae.

The present study is aimed at phylogenetic understanding of prezoea and gill development of some pagurids and brachyurans. Larval development of *Petalomera japonica* (Henderson), *Eurynome*

spinosa Hailstone and ***Atelecyclus rotundatus*** (Olivi) was also studied in terms of their phylogeny.

CHAPTER 2

THE PREZOEAL STAGE IN VARIOUS DECAPOD CRUSTACEANS

INTRODUCTION

In the early period of research on decapod larvae, prezoeas of some brachyuran species were described in some detail. Faxon (1880) was the first who presented detailed descriptions of prezoeas, and Conn (1884) gave a comprehensive discussion on the significance of prezoeas of major decapod groups. Lebour (1927, 1928 b) recognised three groups of brachyuran prezoeas. In the comprehensive review of decapod larvae, Gurney (1942: 51-53) reviewed this stage under the name "embryonic cuticle".

Prezoeas are not easily observable in laboratory hatching because of their short duration, thus they have often been excluded from the detailed descriptions of larval development. Absence of prezoeas in zooplankton samples has also resulted in the neglect of the prezoeal stage. Some authors have questioned the existence of a prezoeal stage, or they have regarded it as an abnormal first larva hatched under the unfavorable conditions (Churchill, 1942; Sandoz and Rogers, 1944; Mir, 1961; Poole, 1966). Nevertheless, morphological descriptions from various decapod groups have been steadily accumulated (Dohrn, 1870; Sars, 1890; Gurney, 1924 a; Lebour, 1928 a, b; 1944; Hart, 1935; Gohar and Al-kholy, 1957; Hartnoll, 1964 a; Greenwood, 1965, Gore, 1968; Wear, 1965, 1968 a, 1970 a, b; Webber and Wear, 1981), and the evidence for recognising the prezoea as a normal stage is now overwhelming (Buchanan and Millemann, 1969;

MacKay, 1942; Knudsen, 1959; Williams, 1968; Alley, 1975; Goudeau and Lachaise, 1980; Quintana, 1984).

Recently several workers have shown particular interest in prezoeas and have presented detailed descriptions (Quintana, 1983, 1984, Quintana and Konishi, 1986; Quintana and Saelzer, 1986; Hong and Williamson, 1986 (Chapter 4 of this thesis); Hong and Ingle, in press (Chapter 6 of this thesis)).

The present study gives detailed descriptions of prezoeas of 20 species of decapod crustaceans, and their phylogenetic relationships are discussed.

MATERIALS AND METHODS

Prezoeas of the following species were examined from laboratory hatching at the Marine Biological Station, Port Erin, Isle of Man: *Pandalus montagui* Leach, *Pagurus prideauxi* Leach, *Pagurus bernhardus* (Linnaeus), *Hyas araneus* (Linnaeus), *Hyas coarctatus* Leach, *Inachus dorsettensis* (Pennant), *Inachus leptochirus* Leach, *Macropodia tenuirostris* (Leach), *Ebalia tuberosa* (Pennant), *Liocarcinus holsatus* (Fabricius), *Liocarcinus marmoreus* (Leach), *Carcinus maenas* (Linnaeus), *Monodaeus couchi* (Couch), *Cancer pagurus* Linnaeus and *Pinnotheres pinnotheres* (Linnaeus). Observations were made on the prezoeas of *Processa canaliculata* Leach and *Munida rugosa* (Fabricius), but these are not described in detail.

Berried females were collected by dredging or beam trawling off Port Erin from October 1984 to July 1986. Intertidal species were obtained under rocks and *Laminaria* hold-fasts at low tide, mainly from Port St. Mary shore.

In Port Erin, berried females were held until hatching in a temperature controlled room at 15 °C with a 12:12 light/dark regime illuminated by fluorescent light. Sea water salinity was about 34.4 (33.86-34.60) ppt. Berried females were slowly acclimatized to 15 °C, and kept in a plastic tank (22x32x20 cm) supplied with running sea water. For 1-2 weeks before hatching the crabs were kept individually in plastic tanks with gentle aeration. The crabs were fed every other day with adductor muscles of scallops or queenies, and after feeding they were transferred to freshly-prepared tanks to maintain water quality.

The following species were examined during September-October, 1984 in the Institute of Marine Sciences (National Fisheries University of Pusan), Pusan, Korea: *Orithyia sinica* (Linnaeus), *Liocarcinus corrugatus* (Pennant), *Portunus gladiator* Fabricius, *Charybdis bimaculata* (Miers) and *Carcinoplax longimana* (De Haan). Observations were also made on the prezoeas of *Neodorippe japonica* (von Siebold) and *Hemigrapsus penicillatus* (De Haan), but these are not described in detail. Berried females were collected by gill nets in the Haewundae area and maintained at 17-19 °C and about 32.8 (32.05-33.27) ppt in ambient light conditions until hatching.

Usually hatching occurs during evening or night. In all cases larvae were released as free-swimming prezoeas. Upon hatching prezoeas swim to the surface by jerking the body backwards using the antennular, antennal and telson processes. Just after hatching prezoeas were individually dipped out and each placed in a glass bowl (170 ml volume, 9 cm diameter) to measure the duration of the prezoea. Duration was based on 5-15 prezoeas, and ranges were taken. The first zoea was easily recognized by the change of swimming pattern from the jerking motion of prezoeas to the continuous perpendicular swimming motion, using maxillipedal setae and telson, of the first zoea.

Larvae were placed on a depression slide with a drop of sea water, and a cover glass was used. When large prezoeas were observed, a square piece of plastic cling film was used instead of a cover glass. In order to anaesthetize the prezoeas a drop of 1 % buffered formalin solution was added to the side of the cover glass. This was also to maintain water level around the larval specimen to prevent damage. Sometimes formalin solution stained by methylene blue was used.

Measurements were made based on at least 5 specimens. Carapace length (CL) was measured from the anterior margin of the forehead to the postero-lateral margin of the carapace (see Fig. 5 A). Telson processes were counted from the outermost.

RESULTS

Hatching, moulting and behaviour of prezoea

Usually hatchings occur during evening and night time. Hatching lasts about 1-2 hours in majids and other species which have few eggs. However, it occurs several times over two or more days in species which have a larger mass of eggs.

Prezoeas hatch from eggs by rupturing the egg capsules. The egg capsule consists of a thin inner membrane and a thick outer membrane (Davis, 1965 a, b). According to the present observations under the microscope, these membranes are connected to each other only at a small area and they do not separate completely even after the emergence of the prezoea. The hatching mechanism was not observed, but prezoeas seems to rupture the two membranes simultaneously.

Upon hatching prezoeas swim up actively to the surface by jerking movements, moving the antennular, antennal and telson processes synchronously. The swimming motion is not continuous and intermittently stops, however they keep themselves near the top of the water column. In the stagnant condition of an experimental tank, some prezoeas are easily trapped on the very surface layer of water by surface tension. Surface trapping probably causes physical damage to delicate structures of prezoeas, and a high density of prezoeas at the top of the water column seems to aggravate physical damage and reduce the proportion moulting to the first zoea. Thus, under laboratory conditions, surface trapping and crowding in the surface layer appear to be major factors controlling prezoeal moulting. Prezoeas which had been accidentally damaged by needles under the microscope never developed into normal first zoeas even if they were safely returned to their original tank. When supplied with vigorous aeration, only damaged prezoeal skins were torn off partially to give abnormal first zoeas with invaginated setae and spines. Such abnormal first zoeas had no fully developed setal structure, and seldom developed into the normal form. In natural conditions in the sea, prezoeas will hardly ever encounter either the surface effect or the crowding effect. In portunids and pinnotherids some larvae emerged from eggs directly as first zoeas, but the majority passed through a prezoeal stage. In some cases it is supposed that the first zoea hatches rupturing the egg capsules and prezoeal membrane almost simultaneously.

General morphology of prezoea

Prezoeas are covered by a transparent outer membrane. Pigmentation and developing setae of the first zoea are clearly visible through the membrane. The carapace is bulbous or ovoid, without processes. The dorsal spine of first zoea is embedded under the dorsal surface of the prezoea, and its protruding tip is sometimes visible under the dorsal surface of the membrane. The rostral spine of the first zoea is embedded in tissue between the eyes and seldom visible. The long rostral spine, when present, is curled up above the mandibles within a bulbous membrane sheath. The transparent cuticle is drawn out into processes on the antennule, antenna and telson. Development of these processes is variable. In some prezoeas, plumose processes were still partially invaginated, but most of them were fully developed at time of hatching.

The antennule and antenna have processes of various sizes and shapes. The mandible is not clearly separated from the epistome and is bulbous in lateral view. The maxillule and maxilla are covered by a membrane with slight lobations only. Maxillipeds are biramous with some minute projections on the tips of the endopod and exopod. The abdomen is without processes and shows the outline of the somites of the first zoea. The telson is bilobed, usually with a median indentation, and is provided with basically 7 pairs of processes. In some species the telson has 4, 5, or 6 processes.

Descriptions

Pandalus montagui Leach

(Fig. 1)

Duration : not measured

Size - CL : 0.82-0.87 mm

Carapace (not shown in figure) - Newly hatched larva covered by transparent outer membrane. Carapace devoid of processes.

Antennule (Fig. 1 A) - With 5 minute naked terminal and 1 subterminal processes.

Antenna (Fig. 1 B) - Endopod with 2 minute naked terminal processes, one of them occupied by spine of endopod. Exopod with 10 naked processes occupied by developing setae of antennal scale.

Mandible, Maxillule, Maxilla and Maxillipeds - Covered by transparent membrane; devoid of processes.

Telson (Fig. 1 C) - With a deep narrow median indentation on distal margin. With 6 pairs of naked marginal processes, conical in shape, occupied by developing spines of first zoea. The 6th process occupied by 6th and 7th processes of first zoea.

Pagurus prideauxi Leach

(Fig. 2)

Duration : 4-15 min

Size - CL : 0.87-1.17 mm

Carapace and Abdomen (not shown in figure) - Covered by transparent prezoeal outer membrane. Carapace devoid of processes. Abdomen without processes and showing outline of abdominal somites of first zoea.

Antennule (Fig. 2 A) - One subterminal and 2 terminal plumose processes: subterminal one occupied by subterminal setae of first zoea; 3 small projections on outer distal margin.

Antenna (Fig. 2 B) - Endopod with 2 long plumose terminal processes occupied by 2 setae of developing antenna. At base of endopod there is a naked process occupied by spinous process of first zoea. Exopod with 9 plumose processes: outermost one occupied by terminal fused spine of antennal exopod of first zoea, 8 processes occupied by 8 marginal setae.

Mandible, Maxillule, Maxilla and Maxillipeds - Covered by transparent membrane; devoid of processes.

Telson (Fig. 2 C) - No distinct median indentation on distal margin. With 7 pairs of marginal processes. Second process short and naked, occupied by fine hair of first zoea. Other processes occupied by developing spines of first zoea, fringed with marginal sub-processes. No distinct demarcations at point of attachment between main and subprocesses.

Pagurus bernhardus (Linnaeus)

(Fig. 3)

Duration : 6-27 min

Size - CL : 0.92-1.12 mm

Carapace and Abdomen (not shown in figure) - Covered by transparent prezoeal outer membrane. Carapace devoid of processes. Abdomen without processes and showing outline of abdominal somites of first zoea.

Antennule (Fig. 3 A) - One subterminal and 2 terminal plumose processes: subterminal one occupied by subterminal seta of first zoea; 3 small projections, occupied by developing aesthetascs, on outer distal margin.

Antenna (Fig. 3 B) - Endopod with 2 small terminal processes: one with fine hairs and empty, the other naked and occupied by tip of endopod of first zoea. A naked process at base of endopod occupied by spinous process of first zoea. Exopod with 1 naked and 8 plumose processes: naked one occupied by terminal fused spine of antennal exopod of first zoea, 8 processes occupied by 8 marginal setae.

Mandible, Maxillule, Maxilla and Maxillipeds - Covered by transparent membrane; devoid of processes.

Telson (Fig. 3 C) - With small median indentation and 7 pairs of marginal processes: 2 outermost processes short and naked, occupied by fused spine and fine hair of first zoea respectively; inner 5 processes fringed with marginal sub-processes. No distinct demarcations at point of attachment between main and subprocess.

Hyas araneus (Linnaeus)

(Fig. 4)

Duration: 10-26 min

Size - CL : 0.83-0.86 mm

Carapace (Fig. 4 A) - Newly hatched larvae covered by transparent outer membrane. Carapace devoid of processes.

Antennule (Fig. 4 B) - With 2 unequal plumose terminal processes, smaller about 1/3 length and less than 1/2 width of larger; 2 minute projections, occupied by aesthetascs of first zoea, at base of larger process.

Antenna (Fig. 4 C) - With 4 terminal plumose processes, with processes of exopod of first zoea projecting towards or into the 3 larger; two smooth subterminal processes, almost filled by spinous process and endopod of first zoea.

Mandible (Fig. 4 A) - Not clearly separated from epistome and labrum, bulbous in lateral view.

Maxillule (Fig. 4 D) - A smooth bud with slight lobations.

Maxilla (Fig. 4 E) - With smooth inner lobes containing developing endites and endopod; smooth outer lobe containing developing scaphognathite.

First Maxilliped (Fig. 4 F) - Biramous; endopod and exopod with 2 and 3 terminal processes respectively, those on endopod minute.

Second Maxilliped (Fig. 4 G) - Biramous; endopod and exopod with 2 and 3 terminal processes respectively.

Telson (Fig. 4 H) - Bilobed, with 7 pairs of marginal processes: 1st smooth; 4th much the shortest, smooth; others plumose; lengths in ratio 4 : 5 : 6 : 1 : 7 : 6 : 3. Developing telson of first zoea clearly visible within prezoeal membrane; processes of first zoea protrude into proximal parts of all prezoeal processes except 2nd. The shortest (4th) process occupied by telson fork of first zoea.

Hyas coarctatus Leach

(Fig. 5)

Duration : 10-47 min

Size - CL : 0.72-0.76 mm

Carapace (Fig. 5 A) - Newly hatched larva covered by transparent outer membrane. Carapace devoid of processes.

Antennule (Fig. 5 B) - With 2 unequal plumose terminal processes, smaller about 1/3 length and about 1/2 width of larger; smaller process occupied by seta of first zoea; 2 minute projections at base of larger process.

Antenna (Fig. 5 C) - With 4 terminal plumose processes, with processes of exopod of first zoea projecting towards or into the 3 outer processes; 2 smooth subterminal processes, occupied by spinous process and endopod of first zoea.

Mandible (Fig. 5 A) - Not clearly separated from epistome and labrum, bulbous in lateral view.

Maxillule and Maxilla (Fig. 5 A) - A smooth bud with slight lobations.

First and Second Maxillipeds (Fig. 5 A) - Biramous; projections on endopod and exopod same as those of *Hyas araneus*

Telson (not shown in figure) - Bilobed, with 7 pairs of marginal processes: size and shape same as *H. araneus*.

Inachus dorsettensis (Pennant)

(Fig. 6)

Duration : 3-23 min

Size - CL : 0.75-0.83 mm

Carapace (Fig. 6 A) - Newly hatched larva covered by transparent outer membrane. Carapace devoid of processes.

Antennule (Fig. 6 B) - With 2 unequal plumose terminal processes, smaller about 2/3 length and about 2/3 width of larger: smaller process occupied by seta of first zoea; 2 minute projections, each occupied by aesthetasc of first zoea, at base of larger process.

Antenna (Fig. 6 C) - With 4 terminal plumose processes, with processes of exopod of first zoea projecting towards or into third process; two smooth subterminal processes, almost filled by spinous process and endopod of first zoea.

Mandible (Fig. 6 A) - Not clearly separated from epistome and labrum, bulbous in lateral view.

Maxillule (Fig. 6 D) - A smooth bud with slight lobations.

Maxilla (Fig. 6 E) - A smooth bud.

First Maxilliped (Fig. 6 F) - Biramous; endopod and exopod with 2 subterminal and 4 terminal minute projections respectively.

Second Maxilliped (Fig. 6 G) - Biramous; endopod and exopod each with a minute projection.

Telson (Fig. 6 H) - Bilobed, with 7 pairs of marginal processes: 4th much the shortest, smooth; others plumose; lengths in ratio 2 : 4 : 4 : 1 : 4 : 3 : 2. Developing telson of first zoea clearly visible within prezoeal membrane; processes of first zoea protrude into proximal parts of all prezoeal processes except 2nd. Shortest (4th) process occupied by protuding telson fork of first zoea.

Inachus leptochirus Leach

(Fig. 7)

Duration : 9-36 mm

Size - CL : 0.98-1.10 mm

Carapace (Fig. 7 A) - Newly hatched larva covered by transparent outer membrane. Carapace devoid of processes.

Antennule (Fig. 7 B) - With 2 unequal plumose terminal processes, smaller about 3/4 length and about 2/3 width of larger: smaller process occupied by seta of first zoea; 2 minute projections, each occupied by aesthetasc of first zoea, at base of larger process.

Antenna (Fig. 7 C) - With 4 terminal plumose processes, with processes of exopod of first zoea projecting towards or into 3rd and 4th processes; two smooth subterminal processes, larger almost filled by spinous process of first zoea, smaller empty.

Mandible (Fig. 7 A) - Not clearly separated from epistome and labrum, bulbous in lateral view.

Maxillule, Maxilla and Maxillipeds (Fig. 7 A) - Similar to *Inachus dorsettensis*.

Telson (Fig. 7 A) - Bilobed, with 7 pairs of marginal processes: size and shape similar to *I. dorsettensis*.

Macropodia tenuirostris (Leach)

(Fig. 8)

Size - CL : not measured

Duration : 5-38 min

Carapace and Abdomen (not shown in figure) - Newly hatched larva covered by transparent outer membrane. Carapace devoid of processes.

Antennule (Fig. 8 A) - With 2 unequal plumose terminal processes, smaller about 2/3 length and equal width of larger: smaller process occupied by seta of first zoea.

Antenna (Fig. 8 B) - With 4 terminal plumose processes, with processes of exopod of first zoea projecting towards or into 3rd and 4th processes; two smooth subterminal processes, almost filled by spinous process and endopod of first zoea.

Mandible (not shown in figure) - Not clearly separated from epistome and labrum, bulbous in lateral view.

Maxillule and Maxilla (not shown in figure) - Smooth buds with slight lobations.

First and Second Maxillipeds (not shown in figure) - Biramous; projections on endopod and exopod similar to *Inachus dorsettensis*.

Telson (Fig. 8 C) - Bilobed, with 7 pairs of marginal processes: size and shape similar to *I. dorsettensis*.

Orithyia sinica (Linnaeus)

(Fig. 9)

Duration : 5-9 min

Size - CL : 0.95-0.98 mm

Carapace (Fig. 9 A) - Newly hatched larva covered by transparent outer membrane. Carapace devoid of processes. Long rostal spine curled within sheath above mandible.

Antennule (Fig. 9 B) - With 3 minute unequal terminal projections.

Antenna (Fig. 9 C) - Membrane covering exopod of first zoea elongate and with 2 minute terminal projections; two smooth subterminal processes, almost filled by spinous process and endopod of first zoea.

Mandible (Fig. 9 A) - Not clearly separated from epistome and labrum, bulbous in lateral view.

Maxillule and Maxilla (Fig. 9 A) - Not clearly visible, but smooth buds with slight lobations.

First Maxilliped (Fig. 9 A, D, E) - Biramous; endopod (Fig. 9 D) and exopod (Fig. 9 E) each with 3 terminal projections.

Second Maxilliped (Fig. 9 A) - Biramous; endopod and exopod similar to first maxilliped.

Telson (Fig. 9 F) - Bilobed, with 5 pairs of naked marginal processes: 1st much the shortest; 2nd massive and occupied by telson fork of first zoea; 3rd-5th lobate, similar in size and shape, innermost occupied by 2 or 3 innermost processes (7-9th) of first zoea (first zoea has 3 or 4 pairs of inner processes: Fig. 9 G).

Ebalia tuberosa (Pennant)

(Fig. 10)

Duration : 8-21 min

Size - CL : 0.45 mm (0.45-0.47 mm)

Carapace (Fig. 10 A) - Newly hatched larva covered by transparent outer membrane; carapace devoid of processes.

Antennule (Fig. 10 B) - With 2 unequal plumose terminal processes, smaller about 3/4 length and equal width of larger; 3 minute projections below base of larger process.

Antenna (Fig. 10 C) - With 2 equal terminal plumose processes and 1 smooth subterminal process occupied by developing endopod.

Mandible (Fig. 10 A) - Not clearly separated from epistome and labrum, bulbous in lateral view.

Maxillule (Fig. 10 D) - A smooth bud with slight lobations containing developing endites and endopod.

Maxilla (Fig. 10 E) - A smooth bud with slight lobations containing developing endites, endopod and scaphognathite.

First Maxilliped (Fig. 10 F) - Biramous; endopod and exopod each with 3 projections, those on endopod minute.

Second Maxilliped (Fig. 10 G) - Biramous; endopod and exopod with 1 and 3 minute projections.

Telson (Fig. 10 H) - Bilobed, with 7 pairs of marginal processes: 1st, 4th and 7th much shorter, smooth; others plumose; lengths in ratio 1.7 : 7 : 9 : 1 : 11 : 10 : 1.5. Developing telson of first zoea clearly visible within prezoeal membrane; processes of first zoea protrude into proximal parts of all prezoeal processes except 1st, 2nd and 4th.

Liocarcinus holsatus (Fabricius)

(Fig. 11)

Duration : 2-10 min

Size - CL : 0.39-0.42 mm

Carapace (Fig. 11 A) - Newly hatched larva covered by transparent outer membrane. Carapace devoid of processes.

Antennule (Fig. 11 B) - With 2 unequal terminal processes, smaller, naked, occupied by seta of first zoea, about 1/5 length and less than 1/2 width of larger; larger plumose on distal half; 2 minute projections at base of larger process.

Antenna (Fig. 11 C) - With 3 terminal plumose processes, outermost much smaller, with processes of exopod of first zoea projecting towards or into outer two; 2 smooth subterminal process, larger filled by tip of spinous process of first zoea, smaller empty.

Mandible, Maxillule and Maxilla (Fig. 11 A) - Not clearly separated from epistome and labrum, bulbous in lateral view.

First Maxilliped (Fig. 11 A, D, E) - Biramous; endopod (Fig. 11 D) with 3 minute projections, exopod (Fig. 11 E) with 3 terminal projections.

Second Maxilliped (Fig. 11 A, F, G) - Biramous; endopod (Fig. 11 F) and exopod (Fig. 11 G) with 2 minute projections.

Telson (Fig. 11 H) - Bilobed, with 7 pairs of marginal processes: 1st shorter and smooth; 4th much the shortest, smooth; others plumose only at tip; lengths in ratio 2 : 2 : 3 : 1 : 6.5: 4 : 2.8. Developing telson of first zoea clearly visible within prezoeal membrane; processes of first zoea protrude into proximal parts of all prezoeal processes except 2nd.

Liocarcinus corrugatus (Pennant)

(Fig. 12)

Duration : 3-15 min

Size - CL : 0.33-0.36 mm

Carapace (Fig. 12 A) - Newly hatched larva covered by transparent outer membrane. Carapace devoid of processes.

Antennule (Fig. 12 B) - With 2 unequal terminal processes; smaller naked, occupied by seta of first zoea, about 1/3 length and less than 1/3 width of larger; 2 minute projections below base of larger process.

Antenna (Fig. 12 C) - With 3 terminal plumose processes, with processes of exopod of first zoea projecting towards or into outer 2 processes; 2 smooth subterminal processes, larger process almost filled by spinous process of first zoea, smaller empty.

Mandible, Maxillule and Maxilla (Fig. 12 A) - Mandible not clearly separated from epistome and labrum, bulbous in lateral view. Maxillule and maxilla simple buds with slight lobations.

First and Second Maxillipeds (Fig. 12 A) - Biramous; projections of endopod and exopod same as those of *Liocarcinus holsatus*.

Telson (Fig. 12 E) - Bilobed, with 7 pairs of marginal processes: size and shape of processes similar to those of *Carcinus maenas*.

Liocarcinus marmoreus (Leach)

(Fig. 13)

Duration : 1-6 min

Size - CL : not measured

Carapace and Abdomen (not shown in figure) - Newly hatched larva covered by transparent outer membrane. Carapace devoid of processes. Abdomen without processes and showing outline of abdominal somites of first zoea.

Antennule (Fig. 13 A, A') - With 2 unequal terminal processes; smaller naked, occupied by seta of first zoea, about 1/5 length and about 1/3 width of larger; larger sparsely plumose; 2 minute projections (Fig. 13 A'), occupied by aethetascs of first zoea, below base of larger process.

Antenna (Fig. 13 B) - With 3 terminal processes, plumose on distal third, outermost process about 1/2 length of 2 inner processes, with processes of exopod of first zoea projecting towards or into the 2 outer processes; 2 smooth subterminal processes, larger process almost filled by spinous process of first zoea.

Mandible (not shown in figure) - Not clearly separated from epistome and labrum, bulbous in lateral view.

Maxillule and Maxilla (not shown in figure) - Smooth buds with slight lobations, similar to ***Liocarcinus holsatus*.**

First and Second Maxillipeds (not shown in figure) - Biramous; projections on endopod and exopod similar to those of ***L. holsatus*.**

Telson (Fig. 13 C) - Bilobed, with 7 pairs of marginal processes: 4th thick, shortest, smooth; others sparsely plumose; lengths in ratio 1.5 : 2 : 2.5 : 1 : 4 : 3.5 : 2. Developing telson of first zoea clearly visible within prezoeal membrane; processes of first zoea protrude into proximal parts of all prezoeal processes except 2nd.

Carcinus maenas (Linnaeus)

(Fig. 14)

Size - CL : 0.32-0.37 mm

Duration : 0.7-6 min

Carapace (Fig. 14 A) - Newly hatched larva covered by transparent outer membrane; carapace devoid of processes.

Antennule (Fig. 14 B, C) - With 2 unequal terminal processes; smaller naked, occupied by seta of first zoea, about 1/3 length and less than 1/3 width of larger; larger plumose; 2 minute projections below base of larger process.

Antenna (Fig. 14 D) - With 3 terminal plumose processes, with processes of exopod of first zoea projecting towards or into outer 2 processes; 2 smooth subterminal process: larger process almost filled by spinous process of first zoea.

Mandible, Maxillule and Maxilla (Fig. 14 A) - Not clearly separated from epistome and labrum, bulbous in lateral view.

First and Second Maxillipeds (Fig. 14 F) - Biramous; projections on endopod and exopod similar to *Liocarcinus holsatus*.

Abdomen (Fig. 14 A) - Without processes and showing outline of abdominal somites of first zoea.

Telson (Fig. 14 E) - Bilobed, with 7 pairs of marginal processes: 4th much the shortest, smooth; others plumose; lengths in ratio 2 : 3.5 : 4 : 1 : 4 : 3 : 2. Developing telson of first zoea clearly visible within prezoeal membrane; processes of first zoea protrude into proximal parts of all prezoeal processes except 2nd; 1st occupied by ultra fine hair of first zoea; 4th by telson fork.

Portunus gladiator Fabricius

(Fig. 15)

Size - CL : 0.31 mm

Duration : not measured

Carapace and Abdomen (not shown in figure) - Newly hatched larva covered by transparent outer membrane. Carapace devoid of processes.

Antennule (Fig. 15 A) - With 2 minute terminal processes, naked; one occupied by seta of first zoea.

Antenna (Fig. 15 B) - Bilobed: one lobe containing exopod processes and the other the spinous process; the exopod lobe with 2 minute terminal processes.

Mandible, Maxillule and Maxilla (not shown in figure) - Not clearly separated from epistome and labrum, bulbous in lateral view.

First and Second Maxillipeds (not shown in figure) - Biramous; projections on endopod and exopod very minute or undiscernible.

Telson (Fig. 15 C) - Bilobed with deep median indentation; 7 pairs of short naked marginal processes: 4th process occupied by tip of telson fork of first zoea; inner 3 pairs by 3 spinous processes.

Charybdis bimaculata (Miers)

(Fig. 16)

Size - CL : not measured

Duration : not measured

Carapace and Abdomen (not shown in figure) - Newly hatched larva covered by transparent outer membrane. Carapace devoid of processes.

Antennule (Fig. 16 A, A') - With 2 minute unequal terminal processes, naked, larger occupied by seta of first zoea. In some specimens a minute subterminal protuberance present.

Antenna (Fig. 16 B) - Bilobed: one lobe containing spinous process and the other the exopod; the latter lobe with two minute naked terminal processess.

Mandible, Maxillule and Maxilla (not shown in figure) - Not clearly separated from epistome and labrum, bulbous in lateral view.

First and Second Maxillipeds (not shown in figure) - Biramous; projections on endopod and exopod very minute or undiscernible.

Telson (Fig. 16 C) - Bilobed with deep median indentation; 7 pairs of short naked marginal processes: outer 3 processes smaller than inner 3 processes, 4th process occupied by tip of telson fork of first zoea, inner 3 processes by 3 spinous processes.

Monodaeus couchi (Couch)

(Fig. 17)

Size - CL : 0.84-0.89 mm

Duration - 8-34 min

Carapace and Abdomen (not shown in figure) - Newly hatched larva covered by transparent outer membrane. Carapace devoid of processes. Abdomen without processes and showing outline of abdominal somites of first zoea.

Antennule (Fig. 17 A) - With 2 unequal plumose terminal processes: smaller less than 1/3 length, about 1/2 width of larger and occupied by a seta of first zoea; 2 minute projections, occupied by developing aesthetasc of first zoea, at base of larger process.

Antenna (Fig. 17 B) - With 4 terminal plumose processes, outermost smaller than other 3; processes of exopod of first zoea project towards or into the 2 outer processes. One smooth subterminal process, almost filled by spinous process of first zoea.

Mandible (not shown in figure) - Not clearly separated from epistome and labrum, bulbous in lateral view.

Maxillule and Maxilla (not shown on figure) - Smooth buds with slight lobations.

First and Second Maxilliped (not shown in figure) - Biramous; projections on endopod and exopod similar to those of *Cancer pagurus*.

Telson (Fig. 17 C) - Bilobed, with 7 pairs of marginal processes: 4th much the shortest, smooth; others plumose; lengths in ratio 2.7 : 3 : 4 : 1 : 5 : 4.7 : 3.4. Developing telson of first zoea clearly visible within prezoeal membrane; processes of first zoea protrude into proximal parts of all prezoeal processes except 2nd.

Cancer pagurus Linnaeus

(Fig. 18)

Duration : 8-32 min

Size - CL : 0.50-0.58 mm

Carapace (Fig. 18 A) - Newly hatched larva covered by transparent outer membrane. Carapace devoid of processes.

Antennule (Fig. 18 B) - With 2 unequal plumose terminal processes, smaller about 1/3 length and less than 1/3 width of larger.

Antenna (Fig. 18 C) - With 4 terminal plumose processes, outermost 2 smaller, with processes of exopod of first zoea projecting towards or into the 3 outer; 2 smooth subterminal process, the larger one filled by spinous process of first zoea.

Mandible (Fig. 18 A, D) - Not clearly separated from epistome and labrum, bulbous in lateral view.

Maxillule (Fig. 18 E) - A smooth bud with slight lobations.

Maxilla (Fig. 18 F) - A smooth bud with slight lobations.

First Maxilliped (Fig. 18 A, G, H) - Biramous; endopod (Fig. 18 G) and exopod (Fig. 18 H) with 4 and 3 projections respectively.

Second Maxilliped (Fig. 18 A, I, J) - Biramous; tip of endopod simple, exopod with 3 terminal projections.

Telson (Fig. 18 K) - Bilobed, with 7 pairs of marginal processes: 4th much the shortest, smooth; others plumose; lengths in ratio 1.5 : 2.5 : 3.5 : 1 : 4.2 : 3.2 : 2.3. Developing telson of first zoea clearly visible within prezoeal membrane;

processes of first zoea protrude into proximal parts of all prezoeal processes except 2nd.

Carcinoplax longimana (De Haan)

(Fig. 19)

Duration : 8-46 min

Size - CL : 0.42-0.47 mm

Carapace (Fig. 19 A) - Newly hatched larva covered by transparent outer membrane. Carapace devoid of processes.

Antennule (Fig. 19 B) - With 2 unequal plumose terminal processes, smaller about 1/2 length and width of larger: smaller process occupied by a setae of first zoea; 2 minute projections, occupied by aesthetascs of first zoea, at base of larger process.

Antenna (Fig. 19 C) - With 4 terminal plumose processes, with processes of exopod of first zoea projecting towards or into 3 outer processes; two smooth subterminal processes, the larger almost filled by spinous process of first zoea, the smaller empty.

Mandible (Fig. 19 A) - Not clearly separated from epistome and labrum, bulbous in lateral view.

Maxillule, Maxilla and Maxillipeds (Fig. 19 A) - Similar to *Monodaeus couchi* and *Cancer pagurus*.

Abdomen (Fig. 19 A) - Without processes and showing outline of abdominal somites of first zoea.

Telson (Fig. 19 D) - Bilobed, with 7 pairs of marginal processes: 4th much the shortest, smooth; others plumose; lengths in ratio 1.1 : 1.5 : 2.5 : 1 : 2.5 : 2.2 : 2.1. Developing telson of first zoea clearly visible within prezoeal membrane; processes of first zoea protrude into proximal parts of all prezoeal processes except 2nd.

Pinnotheres pinnotheres (Linnaeus)

(Fig. 20)

Duration : 1-4 min

Size - CL : 0.35-0.38 mm

Carapace and Abdomen (not shown in figure) - Newly hatched larva covered by transparent outer membrane. Carapace devoid of processes.

Antennule (Fig. 20 A) - A smooth elongate bud containing developing antennule of first zoea.

Antenna (Fig. 20 B) - A smooth conical bud containing developing antenna of first zoea.

Mandible (not shown in figure) - Not clearly separated from epistome and labrum, bulbous in lateral view.

Maxillule and Maxilla (not shown in figure) - Smooth buds with slight lobations.

First and Second Maxillipeds (not shown in figure) - Biramous; projections on endopod and exopod very minute or undiscernible.

Telson (Fig. 20 C, D) - Newly-hatched larva with telson lobes curved ventrally (Fig. 20 C), extending as larva swims to form one lobe with short processes on either side of median projection occupied by median lobe of telson of first zoea. Each of paired lobes with 1+3 pairs of naked marginal processes: inner 3 pairs small and occupied by 3 spines of first zoea; outer process massive, with minute marginal tubercles, occupied by process of telson fork of first zoea.

DISCUSSION

In prezoeas of decapod crustaceans, the prezoeal cuticle is a transparent covering drawn out into processes on the antennule, antenna and telson. The processes are used for swimming, and they present potentially useful taxonomic characters in terms of their numbers, relative lengths and degree of plumosity. It is of considerable interest to consider the extent to which these prezoean features can be used as evidence in the phylogeny of decapod crustaceans.

There are very few descriptions of prezoeas of carideans and thalassinids. Processes on the antennule, antenna and telson are all naked and show little difference in size. The telson has a deep narrow median indentation, and the telson processes are not well separated. Caridean and thalassinid larvae are in many ways more primitive than anomuran and brachyuran larvae (Gurney, 1942), and it might be be expected that their prezoeas would also show primitive features compared to those of anomurans and brachyurans. ***Pandalus montagui*** has 6 pairs of short naked processes on the telson. According to limited observations in the present study, ***Processa canaliculata*** also has 6 pairs of naked processes on the telson. Gurney (1942, Fig. 13 C) described prezoeal telson of ***Hyppolyte varians*** which also shows 6 primary processes on each side.

No thalassinids were examined during the present work. Known prezoeas of this group have 7 pairs of telson processes. Gurney (1938, Fig. 5) described the antennule antenna and telson of prezoeas of *Axius plectorhynchus*, extracted from preserved eggs. The antennule is unsegmented with one process; the antenna has 8 plumose processes on the exopod and 3 on the endopod. The prezoea of *Callianassa uncinata* (described by Aste and Retamal, 1984, Fig. 3) has short and naked processes on the antennule, antenna and telson.

Anomuran prezoeas are easily distinguished from other major groups by the structure of the prezoeal processes. The outermost 2 telson processes (1st and 2nd) are usually naked and reduced to varying extent, while, on the other hand, the 4th process is reduced in prezoeas of most brachyurans. In anomurans the processes on the antennule, antenna and telson are quite variable in size and shape. Some, like *Munida rugosa* (described as *Munida banffica* by Lebour, 1930), *Galathea squamifera* (described by Lebour, 1931) and *Petrolisthes tonsorius* (described by Pellegrini and Gamba, 1985), have a simple sheath on these appendages. However, in most species the processes on the antennule, antenna and telson are well-developed and are equipped with either thick subprocesses or fine hairs. The thick subprocesses are without distinct demarcations at the point of attachment. These can be regarded as more primitive in form than the fine hairs which are found on the prezoeal processes of some anomurans and most brachyurans.

All processes on the antennule and antenna are provided with thick subprocesses in some anomuran species, including *Petrolisthes elongatus* (described by Greenwood, 1965), *Uroptychus* cf. *polytus* (described by Pike and Wear, 1969) and *Pagurus middendorffi* (described by Quintana and Konishi, 1986).

In the present study a limited examination was made of the prezoea of *Munida rugosa*. The telson processes have thick subprocesses, whereas the antennular and antennal processes have fine hairs. *Petrolisthes granulosus* also has this type of prezoeas (Saelzer, Quintana and Quiñones, 1986). In most pagurid species the telson processes are provided with thick subprocesses, while the antennular and antennal processes have fine hairs (Quintana and Konishi, 1986; present study), but fine hairs on the prezoeal telson are not uncommon in other anomurans. Some anomuran species have fine hairs on the processes of the antennule, antenna and telson including *Lithodes maja* (described by Sars, 1890), *Porcellana platycheles* (described by Lebour, 1943), *Porcellana longicornis* (described by Gurney, 1942), *Petrolisthes rufescens* (described by Gohar and Al-kholy, 1957) and *Petrolisthes elongatus* (described by Wear, 1965).

Prezoeas of *Pagurus prideauxi* and *Pagurus bernhardus* show some differences in detail, particularly in the processes of the antennal endopod and telson. Both species have 2 terminal processes on the antennal endopod. In *Pagurus prideauxi* they are long and plumose, while they are short and only one of them is sparsely plumose in ***Pagurus bernhardus***. The telson processes of ***Pagurus prideauxi*** are much shorter and conical in shape. In later development, it was noted that considerable differences occur in the development of larval gills in these two species, in both the late zoea and megalopa stages (see Chapter 3). These differences in prezoeal morphology and larval gills between ***P. prideauxi*** and ***P. bernhardus*** appear to be more distinct than known interspecific differences in congeneric brachyurans. Notable differences have also been found in the zoeal morphology of these two ***Pagurus*** species. MacDonald, Pike and Williamson (1957) and Pike and Williamson (1960) distinguished 3 different groups of pagurid larvae and placed ***P. prideauxi*** and ***P. bernhardus*** in separate groups. Roberts (1970) added another group based on the larvae of ***Pagurus longicarpus***, and Goldstein and Bookhout (1972) suggested that the genus ***Pagurus*** is polyphyletic. Based on the prezoeal morphology and the larval gills, the present study also supports their opinion.

It is interesting to note the similarity in prezoeal features of anomurans and dromiids. In particular, processes on the telson are very similar in both groups. Thick subprocesses which characterize the anomuran telson are also found in dromiid prezoeas, including ***Petalomera wilsoni*** (Wear, 1970 a, Fig. 7) and ***Petalomera japonica*** (see Chapter 4 of thesis). Prezoeal processes of ***Conchoecetes artificiosus***, described by Sankolli and Shenoy (1967, Fig. 1), are very similar in number and size to those of the two ***Petalomera*** species, though the telson processes of

Conchoecetes artificiosus are naked. In addition to the general resemblance of zoeal features, dromiid prezoeas are more similar to pagurid prezoeas than to any brachyuran prezoeas. The systematic position of the Dromioidea has long been a subject of controversy. Those working on the adults have always insisted that they are primitive brachyurans (Guinot, 1977, 1978 and ref.), while those working on the zoeal stages have been equally insistentd that they are anomurans (Gurney, 1924 b, 1942; Lebour, 1934; Pike and Williamson, 1960; Williamson, 1965; Rice, 1980; Williamson, 1982; Rice, 1983; Hong and Williamson, 1986). The present work shows that the prezoea shows the same affinities as the zoeal stages.

Lebour (1928 b) compared brachyuran prezoeas, and she recognised three types agreeing with the major groups Oxystomata, Oxyrhyncha and Brachyrhyncha. She pointed out that the prezoea of *Ebalia tuberosa* (Leucosiidae) is not typical of the Oxystomata. The present study also shows that prezoeas of 2 oxystomatous species show no common features. *E. tuberosa* has 2 terminal plumose processes of equal size on the antennule, 2 on the antennal exopod and 7 on telson. The innermost (7th) process of the telson is naked and markedly reduced. Such a combination of processes is not found in any other known brachyuran prezoea.

Orithyia sinica (Callapidae) shows more atypical features. Prezoeal processes on the antennule, antenna and telson are markedly reduced, without subprocesses or fine hairs. On the telson, only 5 naked processes are present. Considering the well-developed zoeal setae of this species, these prezoeal features are quite unusual. Based on the zoeal characters of *O. sinica,* described by Hong(1976), Rice(1980) discussed this highly characteristic larva in relation to dorippid zoeas, and he recognised the isolated position of this monotypic genus of Calappidae in the Brachygnatha. According to prezoeal characters, *O. sinica* seems to be more advanced than most cyclometopous species in bearing only reduced prezoeal processes.

The prezoea of *Calappa lophos*, described by Raja Bai (1959), has no processes on the antennule, 3 naked processes on the antenna and 5 scantly-plumose process on the telson. It resembles *O. sinica* in the form of the prezoea, but the inclusion of these two species in the same family has been questioned by Rice (1982) and Števčič (1983).

In the present study a limited examination was made of the prezoeal antennule and antenna of *Neodorippe japonica* (Dorippidae). The antennule has two unequal terminal processes: one long and plumose and the other short and naked, with lengths in the ratio 6 : 1. In addition, two minute projections are present near the base of the long process. The antenna has 3 long plumose processes and 2 subterminal processes, one of them occupied by the spinous process.

Although descriptions of telson processes are not available, it is easy to see that this dorippid prezoea is different not only from *E. tuberosa* but also from *O. sinica*. On the other hand it is more similar to most cyclometopous crabs.

Thus, the prezoeal features of these three oxystomatous families are quite different from each other. Similarly diverse characters are also reported in the zoeal features of the oxystomatous families, and Rice (1980) suggested that they should not be placed together. Based on adult features, Guinot(1977, 1978) concluded that the Oxystomata is an artificial group, and it is clear that prezoeal and zoeal characters support this conclusion.

Prezoeas of majids are provided with very well-developed processes on the antennule, antenna and telson. They are very similar to those of most cyclometopous species including cancrids, pirimelids, xanthids, *Atelecyclus* and *Carcinoplax*, but not portunids. Majid prezoeas have 4 subequal plumose process on the antennal exopod, whereas in the foregoing cyclometopous families, 1 or 2 outer processes on the antennal exopod are always considerably reduced in size. Prezoeas of some majid species have reduced processes on the antennule and antenna. In prezoeas of *Chionoecetes bairdi* they are considerably reduced (Haynes, 1973, Fig. 1). In *Microphrys bicornutus* some processes on the antennule, antenna and telson are markely reduced (Hartnoll, 1964 a, Fig. 1). In particular, the prezoeas of *Cancer* *edwardsi* has 4 plumose processes, one of which is almost vestigial (Quintana, 1983, 1984). This suggests that the reduction in the size of processes on the antennal exopod has occurred in varying degrees in the cyclometopous families.

Among the cyclometopous families, prezoeas of the Portunidae show conderable variation compared to those of other families. Two groups of portunid prezoeas are easily recognised. One group has well-developed plumose processes on the antennule, antenna and telson; the other has very reduced processes. In the former group (species of genus *Liocarcinus* and *Carcinus maenas*) there are 3 plumose processes on the antennal exopod, in contrast to 4 in majids and other cyclometopous species. The telson has 7 pair of processes, as in the case of majids and other cyclometopous species. Previous works also described this type of portunid prezoea in *Liocarcinus* (as *Portunus*) *puber* (Dohrn, 1870, Figs. 22-23; Lebour, 1928 b, Fig. 1(1-2)) and *Carcinus maenas* (Faxon, 1880, Figs. 1-14); Lebour (1944, Fig. 1 b) described the prezoea of *Portumnus latipes*, but her descriptions are not adquate to refer to. In the latter group (*Portunus gladiator* and *Charybdis bimaculata*), all the processes on the antennule, antenna and telson are remarkably reduced. The antennal endopod and exopod are of equal size showing more clearly the biramous structure, and antennal exopod has only 2 minute processes. Telson processes are simple and very reduced. This kind of portunid prezoea has previously been reported in *Callinectes hastata* (Conn, 1884, Figs. 2, 14) and

Portunus (as *Neptunus*) *pelagicus* (Prasad and Tampi, 1953, Fig. 8).

Thus, portunid prezoeas appear to show reduction not only in the number of processes on the antennal exopod but also in the size of processes on the antennule, antenna and telson. In *Liocarcinus holsatus* fine hairs on the telson process are limited to the end.

These two groups of portunid prezoeas also corroborate the groupings of adult portunids proposed by Rice and Ingle (1975 b) and Rice (1980), who recognised two evolutionary groups, Carcininae and Portuninae.

In an overall view, it is evident that there has been a gradual reduction in number and size of prezoeal processeses from majids through most of cyclometopous species to some portunids, and further to pinnotherids. This suggests that the Majidae may contain primitive forms, close to the origin of all other Eubrachyura. Also it is suggested that prezoeal features of the telson are more conservative than those of the antennule and antenna.

Little is known of the prezoeas of catometapous species apart from the Grapsidae. Only the antennule and telson of *Hemigrapsus penicillatus* were examined in the present study (not shown in figure). The antennule of this grapsid species has 3 minute projections, and telson processes are remarkably reduced, with only 1+3 naked projections representing the telson fork and 3 inner marginal spines. Conn (1884, Figs. 4-8, 15) described a similar prezoea in *Sesarma* species, having 2 minute projections on the antennule and 1+3 on the telson. Hart (1935) reported that the prezoea of *Hemigrapsus nudus* lacks "the prolongation of the membrane" of the telson. The absence of plumose processes of prezoeas was also reported by Wear (1970 b) in grapsids including *Leptograpsus variegatus*, *Planes marinus*, *Hemigrapsus crenulata*, *Hemigrpsus edwardsi*, *Cyclograpsus lavauxi*, *Cyclograpsus insularum*, *Helice crassa* and *Plagusia chabrus*. Lack of plumose processes in prezoeas was also reported in *Hemiplax hirtipes* (Ocypodidae) by Wear (1968 b).

In addition to the prezoea of *Pinnotheres pinnotheres* described here, berief descriptions of the prezoea of this species and *Pinnotheres pisum* were given by Lebour (1928) and the prezoea of *Pinnotheres ostreum* was described by Conn (1884). Reduction of prezoeal process is very evident in pinnotherids and their prezoal structure is much more simple than in any other brachyuran family. *Pinnotheres pinnotheres* has no terminal projections on the antennule and antenna; there is a simple cuticular sheath covering the developing antennule and antenna of the first zoea. In the zoeal stage the antenna is absent or present as a vestigial spine (Lebour, 1928 a, b; Atkins, 1954), whereas in all cases the antenna is present in the prezoea, even if it is naked. Only 1+3 minute naked processes are present on the telson, corresponding to a modified telson fork and 3 inner marginal spines of the first zoea. The usual 7 pairs of telson processes are no longer traceable in the prezoeal telson, but it has developed a truncate median lobe in the center. This unique feature is also reflected in the armature of the zoeal telson. In the prezoea of ***Pinnotheres ostreum***, reduction of processes are more pronounced (Conn, 1884, Fig. 9). The prezoeal telson has developed a median lobe in centre and nearly lost marginal processes. A cuticular lobe covers developing spines of first zoea.

The Pinnotheridae, as at present constituted, contains species with very atypical larvae, as noted by Bocquet (1965). The species included may also show a range of prezoeal characters, and these features should provide valuable information on the taxonomy and adaptive convergence of the Pinnotheridae.

The biramous nature of crustacean limbs is well established (Calman, 1909; McLaughlin, 1980). However, the antennule is exceptional in being uniramous even in nauplius larvae and in adult crustaceans of all groups except some of the higher Malacostraca. It is still in question whether the flagella of higher Malacostraca represent a biramous structure. On this point it is interesting to note that the prezoeal antennule of all decapods which have so far been described, bears basically 2-3 plumose terminal processes. The presence of these antennular processes of prezoeas does not appear to support the concept of a biramous antennule of decapods, since they are secondary structures on the antennule. Furthermore, the prezoeal antenna has such processes on both the endopod and the exopod. In caridean prezoeas the limited evidence suggests that there are more than 2 processes on the antennule. Prezoeas of anomurans (including dromioids) have 3 (rarely 2 or 4) plumose processes on the antennule (Sars, 1890; Greenwood, 1965; Wear, 1965, 1970 a; Sankolli and Shenoy, 1967; Hong and Williamson, 1986; present study). One of these processes is subterminal in position and occupied by the developing seta of the first zoea. Prezoeas of brachyurans have always 2 processes on the antennule. One of them is usually reduced and always occupied by the subteminal seta of the developing antennule. In all cases developing aesthetascs occupy the minute projections at the base of the plumose processes.

The antenna of prezoeas looks complicated, but its biramous nature is evident, although a varying number of plumose processes (maximum 3-4) obscure its biramous structure. However, these plumous processes are always occupied by the developing exopod, and thus they should be regarded as exopod setae of the first zoea. In addition to the plumose processes, there are two subterminal processes. One of them, representing the endopod, is shorter and obtuse at the tip; the larger represents the spinous process. The spinous process, however, can not be classed as a ramus since it is a secondary growth of the propodus. Similar structures are found in the prezoeal antenna of majids (Lebour, 1927, 1928 b; Gurney, 1942; Hartnoll, 1964 a; Webber and Wear, 1981), cancrids (Quintana, 1983, 1984), pirimelids (Lebour, 1944), xanthids (Conn, 1884; Gurney, 1938; Wear, 1967, Suzuki, 1978), *Atelecyclus rotundatus* (Hong and Ingle, in press) and *Carcinoplax longimana* (present study).

The biramous structure of the prezoeal antenna is more evident in *Ebalia tuberosa* which has an endopod process and an exopod with 2 plumose processes (Lebour, 1928 a; present study). A subterminal process representing the spinous process of the zoeal antenna is absent. In zoeal stages, the antenna of this species is uniramous with an apical process (Lebour, 1928 a, b; Salman, 1982), but in prezoea the antenna retains biramous structure.

From their zoeal characters, phylogenetic relationships of the Pinnotheridae to Leucosiidae (Lebour, 1928 a; Gurney, 1942; Rice, 1980) or to the Hymenosomatidae (Gurney, 1938, 1942; Lucas, 1971; Wear, 1967, 1968 b) have been proposed. Rice (1980: 349) is of the opinion that the Pinnotheridae resemble the Ocypodidae in zoeal morphology. From the prezoeal characters, particularly the trends of reduction of prezoeal processes, it is hard to relate the Pinnotheridae to the Leucosiidae, and instead it is suggested that the Pinnotheridae resemble the Grapsidae and Ocypodidae. Unfortunately information on the prezoeas of Ocypodidae and Gecarcinidae are not suffucient for further discussion. Further information on the prezoeas of catometopous families is very desirable.

Four pairs of telson processes in prezoeas of grapsids and pinnotherids is more comparable to the typical zoeal telson of brachyurans which bears 3 marginal spines and telson fork plus spines. On this point it can be postulated that the lateral and dorsal spines on the telson fork of brachyuran zoeas represent in reduced form the 3 outer processes of the prezoeas. Thus, the spines on the telson fork of brachyuran larvae should be considered as important features bearing evolutionary implications.

On the phylogenetic implications of the prezoea, Conn (1883, 1884: 13) was convinced that "the larval cuticle must refer to some form quite like a protozoea". On the other hand Gurney (1926, 1942) suggested that the embryonic cuticle "must represent the nauplius and not the protozoea". He indicated that the prezoeal stage is "one earlier than the protozoea", since the protozoeal stage has 7 pairs of telson processes, while the embryonic telson of carideans has 6 pairs of telson processes. Also he was of the opinion that the first 3 stages of caridean larvae represent the 3 protozoeal stages of penaeids. He emphasized the similarity of segmentation and setation of natatory antennular exopods of the two groups. Williamson (1957, 1969) pointed out that "the prezoeal stages are certainly too far developed to be regarded as nauplius" and suggested prezoea larvae as "early zoeal stages in which the antennule and antenna retain some nauplius features".

Up to now only few species of caridean prezoeas are known (Gurney, 1942; present study). Since few prezoeal descriptions are available, it is difficult to confirm that the 6 pairs of telson process are a rule in caridean prezoeas. In protozoeas of penaeids and sergestids 6 pairs of telson processes are not uncommon (Bate, 1888; Gurney, 1924 b, 1942; Pearson, 1939; Omori, 1969). Furthermore, some sergestids have even 5 pairs of telson processes. So the naupliar affinity of prezoeas (Gurney, 1926, 1942) is questioned.

Gurney(1942) defined the primary phases of decapod larvae based on the swimming method. According to his definition, nauplius and protozoea are characterised by antennular and antennal propulsion. The nauplius also uses the biramous mandible as a natatory appendage, and prezoeas also use the telson for swimming (Calman, 1909; Gurney, 1942; Williamson, 1957, 1969, 1982). Nauplius larvae have a median nauplius eyes and 3 pairs of natatory appendages: uniramous antennule, biramous antenna and biramous mandible. These nauliar features demonstrate the difficulty in attempting to relate the prezoea to the nauplius. In all prezoeas the mandible is not functional and is covered by simple sheath.

The number of paired processs on the telson in the first zoea (including protozoea) is fairly constant as 7 pairs in most of Decapoda, except minor groups including Sergestoidea (5-7 pairs), Amphionidacea (6 pairs) and Penaeoidea (6 or 7 pairs) (Bate, 1888; Gurney, 1942; Williamson, 1982). The prezoeal telson of Decapoda is basically bilobed with 7 pairs of processes, except some carideans which have 6 pairs.

Gurney (1942: 50) argued that "if the stage represented by the embryonic cuticle actually corresponds to the Protozoea, we should expect to find setae on the maxillae and maxillipeds". On this comment, we have to take into account that, although different prezoeas show different degrees of reductions of the prezoeal process, in all cases, not only are the maxillule and maxillipeds reduced and without setae, but the same applies to the mandibles. It must be remembered that the prezoea is a transient stage which swims but does not feed. The reduced mouth-parts may, therefore, be interpreted as a response to loss of function rather than as an indication of the ancestry of the prezoeal phase. The well developed prezoeal telson is in marked contrast to the poorly defined naupliar telson.

Based on the basic pattern of telson processes and the natatory function of the antennule, antenna and telson, the prezoeal stage of Decapoda is closely comparable to the protozoeal stages as suggested by Conn (1883, 1884) and Williamson (1957, 1969).

Fig. 1. *Pandalus montagui* Montagui, Prezoea

A, antennule; B, antenna; C, telson. Scale = 0.10 mm

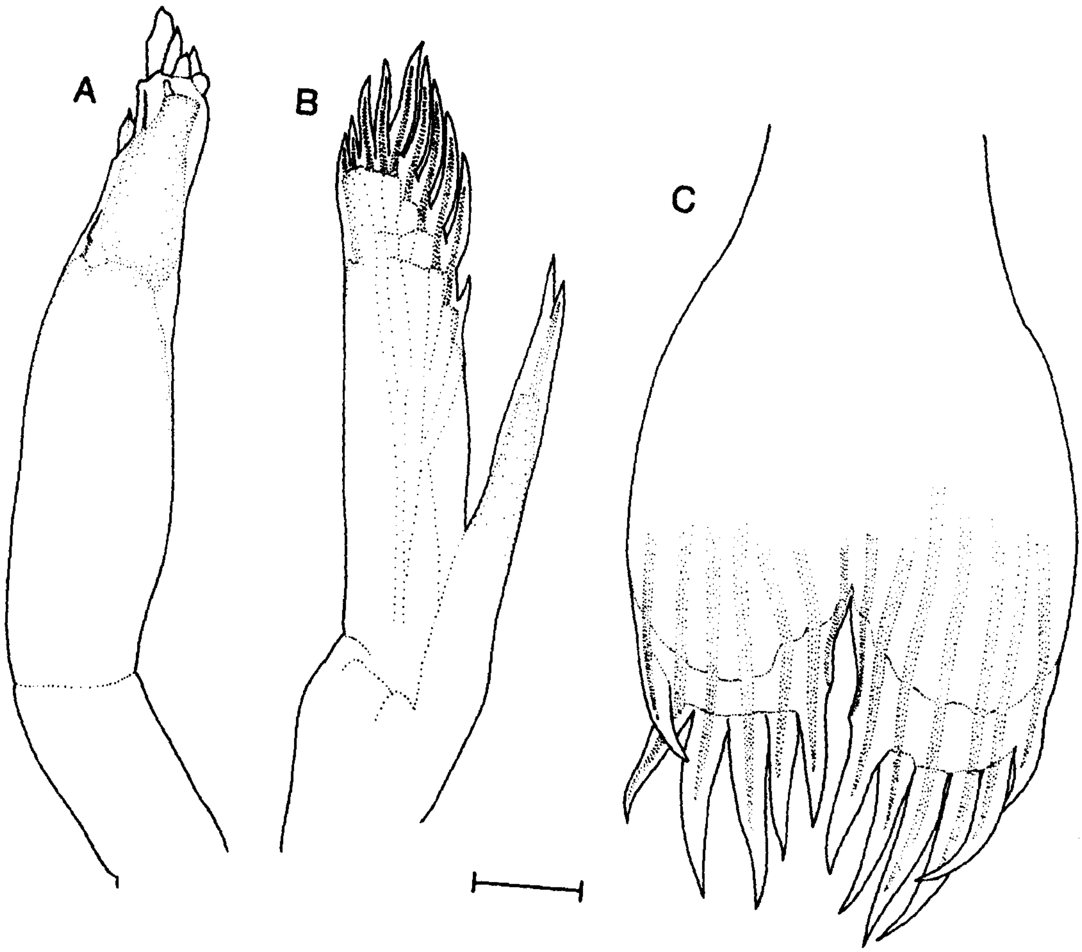

A
B
C

Fig. 2. *Pagurus prideauxi* Leach, Prezoea

A. antennule; B. antenna; C, telson. Scale = 0.10 mm

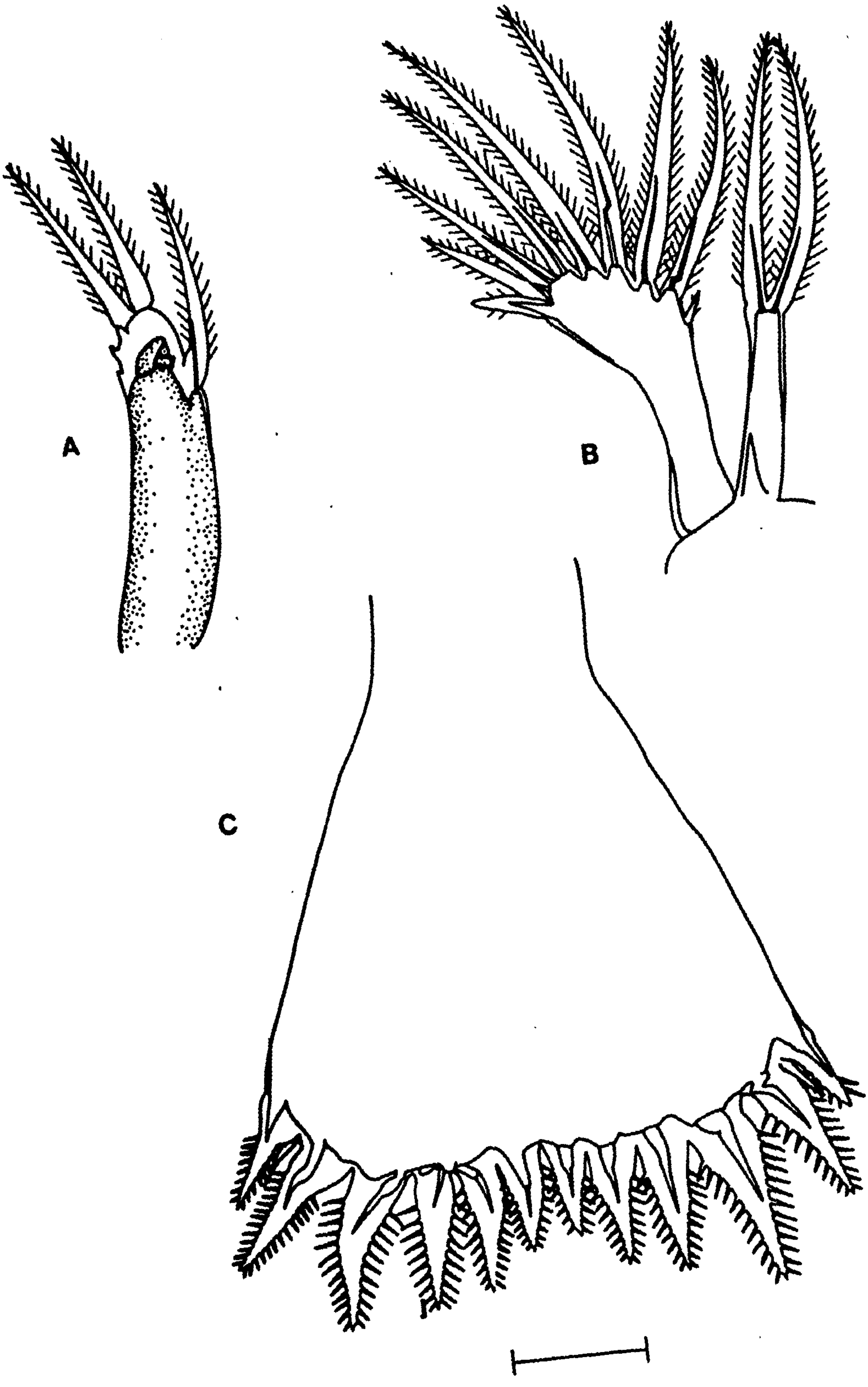

A
B
C

Fig. 3. *Pagurus bernhardus* (Linnaeus), Prezoea

A, antennule; B, antenna; C, telson. Scale = 0.10 mm

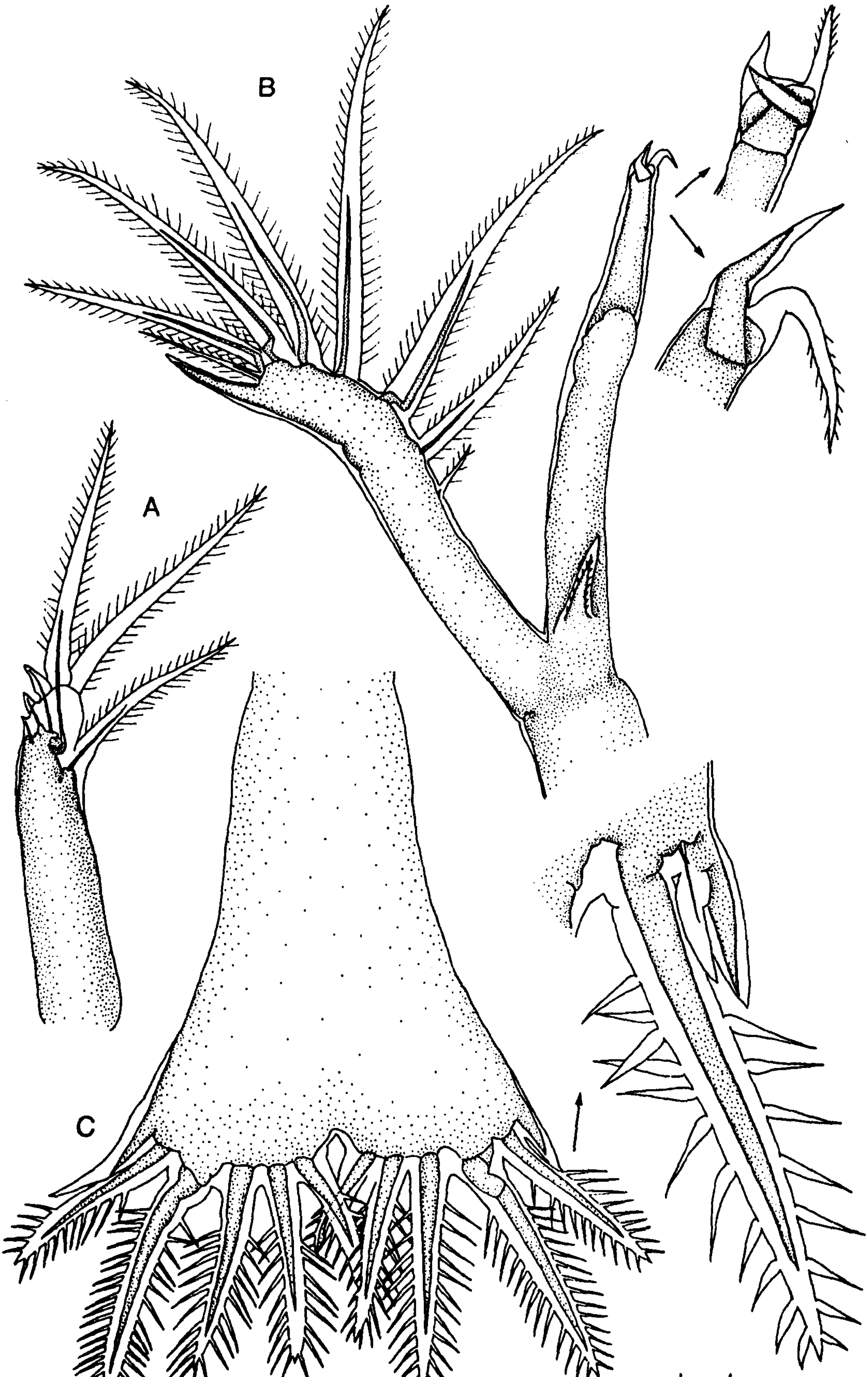

B
A
C

Fig. 4. *Hyas araneus* (Linnaeus), Prezoea

A, lateral view; B, antennule; C, antenna; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, telson. Scales = 0.50 mm


A
B
C
D
E
F
G
H
B-H
A

Fig. 5. *Hyas coarctatus* Leach, Prezoea

A, lateral view; B, antennule; C, antenna; CL: carapace length. Scales = 0.10 mm

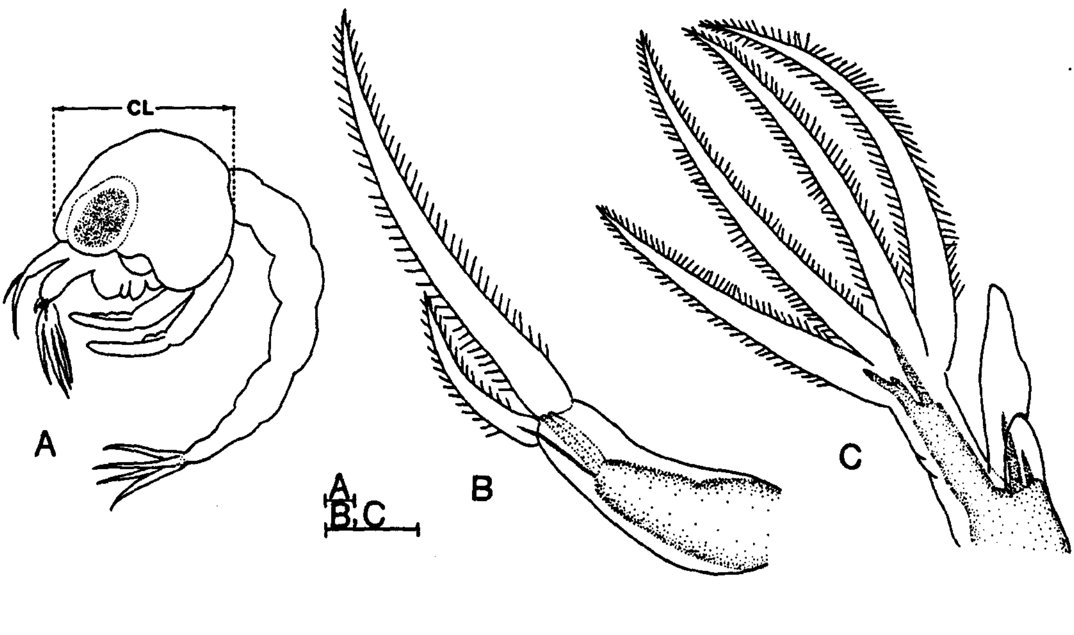

CL
A
A
B,C
B
C

Fig. 6. *Inachus dorsettensis* (Pennant), Prezoea

A, lateral view; B, antennule; C, antenna; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, telson. Scales = 0.10 mm

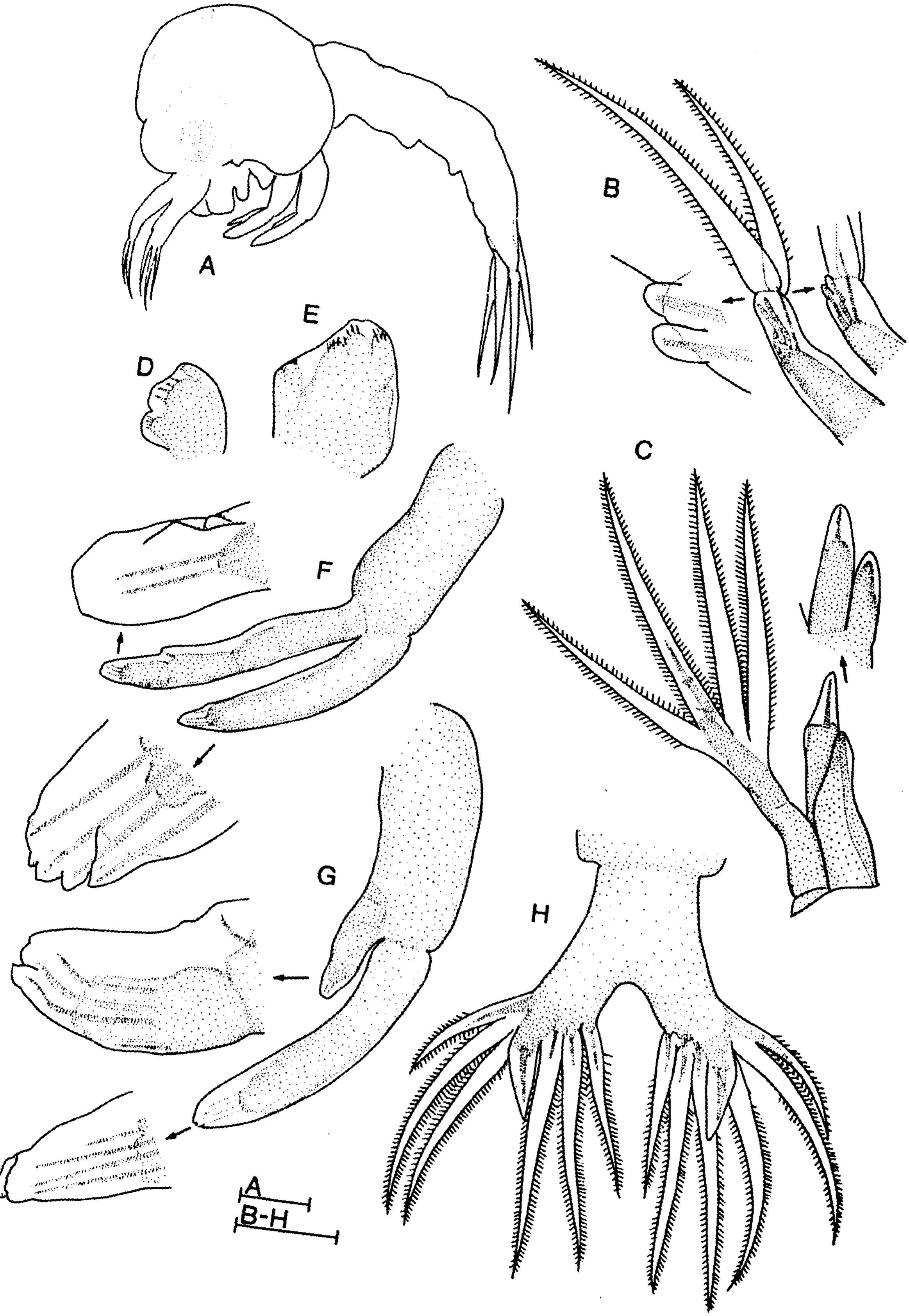
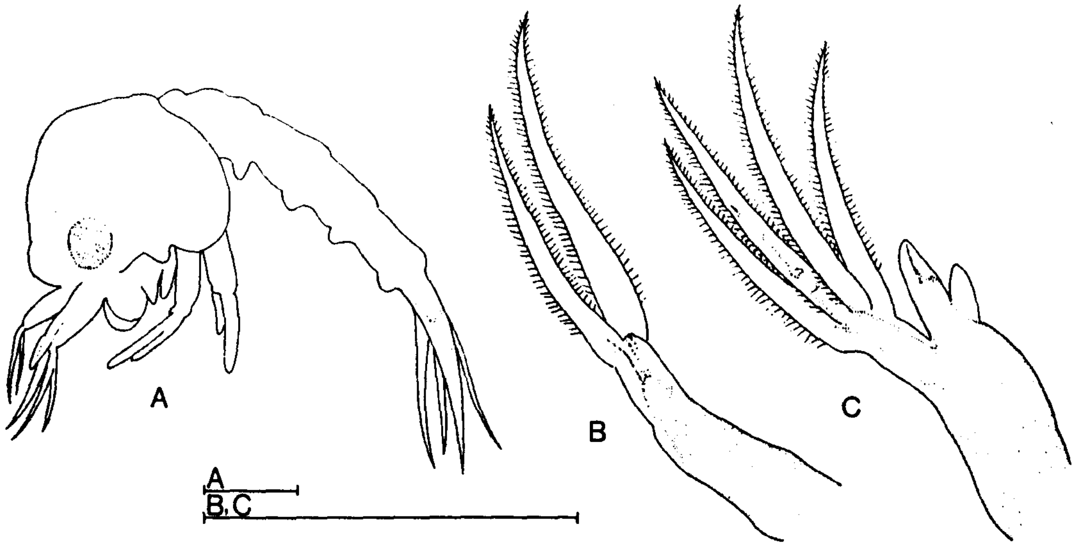

A
B
C
D
E
F
G
H
A
B-H

Fig. 7. *Inachus leptochirus* Leach, Prezoea

A, lateral view; B, antennule; C, antenna. Scales = 0.50 mm

Fig. 8. *Macropoda tenuirostris* (Leach), Prezoea

A, antennule; B, antenna; C, telson. Scale = 0.50 mm


A
B
C
A
B, C

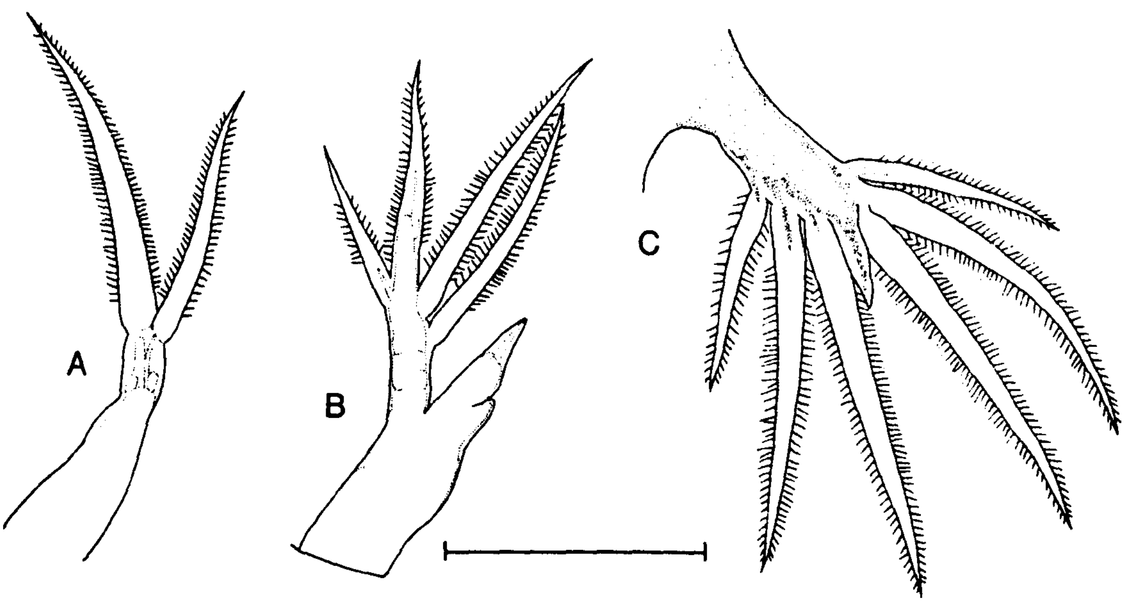
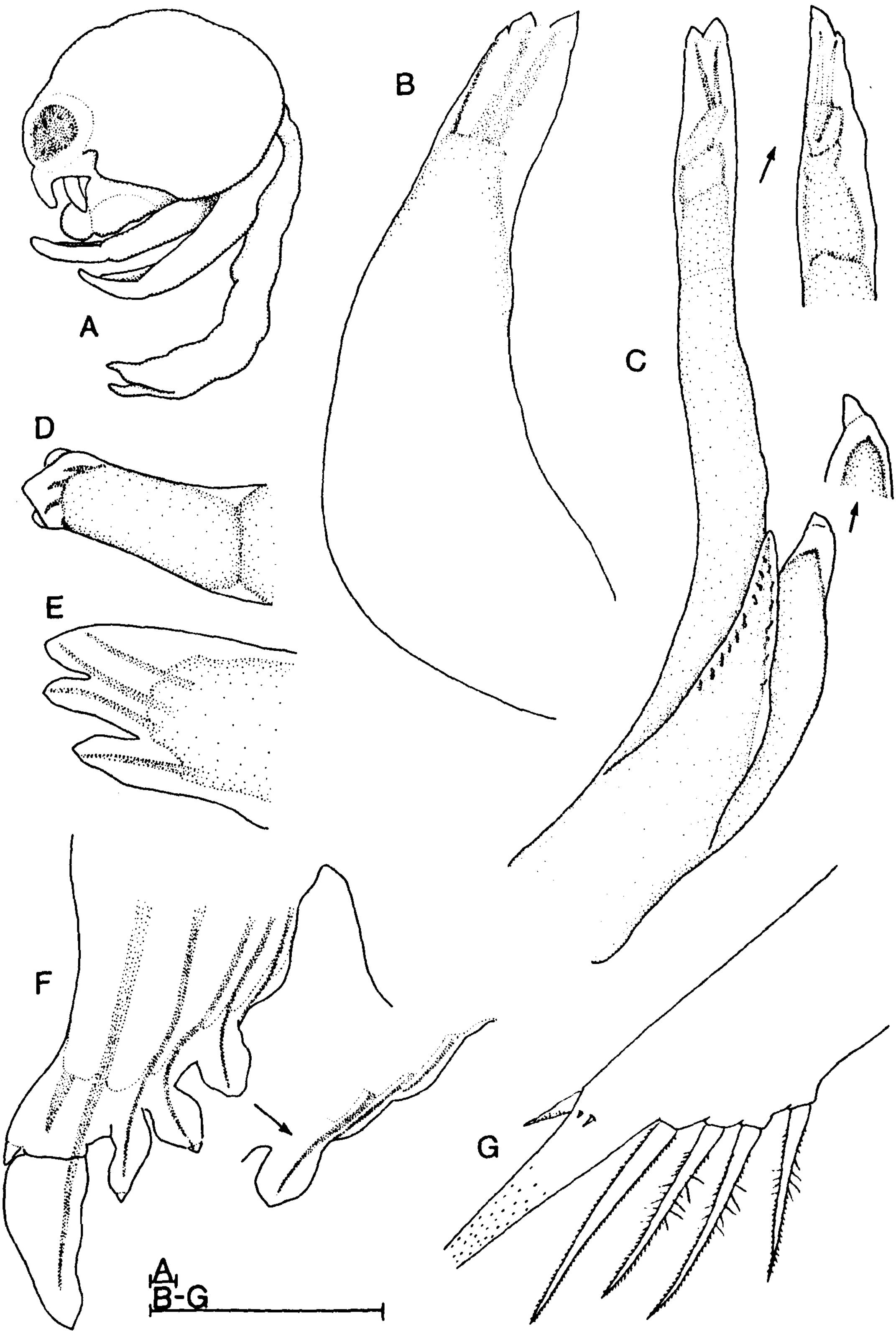

A
B
C

Fig. 9. *Orithyia sinicae* (Linnaeus), Prezoea

A, lateral view; B, antennule; C, antenna; D, endopod tip of first maxilliped; E, exopod tip of first maxilliped; F, telson; G, telson of first zoea. Scales = 0.10 mm



A
B
C
D
E
F
G
A
B-G

Fig. 10. *Ebalia tuberosa* (Pennant), Prezoea

A, lateral view; B, antennule; C, antenna; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, telson. Scales = 0.10 mm

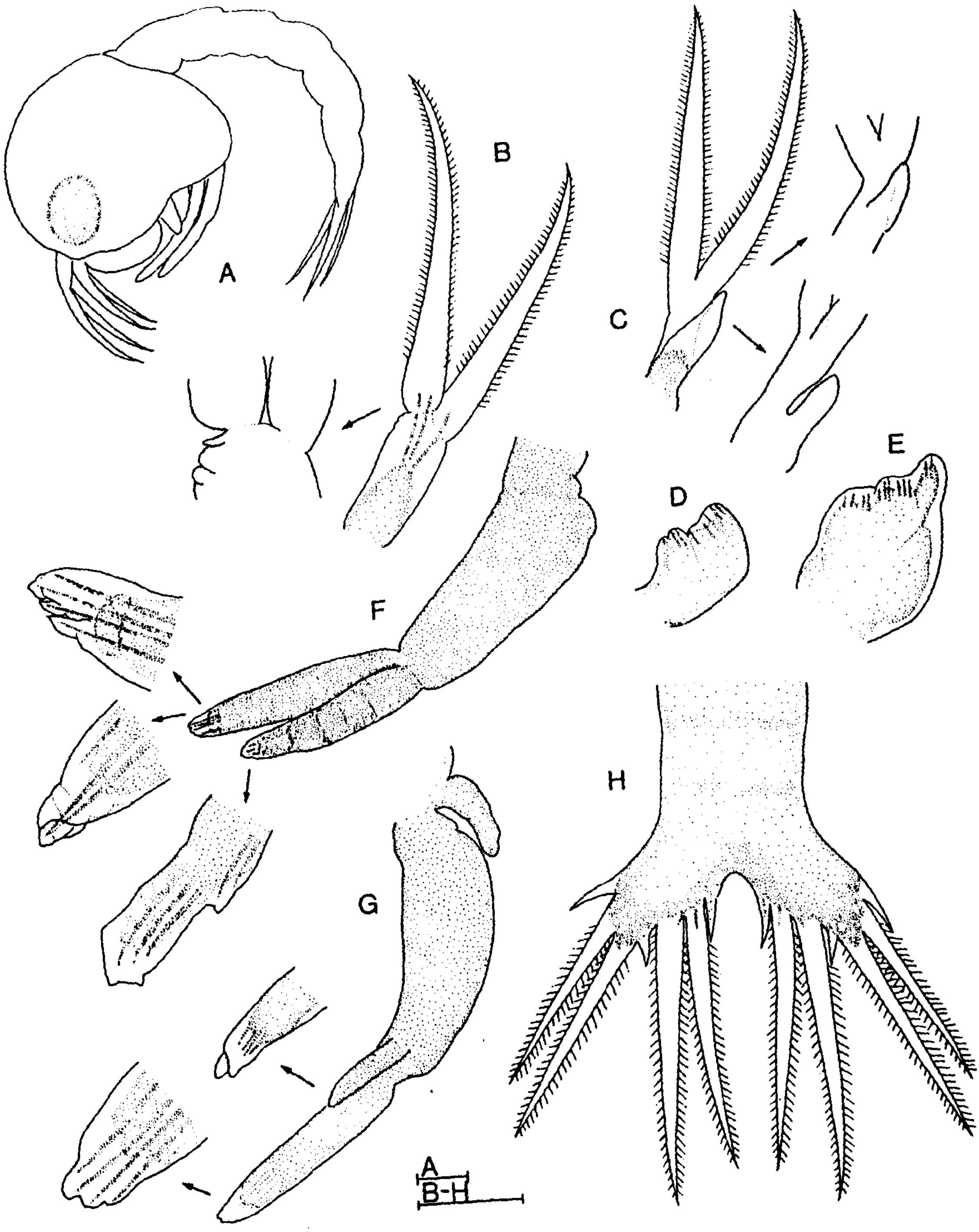

A
B
C
D
E
F
G
H
A
B-H

Fig. 11. *Liocarcinus holsatus* (Fabricius), Prezoea

A, lateral view; B, antennule; C, antenna; D, tip of endopod of first maxilliped; E, tip of exopod of first maxilliped; F, tip of endopod of second maxilliped; G, tip of exopod of second maxilliped; H, telson. Scales = 0.10 mm

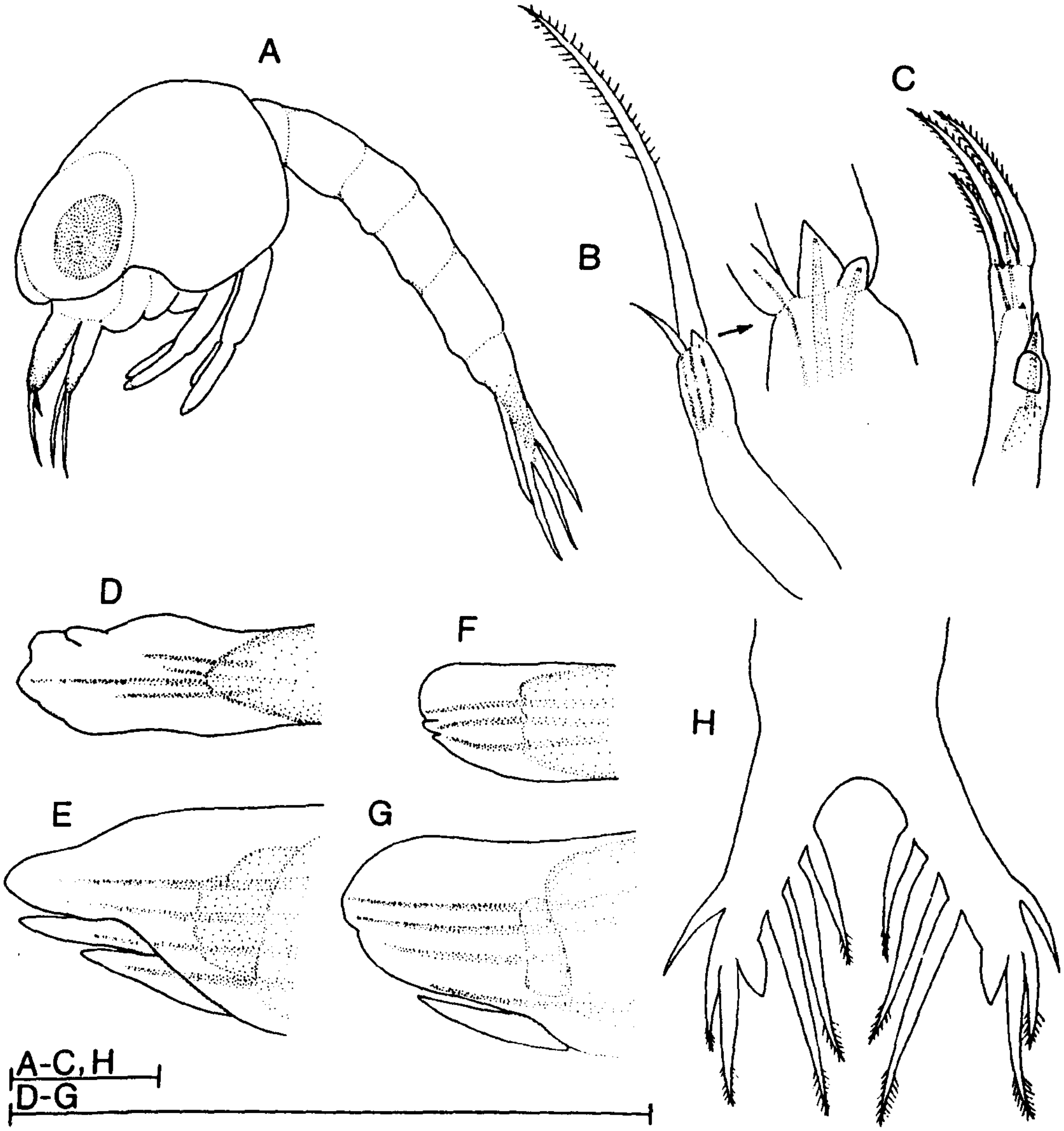
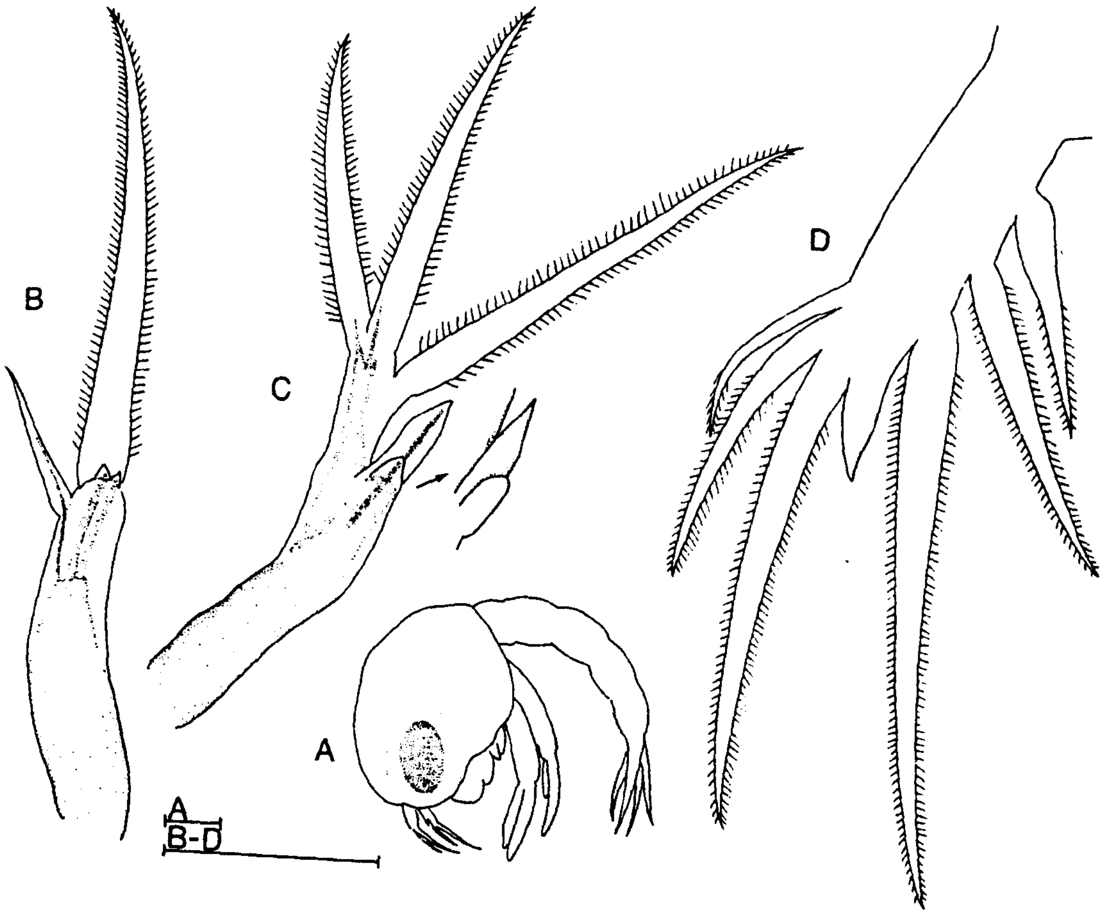

A
B
C
D
F
E
G
H
A-C, H
D-G

Fig. 12. *Liocarcinus corrugatus* (Pennant), Prezoea

A, lateral view; B, antennule; C, antenna; D, telson. Scales = 0.10 mm

Fig. 13. *Liocarcinus marmoreus* (Leach), Prezoea

A, A', antennule; B, antenna; C, telson. Scale = 0.10 mm


B
C
D
A
A
B-D

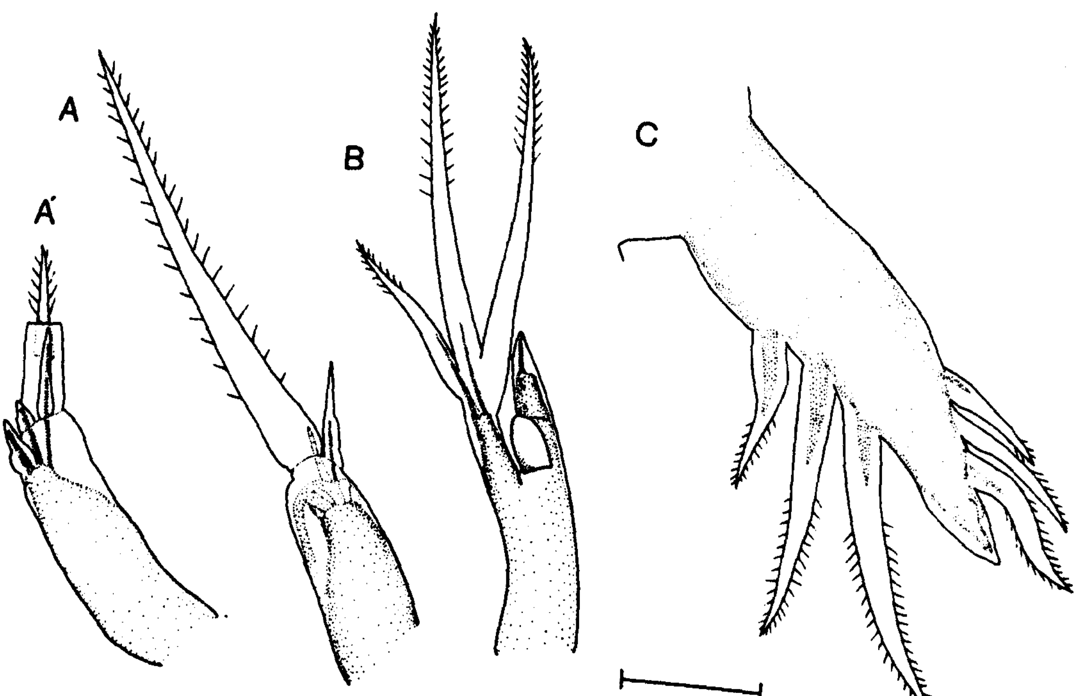

A
A´
B
C

Fig. 14. *Carcinus maenas* (Linnaeus), Prezoea

A, lateral view; B-C, antennule; D, antenna; E, telson. Scales = 0.10 mm

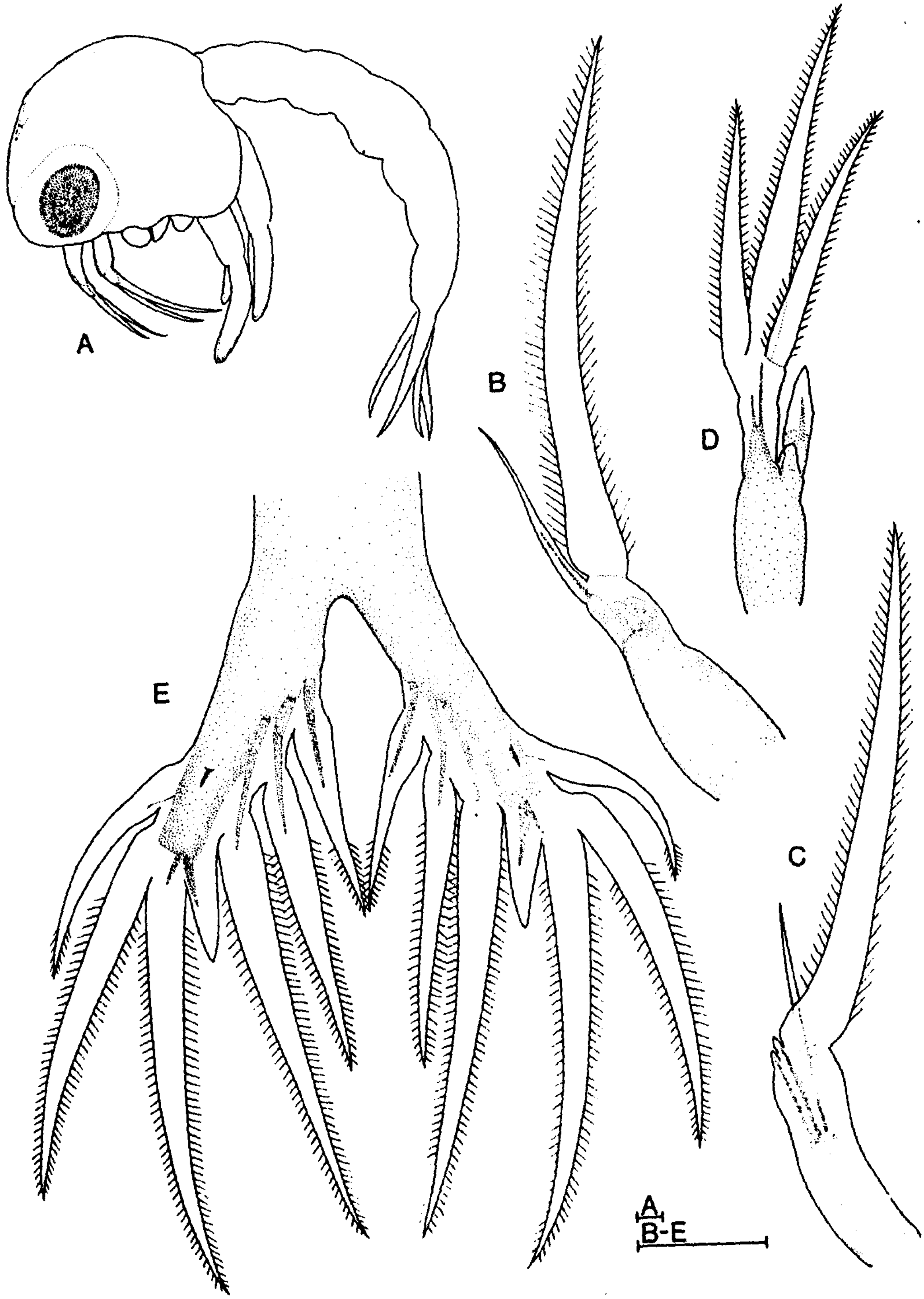
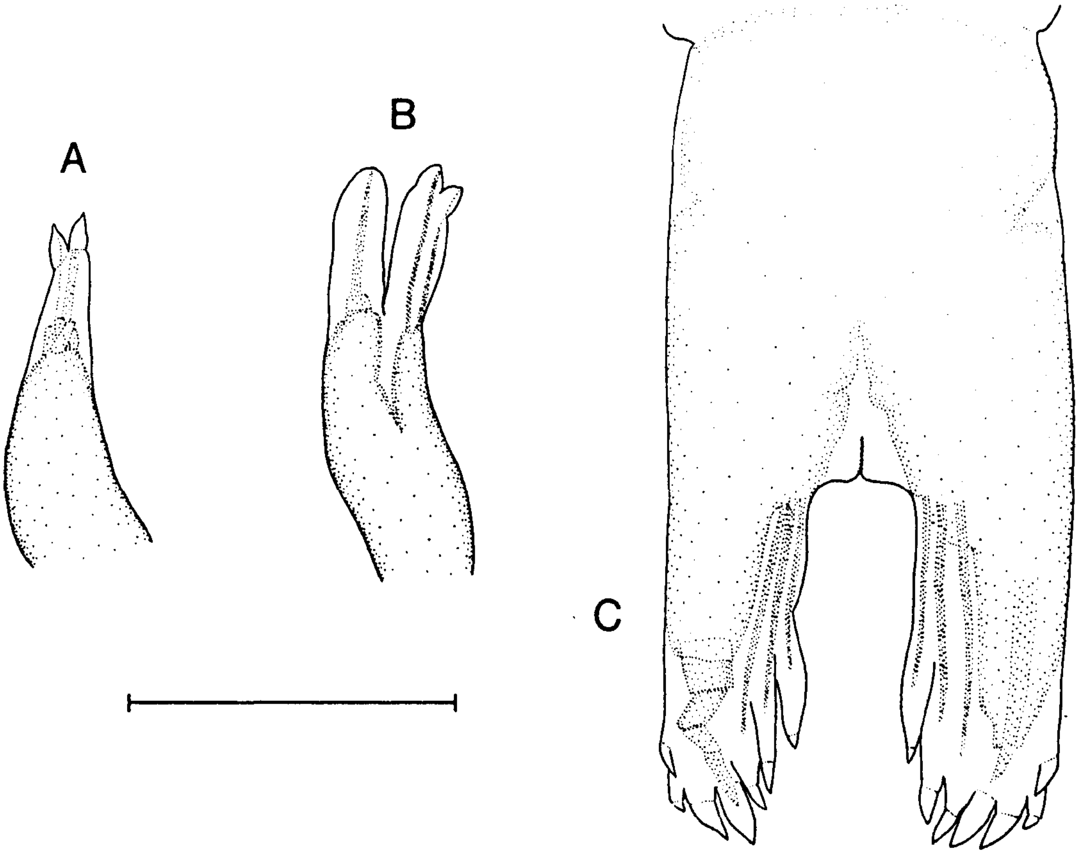

A
B
C
D
E
A
B-E

Fig. 15. ***Portunus gladiator*** Fabricius, Prezoea

A, antennule; B, antenna; C, telson. Scale = 0.10 mm

Fig. 16. ***Charybdis bimaculata*** (Miers), Prezoea

A, A', antennule of different specimens; B, antenna; C, telson. Scale = 0.10 mm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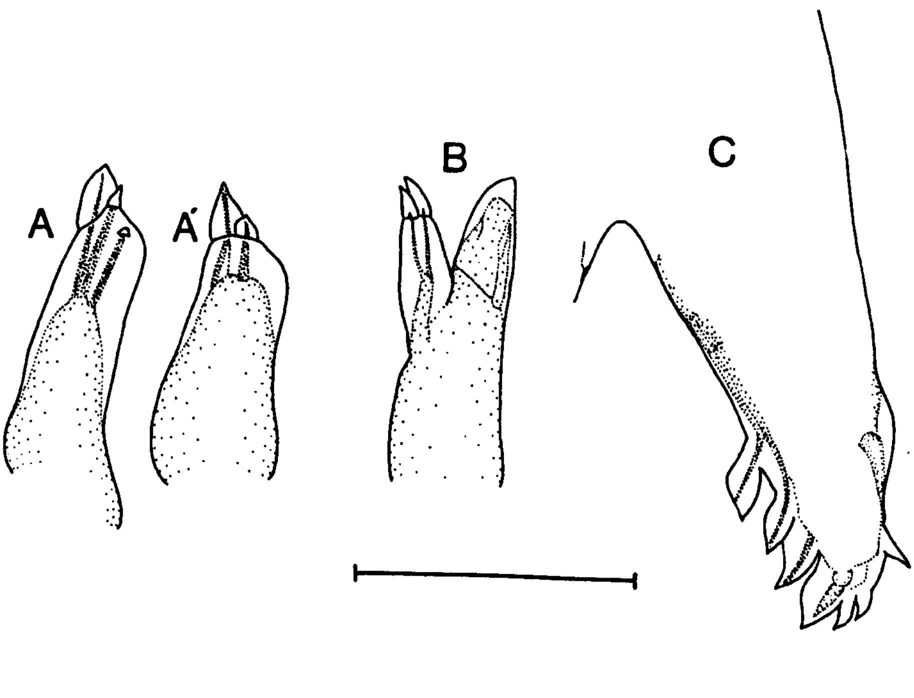

A
A'
B
C

Fig. 17. ***Monodaeus couchi*** (Couch), Prezoea

A, antennule; B, antenna; C, telson. Scales = 0.10 mm

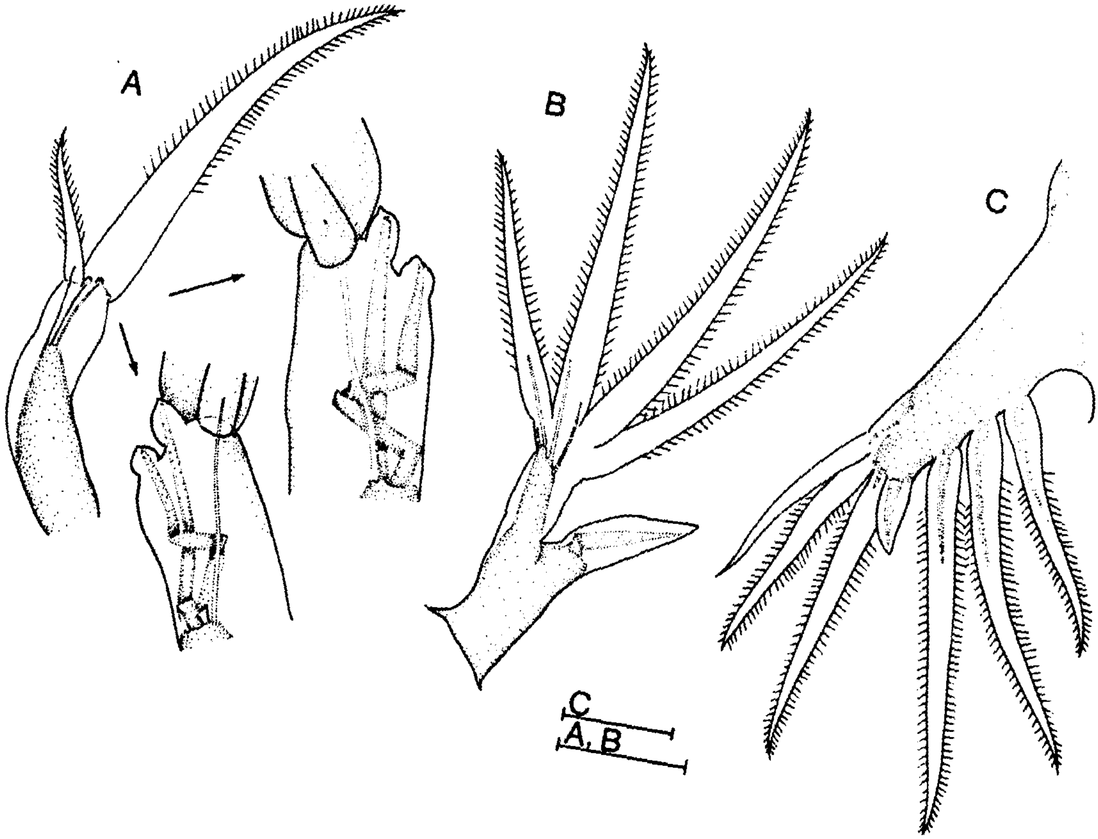

A
B
C
C
A, B

Fig. 18. *Cancer pagurus* Linnaeus, Prezoea

A, lateral view; B, antennule; C, antenna; D, mandible; E, maxillule; F, maxilla; G, tip of endopod of first maxilliped; H, tip of exopod of first maxilliped; I, tip of endopod of second maxilliped; J, tip of exopod of second maxilliped; K, telson. Scales = 0.10 mm

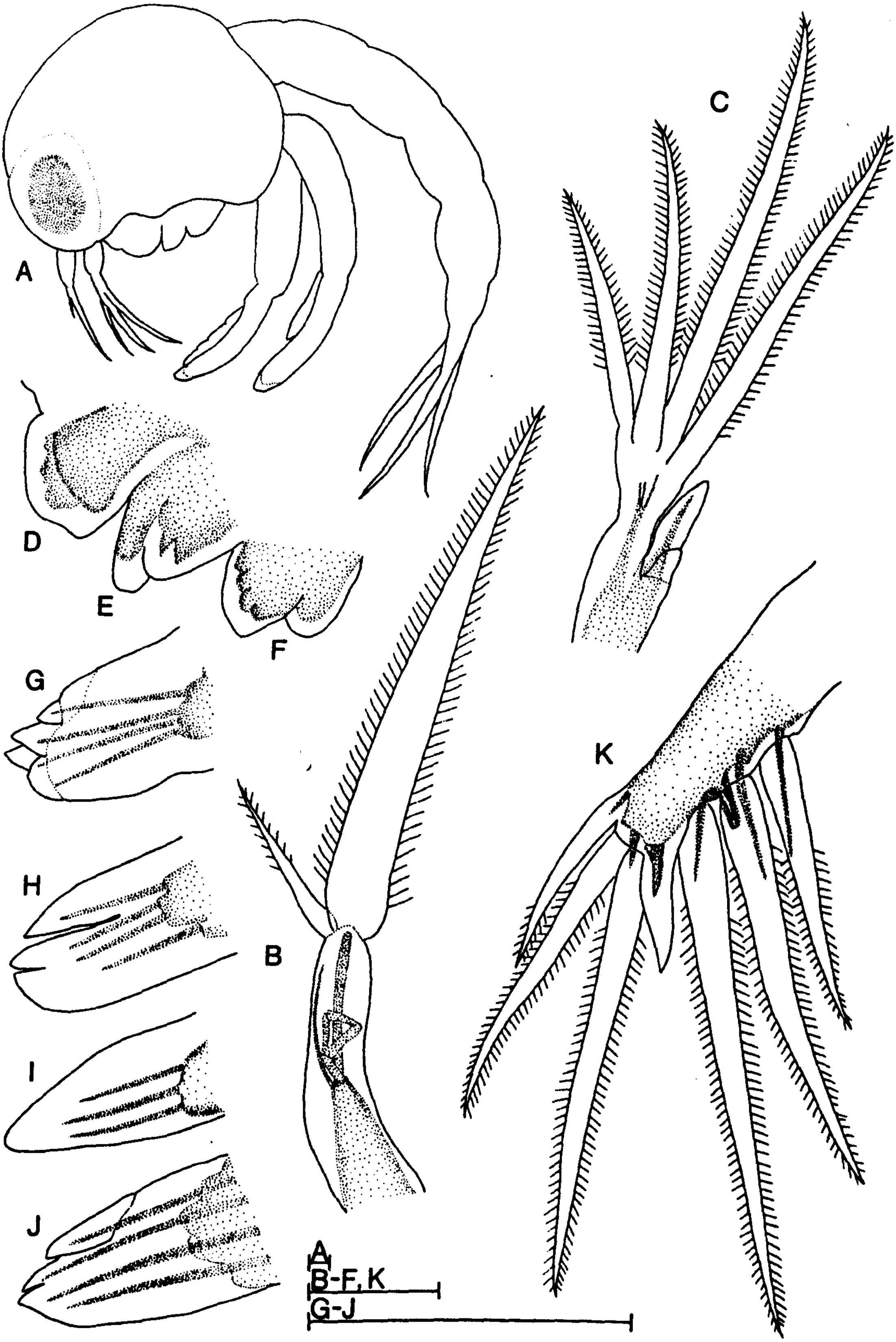
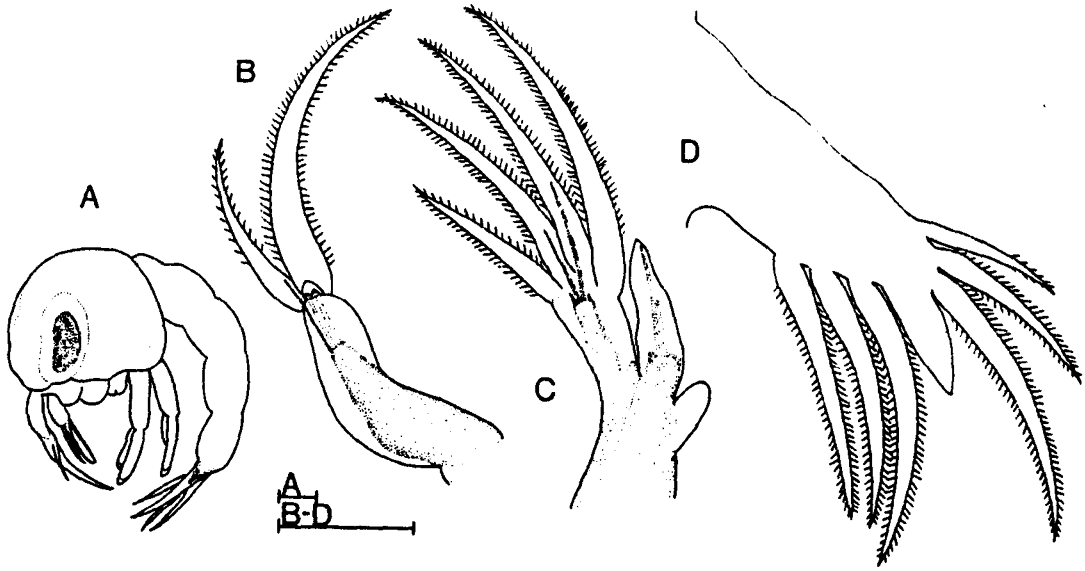

A
B
C
D
E
F
G
H
I
J
K
A
B-F, K
G-J

Fig. 19. *Carcinoplax longimana* (De Haan), Prezoea

A, lateral view; B, antennule; C, antenna, D, telson. Scales = 0.10 mm

Fig. 20. *Pinnotheres pinnotheres* (Linnaeus), Prezoea

A, antennule; B, antenna, C, telson, just after hatching; D, telson, after free swimming. Scale = 0.10 mm


A
B
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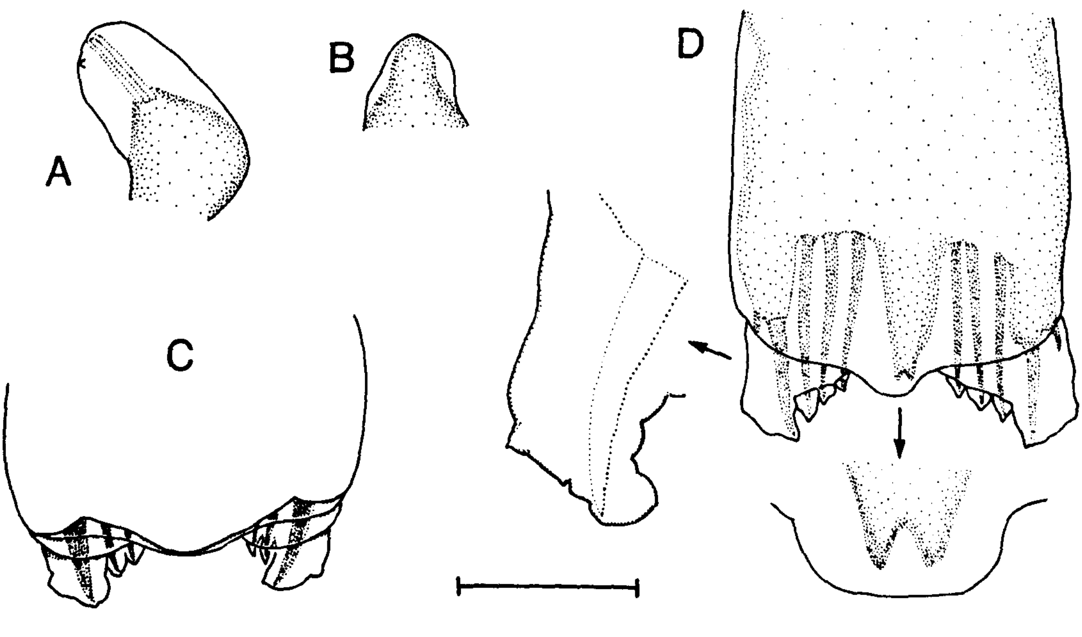
D
A
B-D


A
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D

CHAPTER 3

DEVELOPMENT OF EPIPODS AND GILLS IN SOME PAGURIDS AND BRACHYURANS

INTRODUCTION

The branchial formulae of Decapoda reveal that there are noticeable variations in the number of the gills. In general, penaeid shrimps have the greatest number at 20-24, brachyurans have a maximum of 9 gills, and some pinnotherids have the smallest number, namely 3. Whithin the group reduction in the number of gills with evolution is the general rule (Huxley, 1878; Bate, 1888; Calman, 1909; Gurney, 1942; Balss, 1957; Burkenroad, 1981).

The number of gills is often supposed to be characteristic of a family or family group, and for the taxonomy of groups of Decapoda Burkenroad (1981) used gill formulae as one of the major characters. However, even within a family the number of gills may vary from species to species. Hartnoll (1964 b) reported variations of gill number from 7 to 9 in majid crabs.

Since the monographic works of Calman (1909), Gurney (1942) and Balss (1957), there have been few comprehensive reports on the number of gills of decapod crustaceans. All these works were based on adult material and some fragmented observations on larvae of which moulting stages were incomplete. Even in the detailed developmental studies of larvae, descriptions of larval gills are few. This is probably mainly due to the fact that the proper examination of larval gills is comparatively difficult. Drawings of epipods or some gills on maxillipeds and legs appear in some descriptions of megalopas, but usually no descriptions are given.

Gill formulae of brachyuran larvae have been recorded for a few species (Cano, 1893 a; Gurney, 1942; Williamson 1965; Rice, 1967). Connolly (1923) gave a detailed account of the gill development of *Cancer amoenus* based on plankton material. However, Yang and McLaughlin (1979) were the first to describe the complete gill development of a brachyuran using reared material of the majid *Libinia erinacea*. The description of gills in larval development of the dromiid *Petalomera japonica* is included in Chapter 4 (also Hong and Williamson, 1986).

The present study aims to describe gill development of larvae and some postlarvae of 2 pagurid and 15 brachyuran species, respresenting 6 families, based on reared material. Particular attention is paid to the positions of early attachment and the form of developing gills, and these features are considered in relation to taxonomy and phylogeny.

MATERIALS AND METHODS

Seventeen species representing six families were examined. Most of the larval material was obtained from laboratory rearing at the Marine Biological Station, Port Erin, Isle of Man (IOM), and some larval material was donated by other workers. Sources of material and rearing temperatures are shown in Table 1.

For larval rearing at Port Erin, berried females were collected by dredging or beam trawling between October, 1984 and July, 1986. Larvae were reared by individual culture or mass culture at 15°C or 20°C, and in salinity about 34.4 (33.86-34.60) ppt. Rearing methods were described in Hong and Ingle (in press). Larvae were preserved in 5 % buffered formalin, dissected, and examined in a drop of ethylene glycol solution stained by methylene blue, without cover glass on slide, under microscopes.

A schematic diagram of gill positions is provided (Fig. 20-A). All lateral views are arranged anterior to left, and the developing buds of epipods and gills are stippled. In all legends to figures the gills are denoted by the names of their corresponding appendages, e.g. "third maxilliped" refers to the gills at the base of the third maxilliped.

Table 1. List of species and their sources.

	Locality(sources)	Reared temp. (°C)
Paguridae		
Pagurus priduauxi	IOM (reared)	10.0
Pagurus bernhardus	IOM (reared)	15.0
Majidae		
Inachus dorsettensis	IOM (reared)	15.0
Hyas araneus	IOM (reared)	15.0
Eurynome aspera	IOM (reared)	15.0, 20.0
Pisa armata	IOM (reared)	20.0
Atelecylcidae		
Atelecyclus rotundatus	IOM (reared)	15.0, 20.0
Portunidae		
Carcinus maenas	IOM (reared)	15.0. 20.0
Liocarcinus corrugatus	IOM (reared)	20.0
Liocarcinus holsatus	Helgoland, West Germany (plankton)	
Xanthidae		
Pilumnus hirtellus	IOM (reared)	20.0
Monodaeus couchi	IOM (reared)	20.0
Pinnotheridae		
Pinnotheres pinnotheres	IOM (reared)	15.0
Pinnotheres pisum	IOM (reared)	15.0
Pinnaxodes mutuensis	Hokkaido, Japan (reared)	15.0
Pinnixa rathbuni	Mie, Japan (reared)	15.0
Pinnixa (?)chaetopterana	Rio Grande Sur, Brazil (plankton)	

DESCRIPTIONS

In the following descriptions, the name of each thoracic appendage is used to include the pleural region of the corresponding segment as well as the appendage itself.

Pagurus prideauxi Leach

(Fig. 21)

First and Second Zoea (Fig. 21 A-B) - Devoid of gill buds.

Third Zoea (Fig. 21 C) - Basial part of second to fourth legs extended as gill buds.

Fourth Zoea (Fig. 21 D) - First to third maxillipeds: no gill buds. First leg: a minute gill bud (future posterior arthrobranch). Second and third legs: each with a pair of gill buds (future arthrobranchs). Fourth leg: a pair of arthrobranch buds and a smaller pleurobranch bud between them.

Megalopa (Fig. 21 E, F) - First and second maxillipeds: no gill buds. Third maxilliped: a small biramous gill bud (future arthrobranchs) on coxa. First leg: a pair of small gill buds (future arthrobranchs). Second and third legs: each with a pair of lamellate arthrobranchs, the anterior arthrobranch of the second leg much smaller than the gills of the following legs. Fourth leg: a pair of arthrobranchs and a pleurobranch, all lamellate.

Pagurus bernhardus (Linnaeus)

(Fig. 22)

First and Second Zoea (Fig. 22 A-B) - Devoid of gill buds.

Third Zoea (Fig. 22 C) - Basal parts of second to fourth legs extended as gill buds.

Fourth Zoea (Fig. 22 D, E) - First to third maxillipeds (Fig. 22 D): no gill buds. First leg (Fig. 22 E): a pair of gill buds (future arthrobranchs). Second and third legs (Fig. 22 E): each with a pair of gill buds (future arthrobranchs). Fourth leg (Fig. 22 E): a pair of arthrobranch buds and a smaller pleurobranch bud between them.

Megalopa (Fig. 22 F) - First and second maxillipeds: no gill buds. Third maxilliped: a pair of small gill buds (future arthrobranchs) on basio-coxal part. First leg: anterior and posterior arthrobranchs, lamellate and smaller than the gills of the following legs. Second and third legs: each with a pair of lamellate arthrobranchs. Fourth leg: a pair of arthrobranchs and a pleurobranch, all lamellate.

Inachus dorsettensis (Pennant)

(Fig. 23)

First Zoea (Fig. 23 A-D) - First maxilliped (Fig. 23 A, D): an epipod bud on coxa. Second maxilliped (Fig. 23 B, D): no epipod bud. Third maxilliped (Fig. 23 C, D): two gill buds (future epipod and arthrobranchs) on basio-coxal part. First leg (Fig. 23 D): two gill buds (future anterior and posterior arthrobranchs) on basio-coxal part. Second leg (Fig. 23 D): one gill bud (future pleurobranch) on coxal part. Third leg (Fig. 23 D): devoid of gill bud.

Second Zoea (Fig. 23 E-H) - First maxilliped (Fig. 23 E): epipod bud elongate. Second maxilliped (Fig. 23 F): no epipod bud. Third maxilliped (Fig. 23 G): epipod and arthrobranch buds elongate. First leg (Fig. 23 H): anterior arthrobranch bud much smaller than posterior. Second leg (Fig. 23 H): pleurobranch bud elongate, equal in size to posterior arthrobranch bud of first leg. Third leg (Fig. 23 H): a minute pleurobranch bud appeared.

Megalopa (Fig. 23 I-L) - First maxilliped (Fig. 23 I): epipod elongate. Second maxilliped (Fig. 23 J): epipod bud present.

Third maxilliped (Fig. 23 K, L): epipod and arthrobranch buds elongate, epipod with a terminal seta. First leg (Fig. 23 L): anterior arthrobranch bud elongate, posterior arthrobranch lamellate. Second leg (Fig. 23 L): pleurobranch lamellated. Third leg (Fig. 23 L): pleurobranch bud still minute, more clearly pleural in position.

First Crab (Fig. 23 M-P) - First maxilliped (Fig. 23 M, P): proximal part thick, with 6 setae on distal half. Second maxilliped (Fig. 23 N): basal part with a blunt projection. Third maxilliped (Fig. 23 O): epipod under the gills of following limbs, with 4+3 setae, arthrobranch bud with partial lamellation. First leg (Fig. 23 P): arthrobranchs lamellate, the anterior one smaller than the posterior one. Second leg (Fig. 23 P): pleurobranch lamellate. Third leg (Fig. 23 P): pleurobranch slender with some indication of lamellation.

Hyas araneus (Linnaeus)

(Fig. 24)

First Zoea (Fig. 24 A-D) - First maxilliped (Fig. 24 A, D): an epipod bud on coxa. Second maxilliped (Fig. 24 B, D): a gill bud (future epipod and podobranch) on coxa. Third maxilliped (Fig. 24 C, D): three gill buds (future epipod and anterior and posterior arthrobranchs) on basio-coxal part. First leg (Fig. 24 D): two gill buds (future anterior and posterior arthrobranchs) on coxal part, larger upright and smaller directed downward. Second and third legs (Fig. 24 D): each with a gill bud (future pleurobranch) on coxal part.

Second Zoea (Fig. 24 E-H) - First maxilliped (Fig. 24 E, H): epipod bud elongate. Second maxilliped (Fig. 24 F, H): epipod bud elongate. Third maxilliped (Fig. 24 G, H): epipod bud curved upwards, upper bud (future posterior arthrobranch) upright and markedly larger than lower one (future anterior arthrobranch). First leg (Fig. 24 H): anterior and posterior arthrobranch buds elongate. Second and third legs (Fig. 24 H): each with elongate pleurobranch bud.

Megalopa (Fig. 24 I-L) - First maxilliped (Fig. 24 I): epipod expanded proximally, with 1+6 setae. Second maxilliped (Fig. 24 J): epipod with podobranch bud at base, epipod sometimes with a terminal seta. Third maxilliped (Fig. 24 K): epipod with podobranch bud at base and 1+16 setae. Anterior arthrobranch still a small bud, posterior arthrobranch very large and partially lamellate. First leg (Fig. 24 L): anterior and posterior pleurobranchs on basal part of thoracic pleuron, elongate and lamellate. Second and third legs (Fig. 24 L): each pleurobranch on thoracic pleuron, elongate and lamellate.

Eurynome aspera (Pennant)

(Fig. 25)

First Zoea (Fig. 25 A, B) - First maxilliped (Fig. 25 A): an epipod bud on coxa. Second maxilliped (Fig. 25 A): no epipod bud. Third maxilliped (Fig. 25 A, B): three gill buds (future epipod and anterior and posterior arthrobranchs) on basio-coxal part. First leg (Fig. 25 A): two gill buds (future anterior and posterior arthrobranchs) on coxal part. Second and third legs (Fig. 25 A): each with one gill bud (future pleurobranch) on coxal part, bud on third leg much smaller than that on second.

Second Zoea (Fig. 25 C, D) - First maxilliped (Fig. 25 C): epipod bud elongate posteriorly. Second maxilliped (Fig. 25 C): no epipod bud. Third maxilliped (Fig. 25 C, D): epipod bud curved upwards, upper bud (future posterior arthrobranch) much larger than lower one (future anterior arthrobranch). First leg (Fig. 25 C): anterior and posterior arthrobranch buds enlarged. Second and third legs (Fig. 25 C): pleurobranch bud on second leg enlarged, bud on third leg still small.

Megalopa (Fig. 25 E-I) - First maxilliped (Fig. 25 E, I): epipod, expanded proximally, with 1+4 setae. Second maxilliped (Fig. 25 F, I): an epipod bud on coxal part. Third maxilliped (Fig. 25 G-I): podobranch bud now at base of epipod, epipod with 6-7 setae. Anterior arthrobranch bud still small, posterior arthrobranch very large and lamellate. First leg (Fig. 25 I):

anterior and posterior arthrobranchs on basal part of thoracic pleuron, elongate and lamellate. Second leg (Fig. 25 I): pleurobranch, on thoracic pleuron, elongate and lamellate. Third leg (Fig. 25 I): pleurobranch bud still small.

Pisa armata (Latreille)

(Fig. 26)

First Zoea (Fig. 26 A) - First maxilliped: an epipod bud on coxa. Second maxilliped: no gill bud. Third maxilliped: three gill buds (future epipod and anterior and posterior arthrobranchs). First leg: two gill buds (future two arthrobranchs). Second and third legs: each with a gill bud (future pleurobranch), bud on third leg smaller than that on second.

Second Zoea (Fig. 26 B) - Number of epipod and gill buds unchanged, but most of them increased in size. Third leg: pleurobranch bud much smaller than that of second leg.

Megalopa (Fig. 26 C-F) - First maxilliped (Fig. 26 C): epipod elongate, with 4 setae. Second maxilliped (Fig. 26 D): a minute bud (future epipod and podobranch) on coxal part. Third maxilliped (Fig. 26 E): basal part of epipod now extended as podobranch bud, epipod elongate with 5 setae, anterior arthrobranch bud still small, posterior arthrobranch now partially lamellate. First leg (Fig. 26 F): anterior and posterior arthrobranchs lamellate. Second and third legs (Fig. 26 F): each with lamellate pleurobranch arising at about same level as arthrobranchs on first leg.

First Crab (Fig. 26 G-J) - First maxilliped (Fig. 26 G): epipod flattened and expanded proximally, with 14-15 setae. Second maxilliped (Fig. 26 H): epipod bud elongate. Third maxilliped (Fig. 26 I, J): podobranch bud on inner basal part of epipod still small and smooth, epipod with 8 setae, anterior arthrobranch bud still small and smooth, posterior arthrobranch partially lamellate. First to third legs (Fig. 26 J): all gills larger and more lamellate, pleurobranch of second leg arising at about same level as arthrobranchs.

Atelecyclus rotundatus (Olivi)

(Fig. 27)

First and Second Zoea (Fig. 27 A, B) - No gill buds.

Third Zoea (Fig. 27 C-F) - First maxilliped (Fig. 27 C): minute epipod bud on coxa. Second maxilliped (Fig, 1 D): minute gill bud (future epipod and podobranch) on coxa. Third maxilliped (Fig. 27 E): two gill buds (future epipod and anterior and posterior arthrobranchs). First leg (Fig. 27 F): two gill buds (future anterior and posterior arthrobranchs). Second and third legs (Fig. 27 F): each with a gill bud (future pleurobranch) on coxal part.

Fourth Zoea (Fig. 27 G-J) - First maxilliped (Fig. 27 G): epipod bud triangular. Second maxilliped (Fig. 27 H): epipod bud with minute bud (future podobranch) near base. Third maxilliped (Fig. 27 I, J): epipod bud elongate upwards, posterior arthrobranch bud elongate upwards, with small bud (future anterior arthrobranch) near base. First leg (Fig. 27 J): two arthrobranch buds enlarged. Second and third legs (Fig. 27 J): each pleurobranch bud enlarged, in arthrobranch position.

Fifth Zoea (Fig. 27 K-N) - First maxilliped (Fig. 27 K): epipod bud elongate laterally. Second maxilliped (Fig. 27 L): epipod and podobranch buds unchanged. Third maxilliped (Fig. 27 M, N): epipod and two arthrobranch buds elongate. Legs (Fig. 27 N): arthrobranchs and pleurobranchs enlarged, and pleurobranchs now pleural in position

Megalopa (Fig. 27 O-T) - First maxilliped (Fig. 27 O): epipod thin, extending over gills behind, with 2+9 setae. Second maxilliped (Fig. 27 P): podobranch bud enlarged, epipod with 4 setae. Third maxilliped (Fig. 27 Q): podobranch bud at basal part of epipod as a separate bud; epipod extending between arthrobranchs of first leg and following pleurobranchs, with 1+7 setae; posterior arthrobranch bud enlarged; anterior arthrobranch about half size of posterior arthrobranch. First leg

(Fig. 27 R): anterior and posterior arthrobranch buds enlarged. Second and third legs (Fig. 27 S, T): each pleurobranch bud enlarged, now clearly pleural in position.

Carcinus maenas (Linnaeus)

(Figs. 28-29)

First Zoea (Fig. 28 A) - Devoid of gill buds.

Second Zoea (Fig. 28 B) - First maxilliped: a minute epipod bud on coxa. Second maxilliped: no gill bud. Third maxilliped: three gill buds on basio-coxal part (future epipod and anterior and posterior arthrobranchs). First leg: two gill buds (future anterior and posterior arthrobranchs) on basio-coxal part. Second and third legs: each with a gill bud (future pleurobranch).

Third Zoea (Fig. 28 C) - Now with a gill bud (future epipod and podobranch) on second maxilliped. Number of epipod and gill buds of other appendages unchanged, but all increased in size.

Fourth Zoea (Fig. 28 D) - Basically similar to third zoea. First maxilliped: epipod bud elongate. Second maxilliped: epipod bud enlarged. Third maxilliped: epipod bud elongate upwards, two arthrobranch buds enlarged. First leg: two arthrobranch buds enlarged. Second and third legs: each pleurobranch bud enlarged, arising slightly above base of appendage.

Megalopa (Fig. 28 E-H) - First maxilliped (Fig. 28 E): epipod flattened, with 1+5 setae. Second maxilliped (Fig. 28 F): a biramous bud, future podobranch (lower branch) at right angles to future epipod (upper branch). Third maxilliped (Fig. 28 G): podobranch bud now present as a small separate bud on inner basal part of epipod; epipod elongate, with 4+8 setae; anterior arthrobranch bud still a small bud at base of posterior arthrobranch bud; posterior arthrobranch bud enlarged. First leg (Fig. 28 H): two arthrobranchs partially lamellate. Second and third legs (Fig. 28 H): each pleurobranch partially lamellate, arising from basal part of pleuron.

First Crab (Fig. 29 A-D) - First maxilliped (Fig. 29 A): with 3 spines on proximal angle and 21-25 setae. Second maxilliped (Fig. 29 B-D): podobranch extending posteriorly, proximal part of podobranch partially lamellate; epipod extending upwards, with 0-2 terminal seate. Third maxilliped (Fig. 29 C): podobranch bud present as 2 or 3 lobules on outer basal angle of epipod; epipod with 11 setae; anterior and posterior arthrobranchs partially lamellate. First to third legs (Fig. 29 D): two arthrobranchs on first leg and pleurobranchs on second and third legs all lamellate, arising from same level.

Second Crab (Fig. 29 E) - Epipods and gills almost unchanged except those of second maxilliped (Fig. 29 E): podobranch unchanged, epipod with 6 setae, now with a gill bud (future arthrobranch) near inner base of epipod.

Third Crab (Fig. 29 F) - Epipods and gills similar to second crab, but arthrobranch bud of second maxilliped (Fig. 29 F) extended upwards; epipod with 7 setae.

Fourth Crab (Fig. 29 G) - Epipod and gills basically unchanged except those on second maxilliped (Fig. 29 G): epipod bud directed upwards, with 2 setae on outer proximal angle and 7-9 setae on distal half; arthrobranch bud elongate, at right angles to podobranch.

Fifth Crab (Fig. 29 H) - Epipods more setose and gills enlarged. Second maxilliped (Fig. 29 H): podobranch lamellate almost to distal end, epipod more setose, arthrobranch lamellate on inner margin.

Liocarcinus corrugatus (Pennant)

(Fig. 30)

First Zoea (Fig. 30 A) - No gill buds.

Second Zoea (Fig. 30 B) - First maxillipeds: a minute epipod bud on coxa. Second maxilliped: no gill bud. Third maxilliped: three gill buds on basio-coxal part (future epipod and anterior and posterior arthrobranchs). First leg: two gill buds (future anterior and posterior arthrobranchs) on basio-coxal part, anterior bud curved posteriorly. Second and third legs: each with one gill bud (future pleurobranch).

Third Zoea (Fig. 30 C) - Now with a gill bud (future epipod and podobranch) on coxa of second maxilliped. Number of epipod and gill buds unchanged, but all increased in size.

Fourth Zoea (Fig. 30 D) - Number of epipod and gill buds unchanged, but all increased in size.

Fifth Zoea (Fig. 30 E) - First maxilliped: epipod bud elongate posteriorly. Second maxilliped: now a biramous bud (smaller lower branch: future podobranch; larger upper branch: future epipod). Third maxilliped: epipod with two terminal setae, arthrobranch buds unchanged. First to third legs: two arthrobranch and two pleurobranch buds unchanged; pleurobranchs in arthrobranch position.

Megalopa (Fig. 30 F - I) - First maxilliped (Fig. 30 F, I): epipod flattened, with 2+10 setae. Second maxilliped (Fig. 30 G): podobranch bud almost equal in size to epipod; epipod with 4 setae. Third maxilliped (Fig. 30 H, I): podobranch bud as 3 lobules on the outer basal part of epipod; epipod with 5+16 setae; anterior arthrobranch bud enlarged; posterior arthrobranch bud partially lamellate. First leg (Fig. 30 I): two arthrobranchs lamellate. Second and third legs (Fig. 30 I): each pleurobranch lamellate, still in arthrobranch position.

Liocarcinus holsatus (Fabricius)

(Fig. 31)

Development patterns of epipod and gill buds up to fourth zoea are identical to *Carcinus maenas* and *Liocarcinus corrugatus*, but some differences are found from fifth zoea, particularly in development of arthrobranch on second maxilliped. Descriptions are given from fifth zoea.

Fifth Zoea (Fig. 31 A) - First maxilliped: epipod bud elongate. Second maxilliped: a biramous bud (future epipod and podobranch). Third maxilliped: epipod and two arthrobranch buds elongate. First to third legs: two arthrobranch and two pleulrobranch buds unchanged, all arising at same level as arthrobranchs of first leg.

Megalopa (Fig. 31 B) - Second maxilliped (Fig. 31 B): podobranch bud on base of epipod, at right angles; epipod with terminal seta.

First Crab (Fig. 31 C) - Second maxilliped: podobranch elongate and partially lammelate; epipod with 2 setae; an arthrobranch bud now present.

Second Crab (Fig. 31 D) - Second maxilliped: podobranch elongate; epipod with 8 setae; arthrobranch bud elongate.

Pilumnus hirtellus (Linnaeus)

(Fig. 32)

First Zoea (Fig. 32 A, B) - First and second maxillipeds (Fig. 32 A): no gill buds. Third maxilliped (Fig. 32 A, B): three gill buds (future epipod and anterior and posterior arthrobranchs) on coxal part. Legs (Fig. 32 A): devoid of gill buds.

Second Zoea (Fig. 32 C) - Gill buds unchanged, present only on third maxilliped, as in first zoea.

Third Zoea (Fig. 32 D, E) - First maxilliped (Fig. 32 D): an upright epipod bud on coxa. Second maxilliped (Fig. 32 D): no gill bud. Third maxilliped (Fig. 32 D, E): epipod bud and posterior arthrobranch bud elongate upwards; anterior arthrobranch bud unchanged. First leg (Fig. 32 D): a pair of gill buds (future anterior and posterior arthrobranchs). Second and third legs (Fig. 32 D): each with a gill bud (future pleurobranch), more dorsal than arthrobranchs on first leg.

Fourth Zoea (Fig. 32 F, G) - First maxilliped (Fig. 32 F): epipod elongate posteriorly. Second maxilliped (Fig. 32 F): now with an epipod bud on coxa. Third maxilliped (Fig. 32 F, G): epipod and posterior arthrobranch bud enlarged, anterior arthrobranch bud unchanged and still small. First leg (Fig. 32 F): anterior and posterior arthrobranch buds enlarged. Second and third legs (Fig. 32 F): each pleurobranch bud enlarged, clearly pleural in position.

Megalopa (Fig. 32 H-K) - First maxilliped (Fig. 32 H): epipod flattened, extending over gills behind, with 4 curved setae. Second maxilliped (Fig. 32 I): biramous bud, lower and upper buds representing podobranch bud and epipod bud respectively. Third maxilliped (Fig. 32 J, K): podobranch bud at basal part of epipod as separate bud, epipod extending between arthrobranchs of first leg and following pleurobranchs, with 3+5 setae; anterior arthrobranch bud unchanged; posterior arthrobranch enlarged and partially lamellated. First leg (Fig. 32 K): anterior and posterior arthrobranchs on thoracic pleuron, lamellated. Second and third legs (Fig. 32 K): pleurobranch of second leg lamellate, pleurobranch of third leg partially lamellate, about half length of that of second leg; both pleurobranchs arising from pleuron at about same level as arthrobranchs of first leg.

Monodaeus couchi (Couch)

(Fig. 33)

First Zoea (Fig. 33 A) - First and second maxillipeds: no gill buds. Third maxilliped: two gill buds (future epipod and posterior arthrobranch).

Second Zoea (Fig. 33 B, C) - First and second maxillipeds: no gill buds. Third maxilliped (Fig. 33 C): epipod and arthrobranch buds enlarged. First leg: two gill buds (future anterior and posterior arthrobranchs) on coxal part. Second leg: a small gill bud (future pleurobranch). Third leg: devoid of gill bud.

Third Zoea (Fig. 33 D) - First maxilliped: an epipod bud on coxa. Second maxilliped: no gill bud. Third maxilliped: a small gill bud (future anterior arthrobranch) added between epipod bud and posterior arthrobranch bud. First leg: two arthrobranch buds almost equal in size. Second and third legs: each with a pleurobranch bud arising in arthrobranch position.

Fourth Zoea (Fig. 33 E) - Number of epipod and gill buds unchanged, but all increased in size.

Megalopa (Fig. 33 F-I) - First maxilliped (Fig. 33 F): epipod flattened and elongated, with 8 setae. Second maxilliped (Fig. 33 G): with a biramous bud representing epipod and podobranch buds; epipod with a terminal seta. Third maxilliped (Fig. 33 H): a podobranch bud now at base of epipod as a separate bud, epipod flattened and elongate with more than 14 setae; anterior arthrobranch bud unchanged; posterior arthrobranch partially lamellate. First leg (Fig. 33 I): two arthrobranchs at base of coxa, lamellate. Second and third legs (Fig. 33 I): each pleurobranch on thoracic pleuron, lamellate.

First Crab (Fig. 33 J-L) - First maxilliped (Fig. 33 J): epipod with more than 2+20 setae, proximal half expanded and concave, distal half extending over gills behind. Second maxilliped (Fig. 33 K): podobranch partially lamellate, directed posteriorly, epipod elongate upwards, with 8 setae. Third maxilliped (Fig. 33 L): podobranch with 3 or 4 lamellae, epipod with more than 15 setae; anterior arthrobranch partially lamellate; posterior arthrobranch lamellate almost up to the end. Gills on legs (not shown in figure), similar to megalopa, but increased in size.

Pinnotheres pinnotheres (Linnaeus)

(Figs. 34-35)

First Zoea (Fig. 34 A-C) - First maxilliped (Fig. 34 A: C): an epipod bud on coxa. Second maxilliped (Fig. 34 C): no gill bud. Third maxilliped (Fig. 34 B, C): three gill buds (future epipod and anterior and posterior arthrobranchs) on basio-coxal part. First leg (Fig. 34 C): two gill buds (future anterior and posterior arthrobranchs) on the same level: the posterior bud located on the coxal part of second leg.

Second Zoea (Fig. 34 D-F) - First maxilliped (Fig. 34 D, F): epipod bud elongate posteriorly. Second maxilliped (Fig. 34 F): no gill bud. Third maxilliped (Fig. 34 E, F): epipod bud elongate upwards: anterior arthrobranch bud bulbous and smaller than in first stage; posterior arthrobranch bud larger and elongate upwards; an outgrowth (? future podobranch) developed at base of epipod. First leg (Fig. 34 F): two arthrobranch buds, on the same level, enlarged.

Megalopa (Fig. 34 G-I) - First maxilliped (Fig. 34 G): epipod flattened, roughly triangular, with 5 marginal setae. Second maxilliped (not shown in the figure) without gill bud. Third maxilliped (Fig. 34 H): epipod flattened, more or less triangular, with 6 spines on the outer proximal margin and 3 long setae on distal part; anterior arthrobranch bud (present in the zoeal stages) now represented by two lamellar buds (Fig. 34 H, indicated by arrow) separated by a deep indentation from the proximal part of the posterior arthrobranch; posterior arthrobranch lamellate; the outgrowth at base of epipod elongate downwards (appears to be developing podobranch, but none present in adult). First leg: two arthrobranchs, lamellate.

Adult (Fig. 35, A-C) - First maxilliped (not shown in figure): epipod overlapping gills behind. Second maxilliped (not shown in figure): no gills. Third maxilliped: epipod (not shown in figure), proximal half with numerous stout spines on outer proximal margin, distal half with numerous setae; anterior arthrobranch (Fig. 35 A, B) a small flattened bud about 0.1 times size of posterior arthrobranch and located on inner proximal part of it; posterior arthrobranch (Fig. 35 B) lamellate and as large as the two arthrobranchs of first leg. First leg (not shown in figure): two arthrobranchs on arthromembrane (Fig. 35 C).

Pinnotheres pisum (Linnaeus)

(Figs. 35-36)

First and Second Zoea (Fig. 36 A, B) - Devoid of gill buds.

Third Zoea (Fig. 36 C) - First maxilliped: an epipod bud on coxa. Second maxilliped: no gill bud. Third maxilliped: epipod and gills represented by bulge on proximal part. First leg: two bulges (rudimentary buds of two arthrobranchs) on proximal part.

Fourth Zoea (Fig. 36 D-F) - First maxilliped (Fig. 36 D): epipod bud enlarged. Second maxilliped (Fig. 36 D): no gill bud. Third maxilliped (Fig. 36 D-F): two gill buds (future epipod and arthrobranch). First leg (Fig. 36 D): two arthrobranch buds on coxal part.

Fifth Zoea (Fig. 36 G-H) - First maxilliped: epipod elongate posteriorly. Second maxilliped: no gill bud. Third maxilliped

(Fig. 36 G, H): epipod and arthrobranch bud enlarged. First leg (Fig. 36 G): the two arthrobranch buds elarged.

Megalopa (Fig. 36 I-L) - First maxilliped (Fig. 36 I): epipod flattened, with two setae. Second maxilliped (Fig. 36 J): no gill bud. Third maxilliped (Fig. 36 K, L): epipod with 6 spines on outer proximal margin and 4 setae on distal half, arthrobranch partially lamellate. First leg (Fig. 36 L): two arthrobranchs, posterior one on pleuron of second leg, lamellate.

Adult (Fig. 35 D-F) - First maxilliped (not shown in figure): epipod overlapping gills behind. Second maxilliped (not shown in figure): no gills. Third maxilliped: epipod (not shown in figure), proximal half with numerous stout spines on outer proximal margin, distal half with numerous setae; anterior arthrobranch (Fig. 35 D, E) a small gill about 0.2 times size of posterior arthrobranch and located on inner proximal part of it; posterior arthrobranch (Fig. 35 E) well lamellate and as large as the two arthrobranchs of first leg. First leg (not shown in figure): two arthrobranchs on arthromembrane (Fig. 35 F).

Pinnaxodes mutuensis Sakai

(Fig. 37)

First and Second Zoea (Fig. 37 A, B) - devoid of gill buds.

Third Zoea (Fig. 37 C) - First maxilliped: an epipod bud on coxa. Second maxilliped: no gill bud. Third maxilliped: two gill buds (future epipod and two arthrobranchs), epipod bud curved and directed upwards, an arthrobranch bud directed upwards. First leg: two gill buds (future anterior and posterior arthrobranchs), posterior arthrobranch bud located on second leg.

Fourth Zoea (Fig. 37 D, E) - First maxilliped (Fig. 37 D): epipod, triangular in shape, directed upwards. Second maxilliped: no gill bud. Third maxilliped (Fig. 37 D, E): epipod and arthrobranch buds enlarged. First leg (Fig. 37 D): the two arthrobranch buds enlarged.

Megalopa (Fig. 37 F-K) - First maxilliped (Fig. 37 F): epipod flattened, with 3 setae. Second maxilliped (Fig. 37 G): no gill bud. Third maxilliped (Fig. 37 H-K): epipod with more than 16 spines on outer proximal margin and 4 setae on distal half, extends under anterior arthrobranch of first leg; posterior arthrobranch partially lamellate; anterior arthrobranch represented by a small bud (Fig. 37 I, J indicated by arrows) on basal part of posterior arthrobranch. First leg (Fig. 37 K): two arthrobranchs, on pleuron, lamellate; posterior arthrobranch arising clearly on pleuron of second leg.

First Crab (Fig. 37 L-O) - First maxilliped (Fig. 37 L): epipod, overlapping the gills behind, with 1+3 setae. Second maxilliped (Fig. 37 M): no gill bud. Third maxilliped (Fig. 37 N, O): epipod, proximal half with more than 15 stout spines on outer proximal margin, distal half with 8 setae; arthrobranchs composed of smaller proximal (anterior) part (arrowed in Fig. 37 N, O) and larger distal (posterior) part (demarcation between parts clear in some views and obscure in others). First leg (Fig. 37 O), the two arthrobranchs lamellate; posterior arthrobranch on pleuron of second leg.

Adult (Fig. 37 P, Q) - As in first crab, but the anterior arthrobranch (Fig. 37 P) on the third maxilliped only about 0.15-0.20 times size of the posterior arthrobranch (Fig. 37 Q) and located on inner proximal part of it.

Pinnixa rathbuni Sakai

(Fig. 38)

First Zoea (Fig. 38 A) - Devoid of gill buds.

Second Zoea (Fig. 38 B) - First and second maxillipeds: no gill buds. Third maxilliped: two gill buds (future epipod and arthrobranchs).

Third Zoea (Fig. 38 C) - First and second maxillipeds: no gill buds. Third maxilliped: the two gill buds enlarged. First leg: two gill buds (future arthrobranchs).

Fourth Zoea (Fig. 38 D) - First maxilliped: epipod, directed posteriorly. Second maxilliped: no gill bud. Third maxilliped (Fig. 38 D, E): now three buds present (future epipod and anterior and posterior arthrobranchs). First leg: the two arthrobranch buds enlarged, posterior arthrobranch bud located on second leg.

Fifth Zoea (Fig. 38 F-H) - First maxilliped (Fig. 38 F, H): epipod elongated posteriorly. Second maxilliped: no gill bud. Third maxilliped (Fig. 38 G, H): epipod bud elongated posteriorly and curved over the first leg; anterior arthrobranch bud almost unchanged, posterior arthrobranch bud enlarged. First leg (Fig. 38 H): arthrobranchs further enlarged, both appear to arise posteriorly to base of first leg.

Megalopa (Fig. 38 I-L) - First maxilliped (Fig. 38 I): epipod flattened, with 4 spines on the outer proximal margin and 17-19 setae on distal half. Second maxilliped (Fig. 38 J): no gill bud. Third maxilliped (Fig. 38 K, L): epipod, proximal half curved posteriorly, with more than 25 stout spines on outer proximal margin, distal half extended upwards, with 19-21 setae on distal half; anterior arthrobranch bud now fused to basal part of posterior arthrobranch (Fig. 38 K, L indicated by arrows) to look like sigle gill with asymmetrical lamellar arrangement of basal part. First leg (Fig. 38 L): two arthrobranchs, on thoracic pleuron, lamellate, disposition of lamellae on basal part quite symmetrical.

Pinnixa (?)*chaetopterana* Stimpson

(Fig. 39)

Larvae of this species were sorted from Brazilian plankton by Danilo de Calazans, to whom I am much indebted. There has been no opportunity to confirm the identity of the species by laboratory rearing.

First and Second Zoea (Fig. 39 A, B) - Devoid of gill buds.

Third Zoea (Fig. 39 C) - First maxilliped: an epipod bud on coxa. Second maxilliped: no gill buds. Third maxilliped: three gill buds (future epipod and two arthrobranchs). First leg: two gill buds (future two arthrobranchs).

Fourth Zoea (Fig. 39 D-F) - First maxilliped: epipod elongate posteriorly. Second maxilliped: no gill bud. Third maxilliped (Fig. 39 D-F): epipod and two arthrobranch buds enlarged. First leg (Fig. 39 D): two arthrobranch buds enlarged, posterior bud above base of second leg.

Fifth Zoea (Fig. 39 G-I) - First maxilliped (Fig. 39 G): epipod elongate. Second maxilliped: no gill bud. Third maxilliped (Fig. 39 G-I): epipod bud elongated and extending over first leg, anterior arthrobranch bud unchanged, posterior arthrobranch bud enlarged. First leg (Fig. 39 G): arthrobranchs further enlarged; posterior arthrobranch arising at pleuron of second leg.

Megalopa (Fig. 39 J-L) - First maxilliped (Fig. 39 J): epipod flattened, with 2 spines on outer proximal margin and 10-12 setae on distal half. Second maxilliped (Fig. 39 K): no gill bud. Third maxilliped (Fig. 39 L): epipod, proximal half curved posteriorly with numerous spines on outer proximal margin and 14-17 setae (not shown in figure) on distal half, anterior arthrobranch bud now fused to the proximal part of posterior arthrobranch and indistinguishable, the posterior arthrobranch lamellate. First leg (not shown in figure): two arthrobranchs, on thoracic pleuron, lamellate.

DISCUSSION

Gills of decapods are named according to their position of attachment on the adult, namely podobranch on coxa, arthrobranch on arthromembrane between coxa and pleuron, and pleurobranch on pleuron.

Borradaile (1907: 462-463), in elaboration of Coutière (1905), expressed the view of that the mastigobranch, setobranch and anterior arthrobranch have been derived from the distal *epipodite* and the posterior arthrobranch and pleurobranch from a proximal *proepipodite* (see Fig. 20-A).

In penaeids and carideans, a horizontal arrangement of 3 series of gill buds are recognised in addition to epipod buds. From lower to upper, the series represents anterior arthrobranch, posterior arthrobranch and pleurobranch (Claus, 1885; Calman, 1909; Kemp, 1910; Gurney, 1924 b, 1942; Burkenroad, 1934). Of these, it is known that pleurobranch buds are added later than the others.

So far little is published on the larval gills of pagurids and brachyurans, particularly in terms of variation in position and in number during development.

Adults of *Pagurus prideauxi* and *Pagurus bernhardus* have 11 gills in the following pattern:

Third maxilliped	2 arthrobranchs
First leg	2 arthrobranchs
Second leg	2 arthrobranchs
Third leg	2 arthrobranchs
Fourth leg	2 arthrobranchs, 1 pleurobranch

During larval development, gill buds appear in the fourth zoea as elongated buds on the coxa or basio-coxal part of the legs, and they are lamellate in the megalopa. The arthrobranch buds of the third maxilliped do not appear until the megalopa, and become lamellate in the crab stages. There is some dorsal migration of the arthrobranchs during development.

In *P. prideauxi*, the arthrobranchs of first leg are also delayed. They appear as a small single bud in the fourth zoea and as a pair of small buds in the megalopa. It is also noted that arthrobranchs of the first and second legs are noticibly smaller than those of the following legs. In both *P. prideauxi* and *P. bernhardus*, all arthrobranchs arise on the same level on the coxa, but the pleurobranch arises in the pleural position.

The gill lamellae of megalopas of these pagurid species are different from those of brachyurans. The gills of pagurid megalopas are slightly narrower, and the lamellae are rather lobule-like buds on both lateral margins. Such differences foreshadow the difference in gill forms of adult pagurids and brachyurans, which have trichobranchiate gills and phyllobranchiate gills respectively (see Calman, 1909).

The present study shows that the podobranchs of brachyuran larvae always develop by the branching of an epipod bud or of a well-developed epipod; also the anterior and posterior arthrobranchs always appear as separate buds from the early stages, revealing their separate origins from *epipodite* and *proepipodite*. This applies to all brachyran larvae, as suggested by Coutière (1905) and Borradaile (1907), but the developmental pattern of arthrobranchs and pleurobranch shows some differences between families or family groups.

Generally in brachyuran larvae, one of the arthrobranchs of the anterior appendages (second and third maxillipeds) tends to be delayed; also, once the epipod and arthrobranchs appear, pleurobranch buds also appear at the same time on the second or third legs. However, some exceptions are found, particularly in the position of arthrobranch buds of the first leg and pleurobranchs of the second and third legs.

In most brachuran larvae, the two arthrobranch buds of the first leg lie one above the other at their first appearance (first or second zoea), showing a clear pattern of serial tiering of gill buds, as suggested by Claus (1885), Calman (1909), Kemp (1910) and Gurney (1942). However, in later zoeas these two gill buds come to lie at the same level, in the arthrodial position at the base of the appendage, and so their levels of attachment are no longer different.

In general, the pleurobranchs of the second and third legs are present on the same level as the posterior arthrobranch of the first leg until the penultimate zoeal stage, however, the pleurobranchs shift their position up to the pleuron in the last zoea or in megalopa, whereas the posterior arthrobranch of the first leg remains in the original position, at the side of the anterior arthrobranch. In some majids, arthrobranchs also shift to the pleural position. In ***Carcinus maenas, Liocarcinus corrugatus*** and ***Liocarcinus holsatus***, it is not clear when the pleurobranch buds shift to the pleuron. The arthrobranchs and pleurobranchs are all located on the arthrobranch level in the megalopa.

Hartnoll (1964 b) found a variation of gill number from 9 to 7 in 17 species of 8 majid subfamilies. This variation is mainly due to the presence or absence of the gills of the second maxilliped, which has 1 podobranch and 1 arthrobranch as the maximum number. Of these, one or both gills are absent or modified in most of the species examined. He found that only ***Pisa armata*** (as ***Pisa gibbsi***) has 9 gills without any modification and ***Eurynome aspera*** and ***Eurynome spinosa*** have a reduced arthrobranch, with one row of lamellae, on the second maxilliped.

In *Inachus dorsettensis*, which has 7 pairs of gills in the adult, the anterior arthrobranch of the third maxilliped is the most anterior gill. It is interesting that even a bud of the anterior arthrobranch of the third maxilliped does not appear up to the megalopa stage. It is assumed to appear in the crab stages. In *Hyas araneus*, which has 8 pairs of gills in the adult, only the podobranchs of the second and third maxillipeds are delayed in the zoeas, and appear as buds in the megalopa. *E. aspera* and *P. armata* have 9 pairs of gills. Gurney (1924 a, Fig. 2) observed the gill buds of the first zoea of *E. aspera*, but he missed those on the first maxilliped and second leg. In these two species gill buds appear from the first zoea as small rudimentary buds on the coxa or basio-coxal part, and these gill buds represent most of the corresponding gills of the adult except the podobranchs of the second and third maxillipeds. These two podobranchs appear in the megalopa as small buds at the base of the epipods, and the arthrobranch of second maxilliped is assumed to appear in the crab stages, as in other brachyuran species except pinnotherids.

Yang and McLaughlin (1979) reported that *Libinia erinacea* has 9 pairs of gills in the adult, but the megalopa has only 5 pairs of lamellar gills. The epipod of the second maxilliped was still absent in the megalopa and appeared as "a single lobate bud" in the first crab. Arthrobranch buds appeared in the second crab and lamellation started in the fourth crab. They found a similar pattern of epipod and gill development in 13 other majid species. In *Epialtus dilatatus*, which has 8 gills and 3 epipods in the adult, only 4 pairs of gills were present in the megalopa (Yang, 1968). In the present studies, larvae of *E. aspera* and *P. armata* showed the same pattern of development for the epipod of the second maxilliped as in *L. erinacea* (Yang and McLauglin, 1979), but in *H. araneus*, this epipod bud appeared in the first zoea, and the podobranch bud branched out of the epipod bud in the megalopa. Based on these findings, it is suggested that the delayed development of the epipod on the second maxilliped probably occurs only in those majid species which have 9 pairs of gills. In regard to this, it is interesting to note that no epipod and gill buds were shown on the second maxilliped in figures of majid larvae described by Yang (1968), Christiansen (1973), Ingle (1977), Ingle and Clark (1980), Scotto and Gore (1980), Webber and Wear (1981), Gore, Scotto and Yang (1982) and Salman (1982).

Based on these findings, one conclusion is that the absence of a podobranch or arthrobranch or both on the second maxilliped is likely to be common in majid crabs, and, in case of their presence, they usually develop after the megalopa stage. The most anterior arthrobranch, whether it is present on the second or third maxilliped, is always delayed and appears in the crab stages.

In *I. dorsettensis*, it is also noted that the pleurobranch of the second leg appears in the second zoea, becomes a small bud in the megalopa, and remains as a single lamella in the first crab, whereas other gills on the preceding appendages have well developed lamellae. Similar delayed development of the pleurobranch of second maxilliped was also seen in *E. aspera*, in which the gill bud (future pleurobranch) of the second leg is much smaller than that of the first leg, and remains as a simple bud even in the megalopa. These provide good examples of delayed development of pleurobranchs in brachyuran larvae. It is not known whether such delayed development and reduction of the posterior pleurobranch is common in majids or not. However, such phenomena draw attention to the fact that there is a tendency to reduction of the number of pleurobranchs in brachyurans. Dromiids have 4 pleurobranchs, and this probably represents the primitive condition, but some ocypodids and all pinnotherids have no pleurobranchs at all (Calman, 1909; Balss, 1957; Burkenroad, 1981).

It is generally accepted that most Cyclometopa, including Atelecyclidae, Cancridae, Xanthidae and Portunidae, have 9 gills and 3 epipods (Huxley, 1878; Pearson, 1908; Calman, 1909; Borradaile, 1922; Gurney, 1942; Balss, 1957; Crothers, 1967). Few exceptions are known. Wear (1968 a: 321) reported 8+3 gills in *Ozius truncatus* (Xanthidae). The usual pattern in these 4 families, confirmed in *A. rotundatus*, *C. maenas*, *L. corrugatus*, *L. holsatus*, *Pilumnus hirtellus*, and *Monodaeus couchi*, is as follows:

First Maxilliped	1 epipod
Second Maxilliped	1 epipod, 1 podobranch 1 arthrobranch
Third Maxilliped	1 epipod, 1 podobranch, 2 arthrobranchs
First Leg	2 arthrobranchs
Second Leg	1 pleurobranch
Third Leg	1 pleurobranch

On the second maxilliped, the podobranch is a branchial plume lying horizontally and the arthrobranch is the most anterior of the gills which point vertically.

Although there are some differences in the sequence of appearance of gill buds in the larval stages, basically the developmental patterns are very similar. Most gill buds first appear before the antepenultimate or penultimate zoeal stage (third or fourth zoea) except those corresponding to the podobranch and arthrobranch of the second maxilliped. The important common pattern is that the epipod bud of the second maxilliped appears in the last zoea, whereas the arthrobranch (the most anterior gill) does not appear even up to the megalopa. In *L. holsatus* the arthrobranch appears as a simple bud in the first crab, and in *C. maenas* it appears as a simple bud in the second crab and becomes lamellate in the fifth crab. Megalopas of *C. maenas, Liocarcinus puber* and *L. holsatus* described by Rice and Ingle (1975 a, b) show only bilobed epipods on the second maxilliped. Connolly (1923, Fig. 32) and Wear (1968 a, Fig. 68) found such absence of arthrobranch of the second maxilliped in *Cancer amoenus* and *O. truncatus* respectively.

Similar delayed development of the arthrobranch of the second maxilliped was also found in two majid crabs, ***E. aspera*** and ***P. armata***, which have 9 gills and 3 epipods. In regard to this, it will be interesting to know whether all brachyurans which have 9 gills and 3 epipods show such a pattern of gill development.

Since the earlier works of Claus (1885), Calman (1909), Gurney (1942) and Balss (1957), pinnotherids have been known to have 3 gills and 2 epipods in the following pattern:

First Maxilliped	1 epipod
Second Maxilliped	--
Third Maxilliped	1 epipod 1 arthrobranch
First Pereiopod	2 arthrobranchs

This formula was based mainly on ***Pinnotheres pinnotheres*** and ***Pinnotheres pisum***. But they missed another arthrobranch (anterior arthrobranch) on the third maxilliped of these two pinnotherids. According to the detailed examinations of some pinnotherid adults, this gill formula can be used for only some pinnotherid species. The author found that ***P. pinnotheres, P. pisum, Pinnaxodes mutuensis*** and ***Pinnaxodes major*** have 2 arthrobranchs on the third maxilliped, and thus have a total of 4 pairs of gills and 2 pairs of epipods. Of the two arthrobranchs on the third maxilliped, the anterior arthrobranch is very reduced and of varying sizes (Fig. 15 A, B, D, E; Fig. 17 P, Q) when compared to the posterior arthrobranch. Probably because of its reduced size, it is asummed, the previous workers have missed it. On the other hand, *Pinnotheres pholadis*, *Pinnotheres sinensis* and *Pinnaxodes rathbuni* have no anterior arthrobranch at all on the third maxilliped, and they have a total of 3 pairs of gills. Even within a genus there are variations in number of gills, and it appears to be common within the family Pinnotheridae. When the third maxilliped has two arthrobranchs, the anterior arthrobranch appears to be reduced in varying degree. Variations of gill numbers in pinnotherids have been also suggested by K. Konishi (personal communication).

The major difference between the gill formulae of pinnotherids and other brachyurans is the total loss of pleurobranchs on the second and third legs and the occurrence of arthrobranchs only on the third maxilliped and first leg.

Unfortunately descriptions of larval gills are not included in the published developmental studies on pinnotherids (Hyman, 1924; Sandoz and Hopkins, 1947; Atkins, 1954; Costlow and Bookout, 1966; Hong, 1974; Noble, 1974; Rice, 1975; Roberts, 1975; Muraoka and Konishi, 1977; Sekiguchi, 1978; Konishi, 1981; Pohle and Telford, 1981, 1983).

Despite the delayed development of the arthrobranch of the second and third maxillipeds in the above-mentioned majids and brachyrhynchs, it is very interesting to note that developmental patterns of gills of pinnotherids show greater differences than those of other families. Particulary, as mentioned the anterior arthrobranch on the third maxilliped tends to be reduced in size or fused to the posterior arthrobranch, as a result, in some species the adults have only one arthrobranch on the third maxilliped.

Gurney (1942: 27, 144) stated that "when the gill formula of the adult is reduced there is no trace of the lost gills in the larvae", although rudiments of such gills might be expected. Burkenroad (1981: 258) also expressed the same view. It is, therefore, most important to note that in the present study some evidence is found of the disappearance or reduction of gill buds during the larval development of some pinnotherid larvae.

In *P. pinnotheres*, which has 4 gills and 2 epipods in the adult, gill buds first appear in the first zoeal stage as small rudiments on the coxal region of the limbs. These gill buds represent exactly the same gills as occur on all appendages in the adult. In the first zoea, the third maxilliped bears 3 gill buds corresponding to an epipod and two arthrobranchs. Of these buds, the middle one (future anterior arthrobranch) becomes smaller in the second zoea, and eventually fused to the proximal part of the posterior arthrobranch in the megalopa. As a result, the adult has a reduced anterior arthrobranch on the third maxilliped (Fig. 35 A, B, D, E). Also it is noted that there is an outgrowth at the base of the epipod from the second zoeal stage (Fig. 34 E, H), but none in adult. By its shape and position on the third maxilliped, the outgrowth can be easily recognised as the early development of a podobranch. In other crabs podobranchs appear in the same pattern as a bud at the base of the epipod. If the outgrowth were to develop as a podobranch, it means that during the crab stages this species would have either a fully developed podobranch or a simple rod, as in the megalopa (as shown in Fig. 34. H). Considering the absence of the podobranch on the third maxilliped in the adults, it can be postulated that the podobranch degenerates by the adult stages. Reduction or disappearance of the anterior arthrobranch bud and the assumed degeneration of the podobranch on the third maxilliped is very unusual in regard to the gill development of other families.

In ***P. pisum***, which has 4 pairs of gills, appearance of the anterior arthrobranch of the third maxilliped is delayed. It is interesting to note that the gill bud corresponding to the anterior arthrobranch of third maxilliped does not appear even up to the megalopa. It is assumed to appear in crab stages. Such delayed developments of gills were found in case of arthrobranch of second maxilliped of other brachyurans. From the fourth zoea there is one arthrobranch bud on the third maxilliped and 2 arthrobranch buds on the first leg, and megalopa also has the same 3 pairs of gills.

In ***P. mutuensis***, which has 4 gills and 2 epipods in the adult, the anterior and posterior arthrobranchs of the third maxilliped is very similar to those of ***P. pinnothers*** and ***P. pisum***, but developmental pattern of the anterior arthrobranch is quite different. The gill bud corresponding to the anterior arthrobranch of the third maxilliped does not appear in zoeal stages. It appears as a small bud on basal part of posterior arthrobranch in megalopa.

In *Pinnixa rathbuni* and *Pinnixa (?)chaetopterana*, which have 3 pairs of gills, reduction or fusion of the anterior arthrobranch of the third maxilliped was observed. Three gill buds are found in the zoeal stages, however, the anterior arthrobranch bud develops as a small gill with one or two lamellae which is fused to the bottom of the posterior arthrobranch. In the adult the anterior arthrobranch is absent, and only one arthrobranch is found on the third maxilliped.

Reduction in the number of gills as well as the disappearence of some gills during the ontogeny of pinnotherids might be closely related to the adaptive strategy of such species to commensal life. The reduced gills are adequate to meet the respiratory requirements of a inactive commensal crab, and space is at premium.

Thus reduction in the number of gills would be probably common among commensal pinnotherids. It is suggested that reduction of gills has been achieved in the evolution of pinnotherids, and ontogeny recapitulates this reduction process in some pinnotherids. The evidence which Gurney (1942) regarded as missing, does therefore exist.

Pinnotherid larvae show another interesting character in the position of the gill buds. It was found that the two arthrobranch buds of the first leg never appear one above the other, as in the case of other brachyurans, but always appear side by side on the same level even in the first zoea. In other brachyurans, the appearance of these arthrobranchs one above the other is thought to represent their origins from separate epipodites.

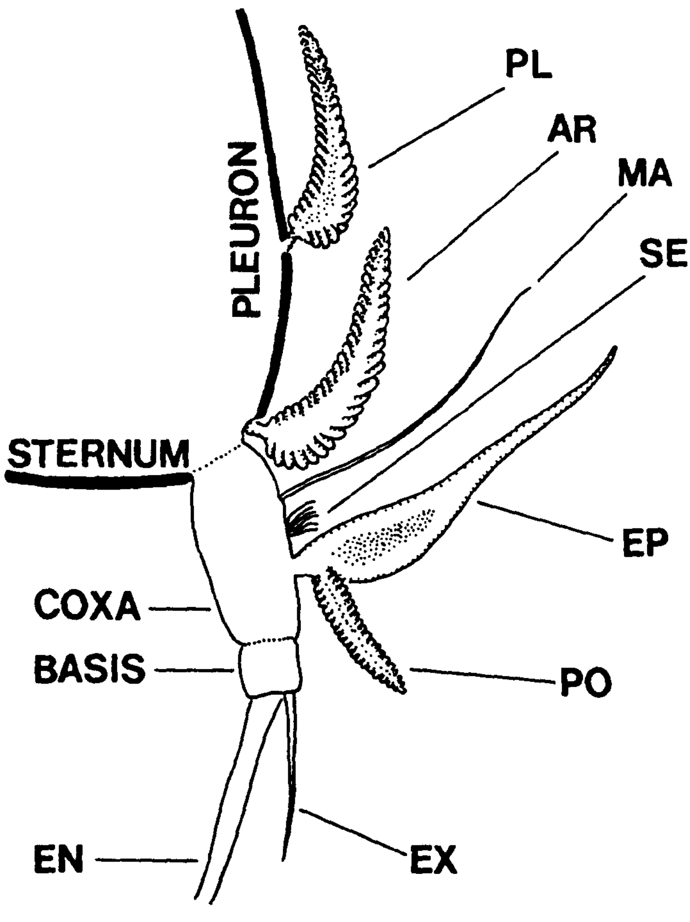
It is also interesting to note that in all pinnotherid zoeas, the posterior arthrobranch of the first leg is always located at the base of the coxal part of the second leg. In megalopas and first crabs this gill is clearly located on the pleuron of the second leg or even further back on the pleural surface. The pleural position of the posterior arthrobranch and its tendency to migrate during development raises the question of whether it is really an arthrobranch, and whether the conventional classification of brachyuran gills is well founded.

The present work shows important differences between the Pinnotheridae and other Brachyura not only with number of gills but in the way in which they develop. In many Majidae, Atelecyclidae, Portunidae and Xanthidae investigated, the pleurobranchs of the adults tends to be indistinguishable from arthrobranchs in their location at first appearance, while in the

Pinnotheridae the posterior arthrobranchs of the adults occupy the position of pleurobranchs in some of the early developmental stages of the crabs. This clearly raises important questions on the distinctions between different types of gills and their evolutionary origins. To answer them, it will be necessery to review the development of gills and variations in adult gill formulae in many more various species of decapods, but the Pinnotheridae emerge as a group of particular interest and importance.

Fig. 20-A. A schematic drawing of gill position.

AR: arthrobranch; EN: endopod; EP: epipod; EX: exopod; MA: mastigobranch; PL: pleurobranch; PO: podobranch; SE: setobranch.


PL
AR
MA
SE
PLEURON
STERNUM
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BASIS
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Fig. 21. *Pagurus prideauxi* Leach, Development of gills

A-D, maxillipeds and legs: A, first zoea; B, second zoea; C, third zoea; D, fourth zoea; E-F, megalopa: E, third maxilliped; F, maxillipeds and legs. Scale = 0.25 mm

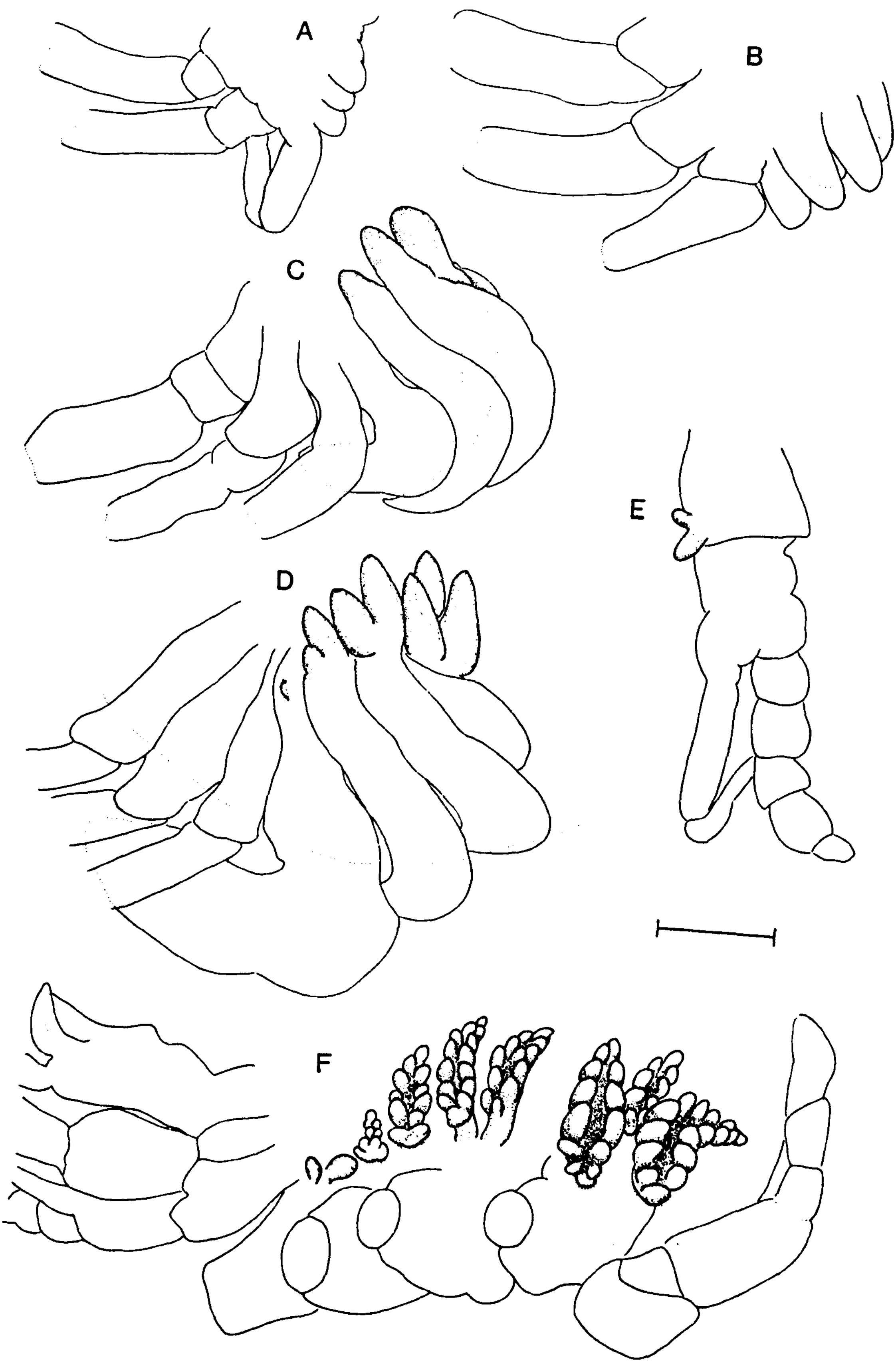
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Fig. 22. *Pagurus bernhardus* (Linnaeus), Development of gills

A-F, maxillipeds and legs: A, first zoea; B, second zoea; C, third zoea; D-E, fourth zoea; F, megalopa. Scale = 0.50 mm

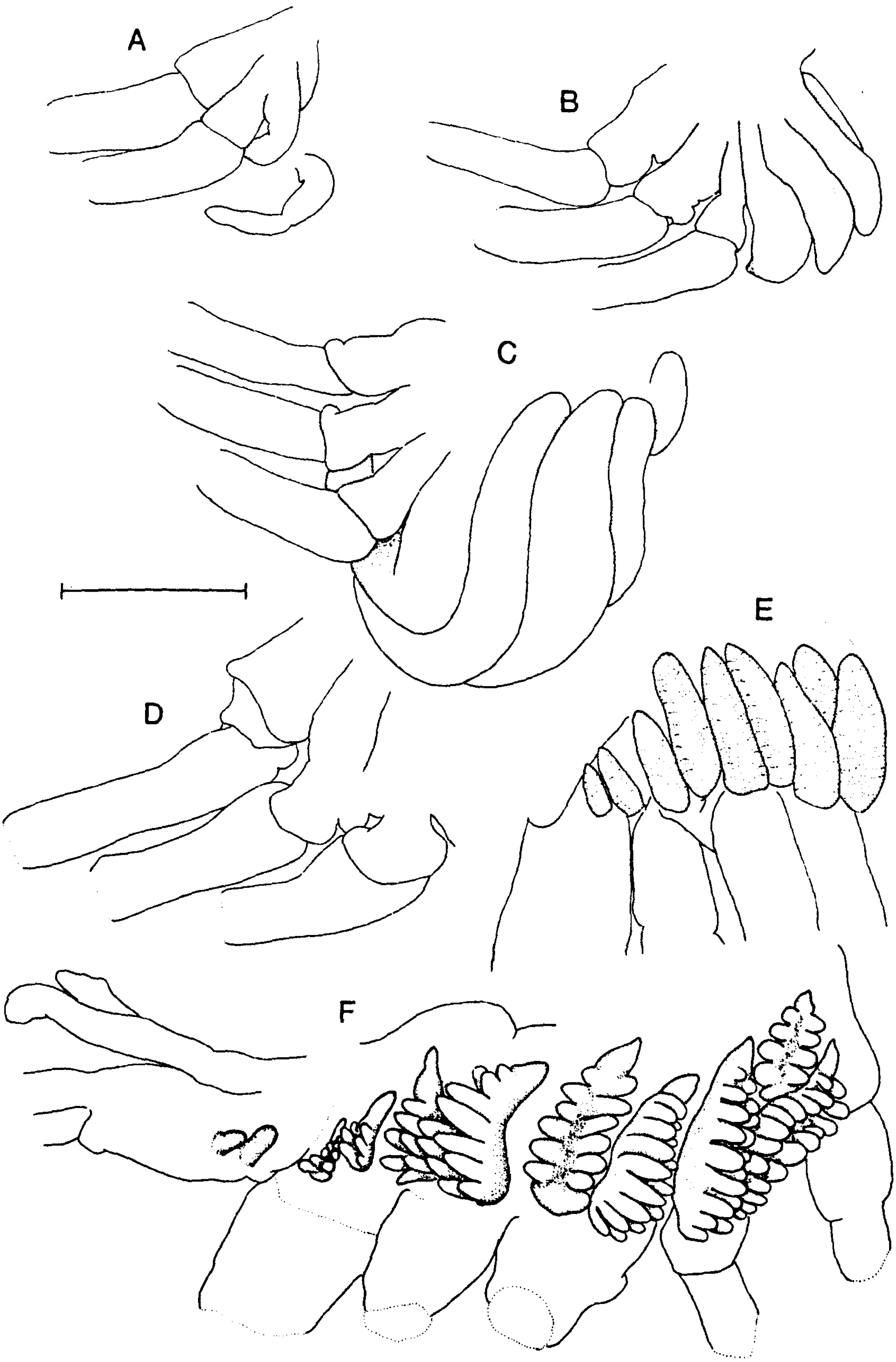

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Fig. 23. *Inachus dorsettensis* (Pennant), Development of gills A-D, first zoea: A, first maxilliped; B, second maxilliped; C, third maxilliped; D, maxillipeds and legs; E-H, second zoea: E, first maxilliped; F, second maxilliped; G, third maxilliped; H, legs; I-L, megalopa: I, first maxilliped; J, second maxilliped; K, third maxilliped, L, third maxilliped and thoracic pleura; M-P, first crab: M, first maxilliped; N, second maxilliped; O, third maxilliped; P, third maxilliped and thorax. Scale = 0.25 mm


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Fig. 24. *Hyas araneus* (Linnaeus), Development of gills

A-D, First zoea: A, first maxilliped; B, second maxilliped; C, third maxilliped; D, maxillipeds and legs; E-H, second zoea: E, first maxilliped; F, second maxilliped; G, third maxilliped; H, maxillipeds and legs; I-L, megalopa: I, first maxilliped; J, second maxilliped; K, third maxilliped; L, thorax. Scale = 0.50 mm

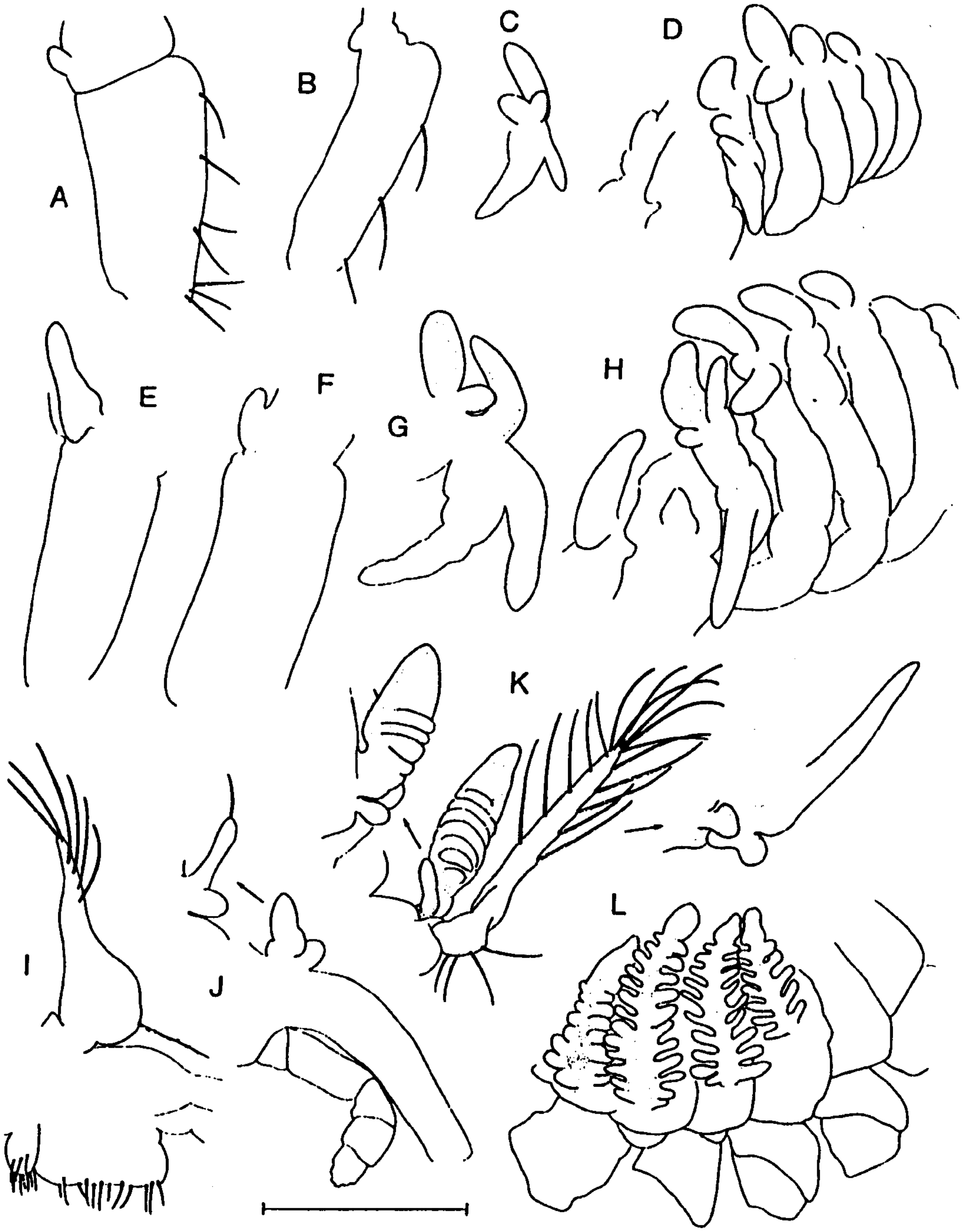

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Fig. 25. *Eurynome aspera* (Pennant), Development of gills

A-B, first zoea: A, maxillipeds and legs; B, third maxilliped; C-D, second zoea: C, maxillipeds and legs: D, third maxilliped; E-I, megalopa; E, first maxilliped; F, second maxilliped; G, third maxilliped; H, podobranch bud of third maxilliped; I, maxillipeds and thorax. Scale = 0.10 mm


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Fig. 26. *Pisa armata* (Latreille), Development of gills

A, first zoea; B, second zoea; C-F, megalopa: C, epipod of first maxilliped; D, second maxilliped; E, third maxilliped; F, maxillipeds and legs; G-J, first crab: G, first maxilliped; H, second maxilliped; I, third maxilliped; J, maxillipeds and thorax showing arthrobranch bud and arthrobranch of third maxilliped and two arthrobranchs and two pleurobranchs of legs. Scale = 0.25 mm

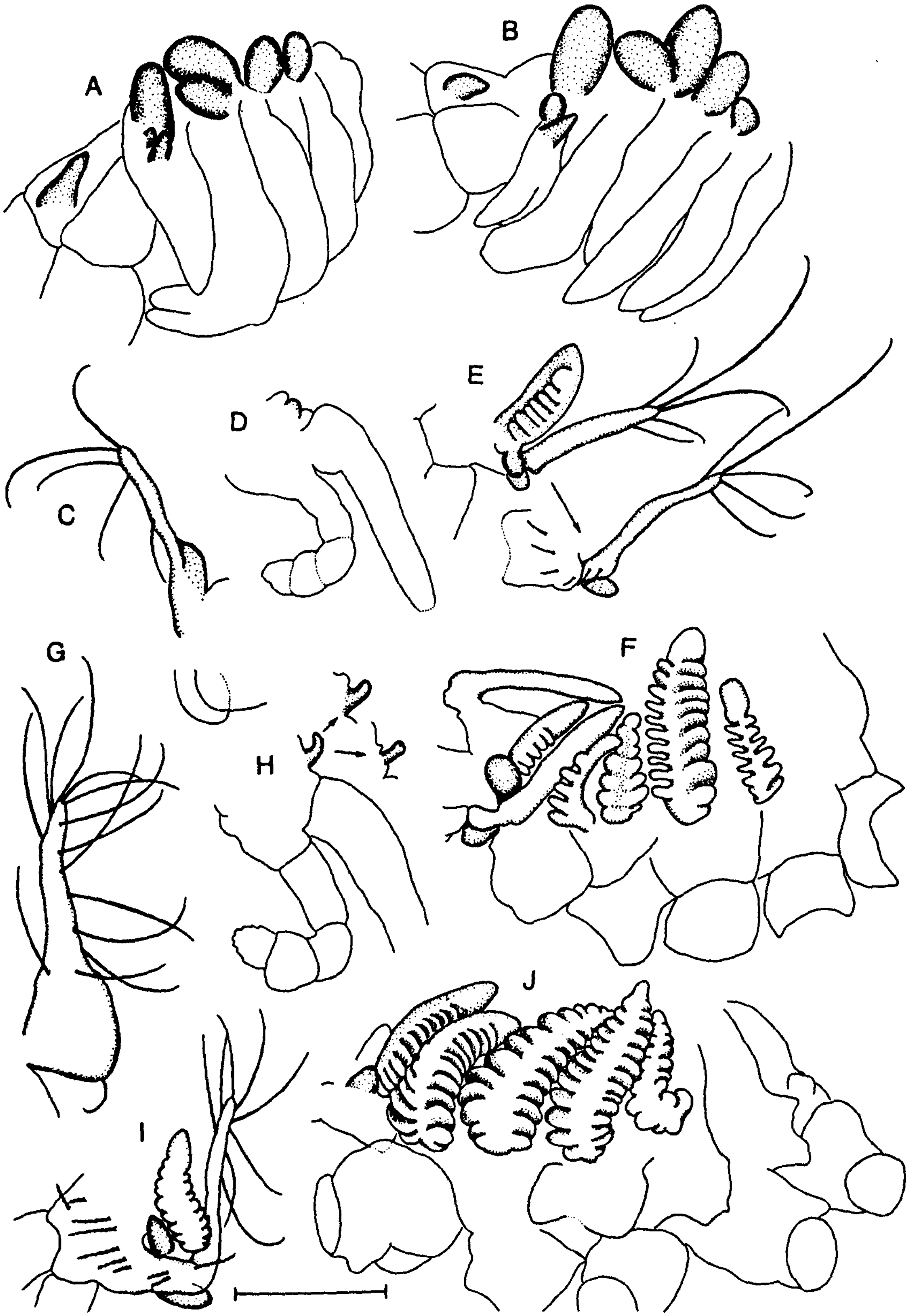
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Fig. 27. ***Atelecyclus rotundatus*** (Olivi), Development of gills A-B, maxillipeds and legs: A, first zoea; B, second zoea; C-F, third zoea: C, first maxilliped; D, second maxilliped; E, third maxilliped; F, legs; G-J, fourth zoea: G, first maxilliped; H, second maxilliped; I, third maxilliped; J, legs; K-N, fifth zoea: K, first maxilliped; L, second maxilliped; M, third maxilliped; N, legs; O-T, megalopa: O, first maxilliped; P, second maxilliped; Q, third maxilliped; R, first leg; S, second leg; T, third leg. Scale = 0.50 mm


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Fig. 28. *Carcinus maenas* (Linnaeus), Development of gills A-D, maxillipeds and legs: A, first zoea; B, second zoea; C, third zoea; D, fourth zoea; E-H, megalopa: E, first maxilliped; F, second maxilliped; G, third maxilliped; H, thorax. Scale = 0.25 mm

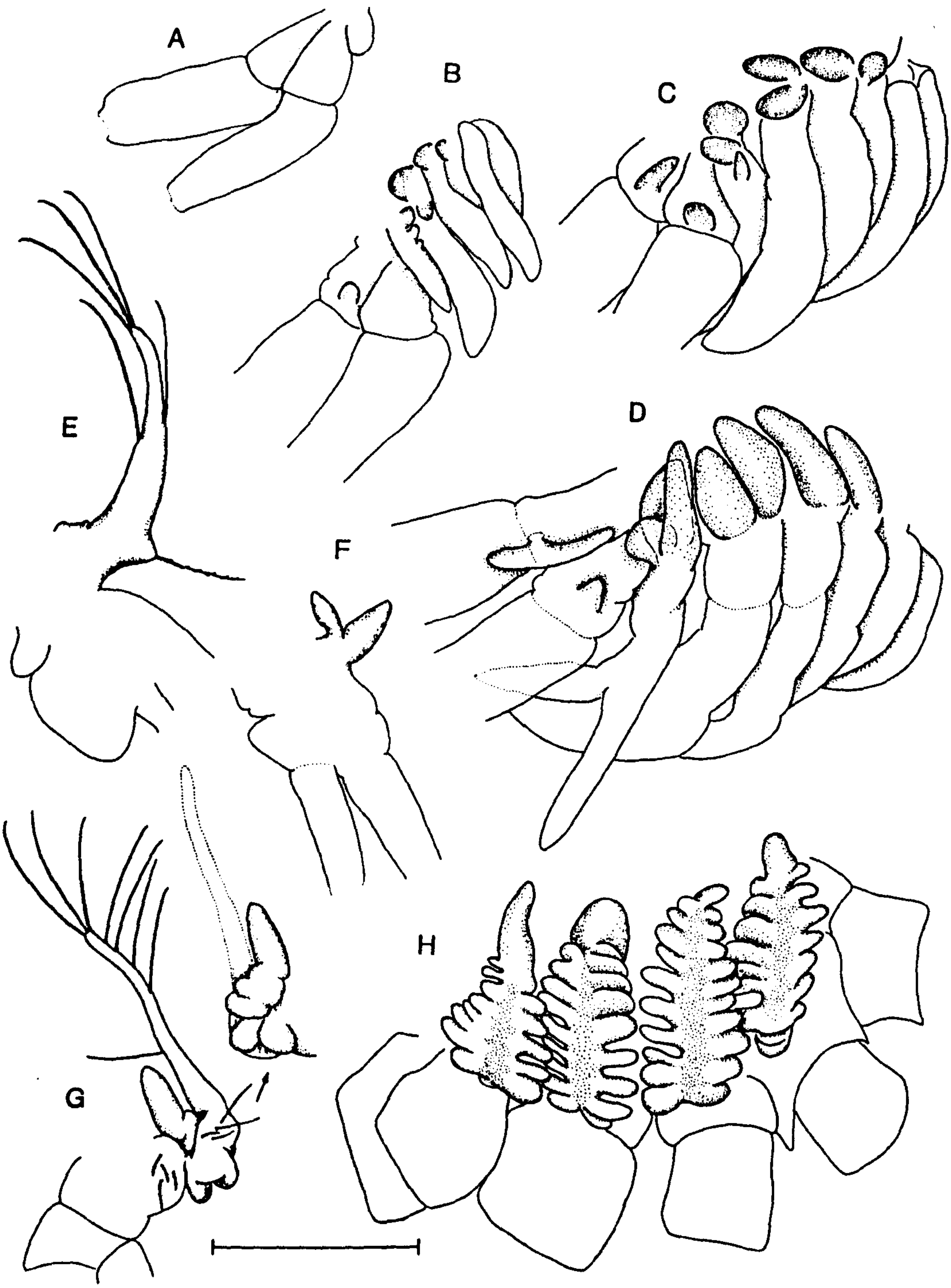
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Fig. 29. *Carcinus maenas* (Linnaeus), Development of gills A-D, first crab: A, first maxilliped; B, second maxilliped; C, third maxilliped; D, podobranch and posterior arthrobranch of third maxilliped and gills of legs; E-H, second maxilliped showing development of podobranch, epipod and arthrobranch; E, second crab; F, third crab; G, fourth crab; H, fifth crab. Scale = 0.25 mm

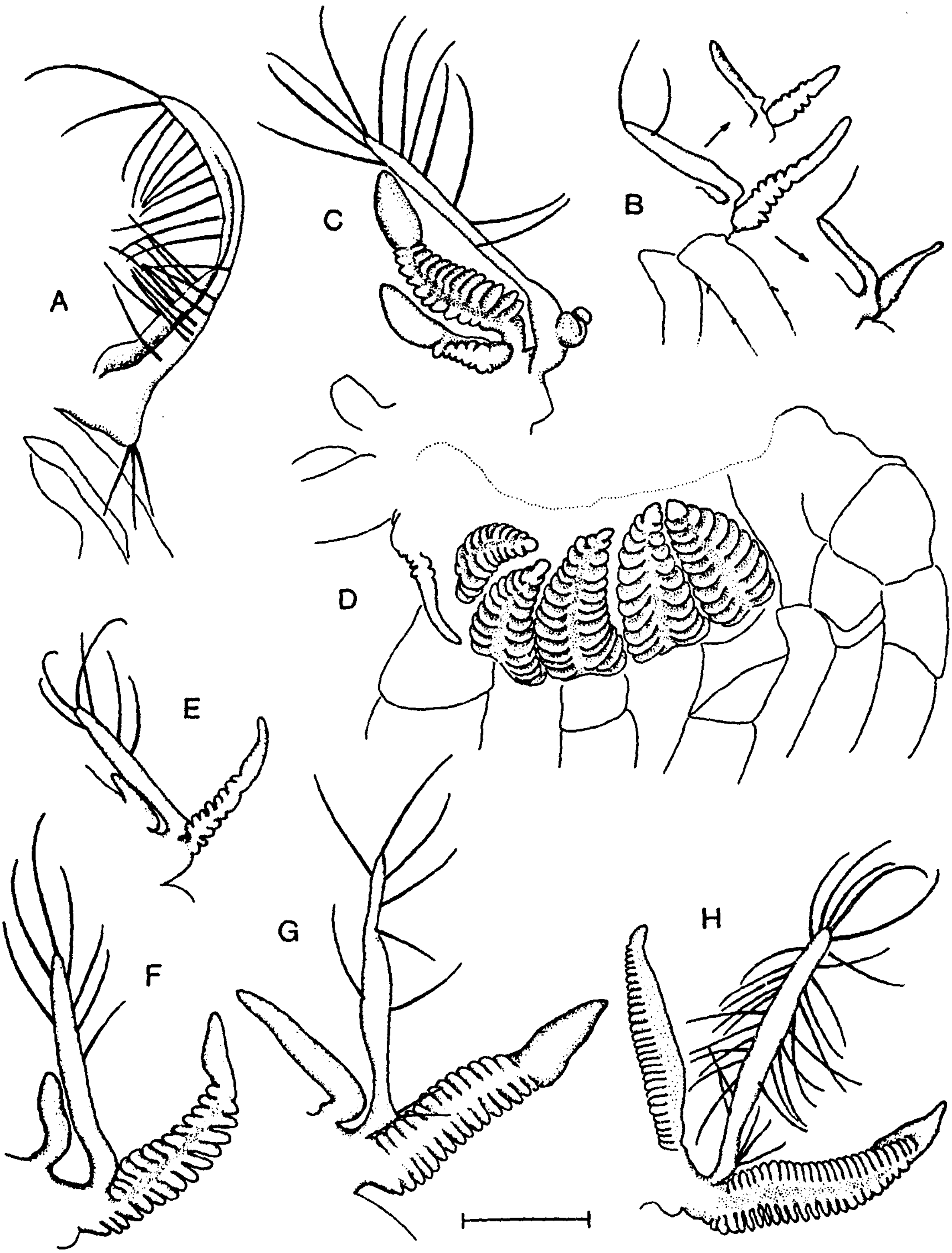
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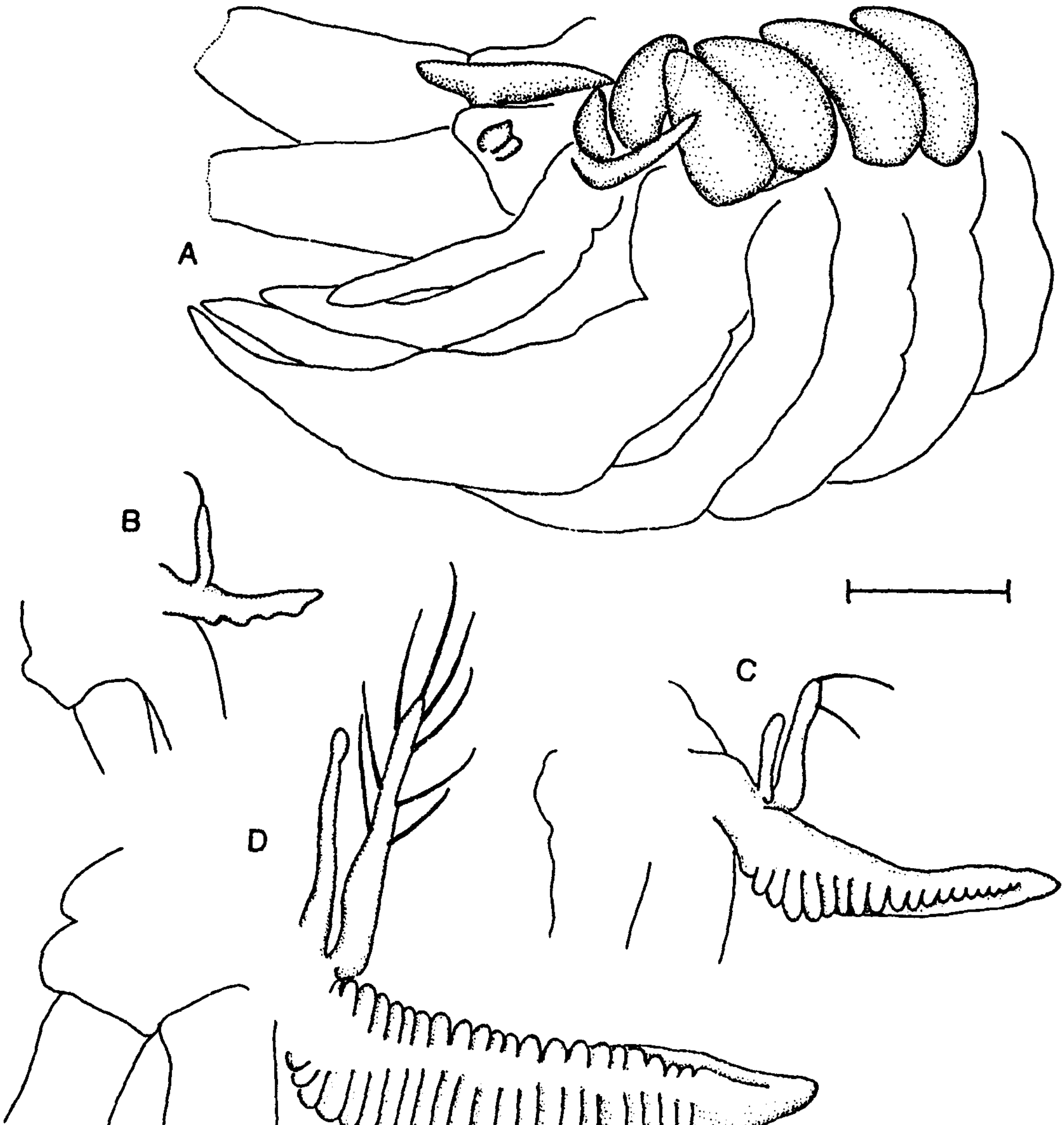
Fig. 30. *Liocarcinus corrugatus* (Pennant), Development of gills

A-D, maxillipeds and legs: A, first zoea; B, second zoea; C, third zoea; D, fourth zoea; E, fifth zoea; F-I, megalopa: F, first maxilliped; G, second maxilliped; H, third maxilliped; I, maxillipeds and thorax. Scale = 0.25 mm

Fig. 31. *Liocarcinus holsatus* (Fabricius), Development of gills

A, maxillipeds and legs of fifth zoea; B-D, second maxillipeds showing development of podobranch, epipod and arthrobranch bud. B, megalopa; C, first crab; D, second crab. Scale = 0.25 mm


A
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C
D

Fig. 32. *Pilnumnus hirtellus* (Linnaeus), Development of gills. A-G, maxillipeds and legs: A, first zoea; B, third maxilliped of first zoea; C, second zoea; D, third zoea; E, third maxilliped of third zoea; F, fourth zoea; G, third maxilliped of fourth zoea, H-K, megalopa: H, first maxilliped; I, second maxilliped; J, third maxilliped; K, third maxilliped and thorax. Scale = 0.50 mm

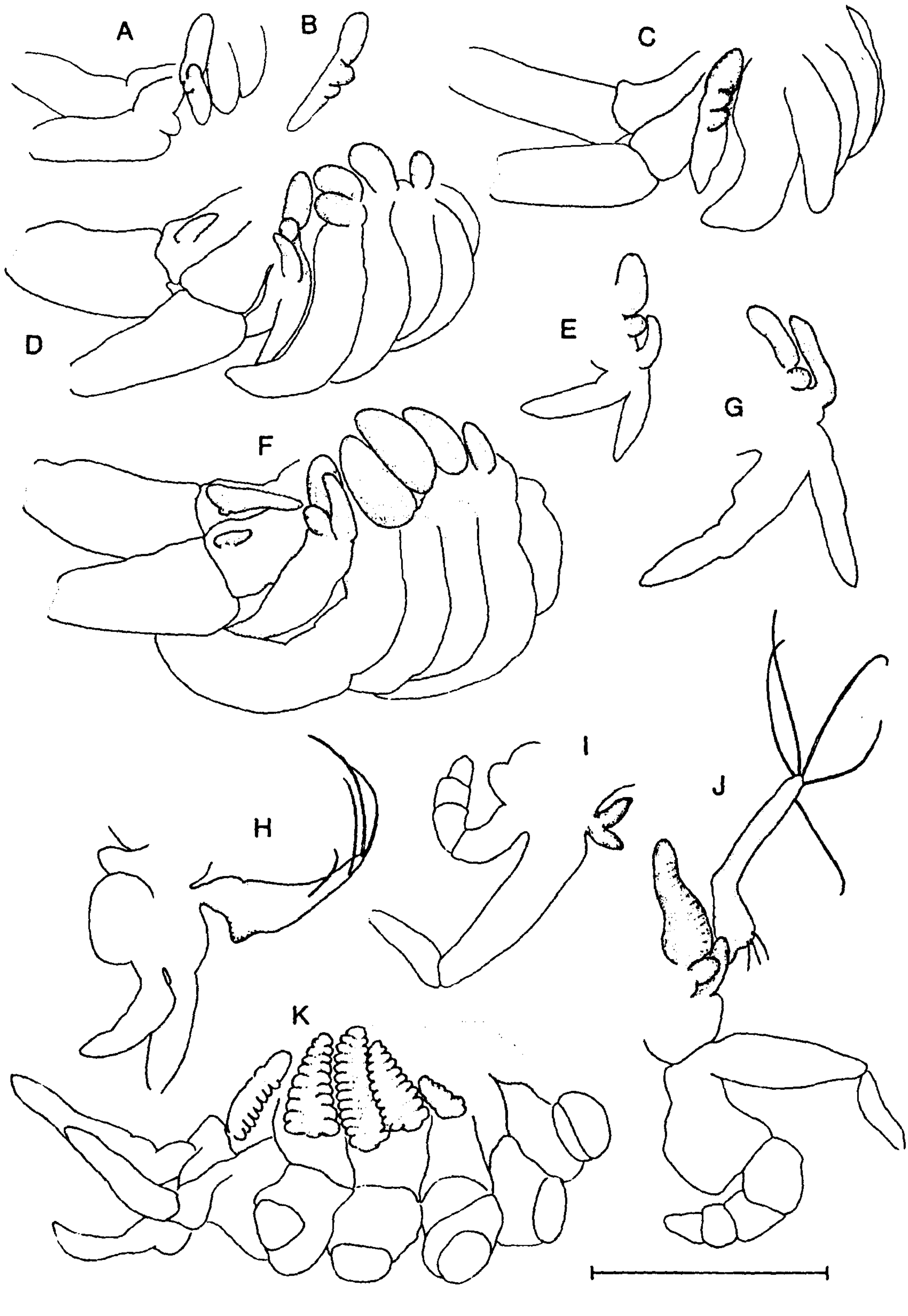
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Fig. 33. *Monodaeus couchi* (Couch), Development of gills

A-E, maxillepeds and legs: A, first zoea; B, second zoea; C, first leg bud of second zoea; D, third zoea; E, fourth zoea; F-I, megalopa: F, first maxilliped; G, second maxilliped; H, third maxilliped; I, thorax; J-L, first crab: J, first maxilliped; K, second maxilliped; L, third maxilliped. Scale = 0.25 mm

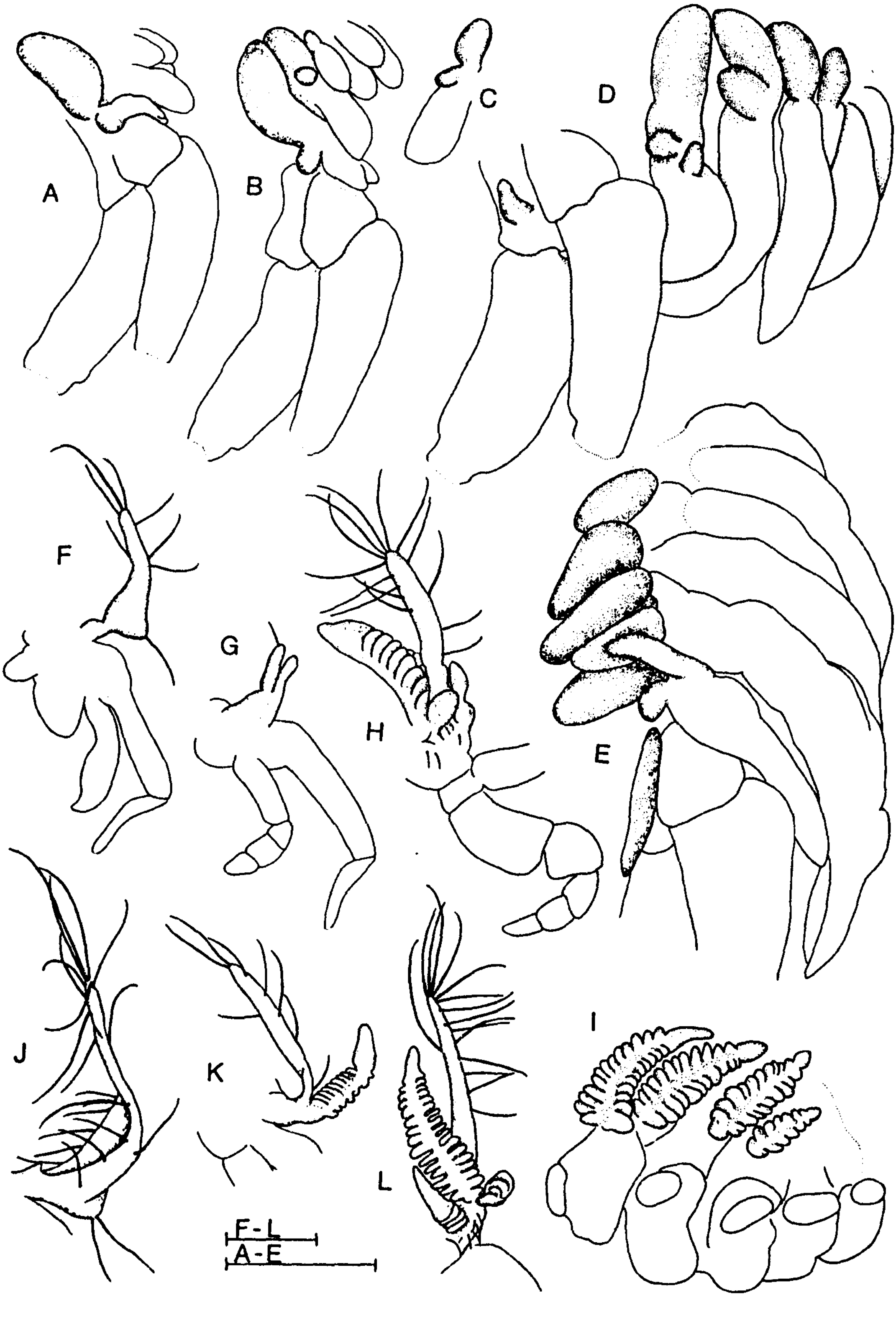
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Fig. 34. *Pinnotheres pinnothers* (Linnaeus), Development of gills

A-C, first zoea: A, first maxilliped; B, third maxilliped; C, maxillipeds and legs; D-F, second zoea: D, first maxilliped; E, third maxilliped; F, maxillipeds and legs; G-I, megalopa: G, first maxilliped; H, third maxilliped; I, thorax showing two arthrobranchs on first leg. Scale = 0.20 mm

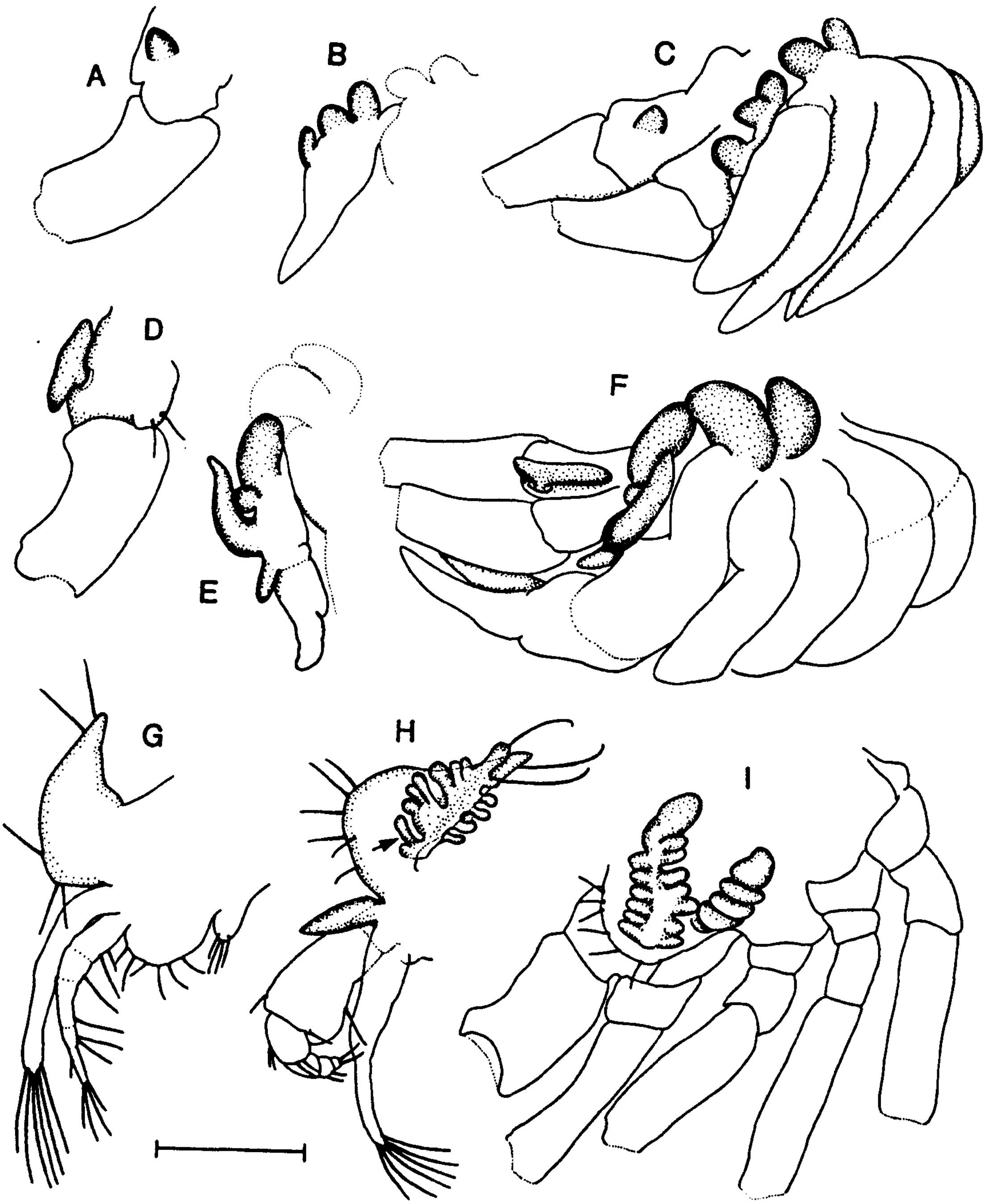
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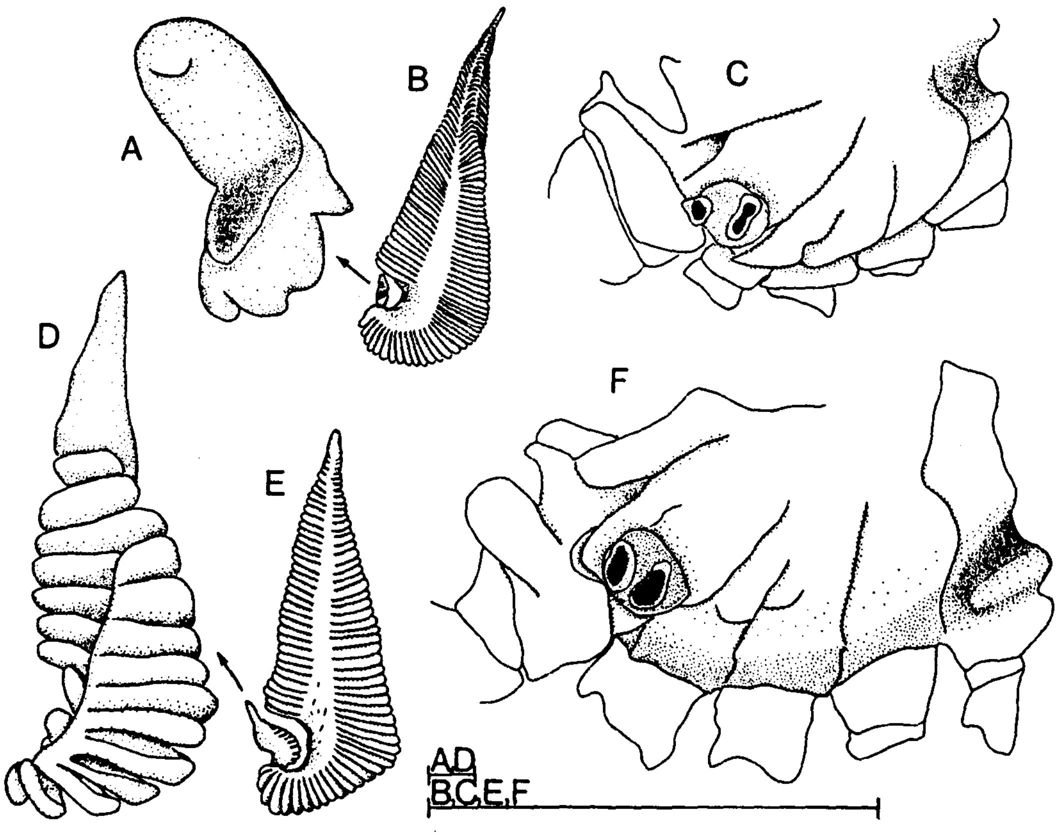
Fig. 35. Gills of adult pinnotherids.

A-C, *Pinnotheres pinnotheres* (Linnaeus), adult female, carapace length: 6.50 mm: A, anterior arthrobranch of third maxilliped; B, anterior and posterior arthrobranchs of third maxilliped; C, thoracic pleura showing the position of attachment of arthrobranchs of first leg; D-F, *Pinnotheres pisum* (Linnaeus), adult female, carapace length: 8.60 mm: D, anterior arthrobranch of third maxilliped; E, anterior and posterior arthrobranchs of third maxilliped; F, thoracic pleura showing the position of attachment of arthrobranchs of first leg. Scales = 0.50 mm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B,C,E,F

Fig. 36. *Pinnotheres pisum* (Linnaeus), Development of gills A-H, maxillipeds and legs: A, first zoea; B, second zoea; C, third zoea; D, fourth zoea; E-F, third maxilliped of fourth zoea; G, fifth zoea; H, third maxilliped of fifth zoea; I-L, megalopa: I, first maxilliped; J, second maxilliped; K, third maxilliped; L, maxillipeds and thorax showing three gills including arthrobranch of third maxilliped and two arthrobranchs of first leg. Scale = 0.20 mm


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Fig. 37. *Pinnaxodes mutuensis* Sakai, Development of gills

A-E, maxillipeds and legs: A, first zoea; B, second zoea; C, third zoea; D, fourth zoea; E, third maxilliped of fourth zoea; F-K, megalopa: F, first maxilliped; G, second maxilliped; H, third maxilliped; I, J, lamellated posterior arthrobranch and bud of future anterior arthrobranch (indicated by arrows) of third maxilliped; K, third maxilliped and thorax showing epipod (partially obscured), posterior arthrobranch of third maxilliped and two arthrobranchs of first leg; L-O, first crab: L, first maxilliped; M, second maxilliped; N, third maxilliped showing anterior arthrobranch (indicated by arrow) at base of posterior arthrobranch; O, thorax showing epipod (partially obscured), arthrobranchs of third maxilliped and two arthrobranchs of first leg (arrow indicates anterior arthrobranch of third maxilliped); P-Q, adult: anterior and posterior arthrobranchs of third maxilliped. Scales = 0.50 mm

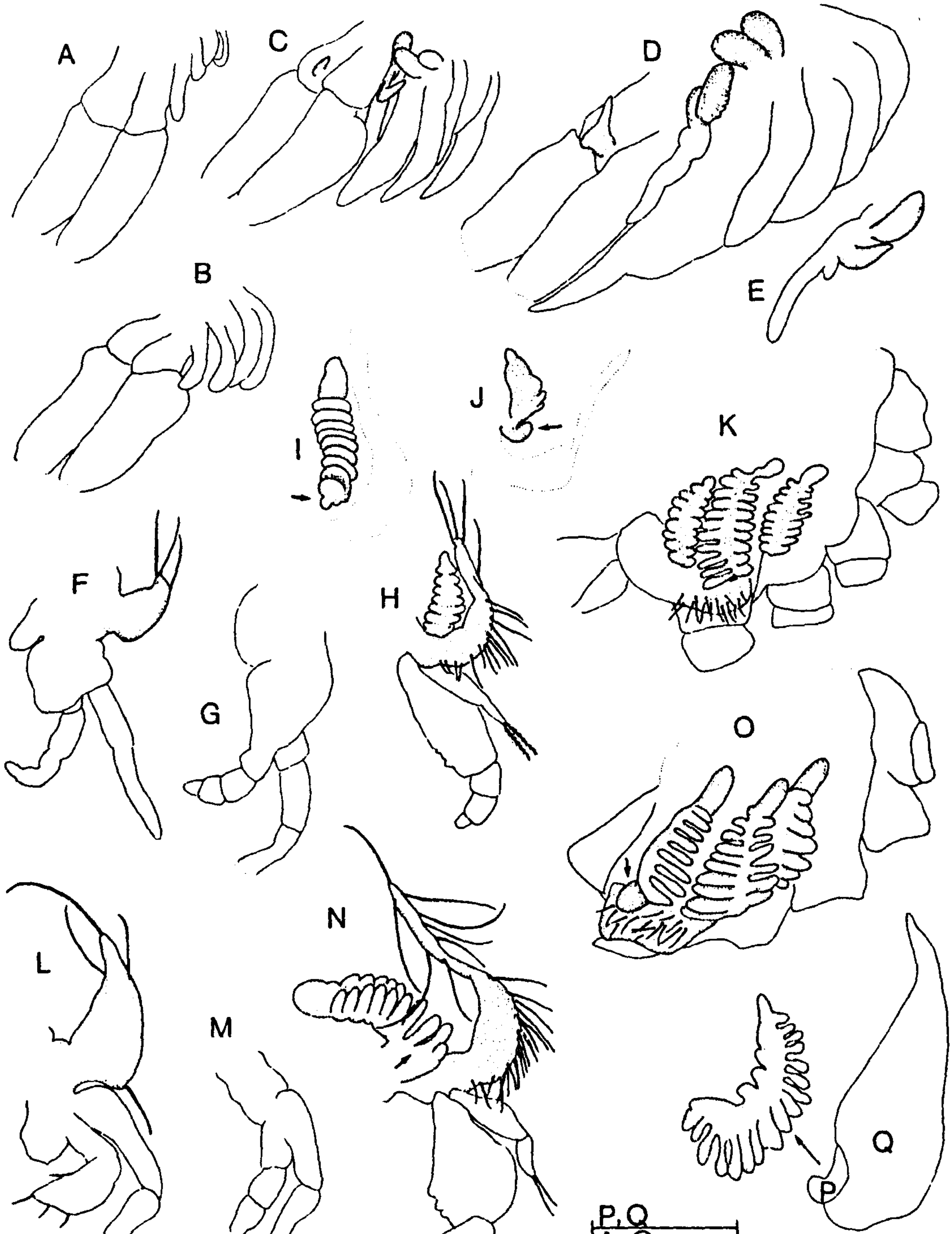
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Fig. 38. *Pinnixa rathbuni* Sakai Development of gills

A-E, maxillipeds and legs: A, first zoea; B, second zoea; C, third zoea; D, fourth zoea; E, third maxilliped of fourth zoea; F-H, fifth zoea: F, first maxilliped; G, third maxilliped; H, maxillipeds and legs; I-L, megalopa: I, first maxilliped; J, second maxilliped, K, third maxilliped, L, adult female, arthrobranchs of third maxilliped and first leg. Scales = 0.25 mm

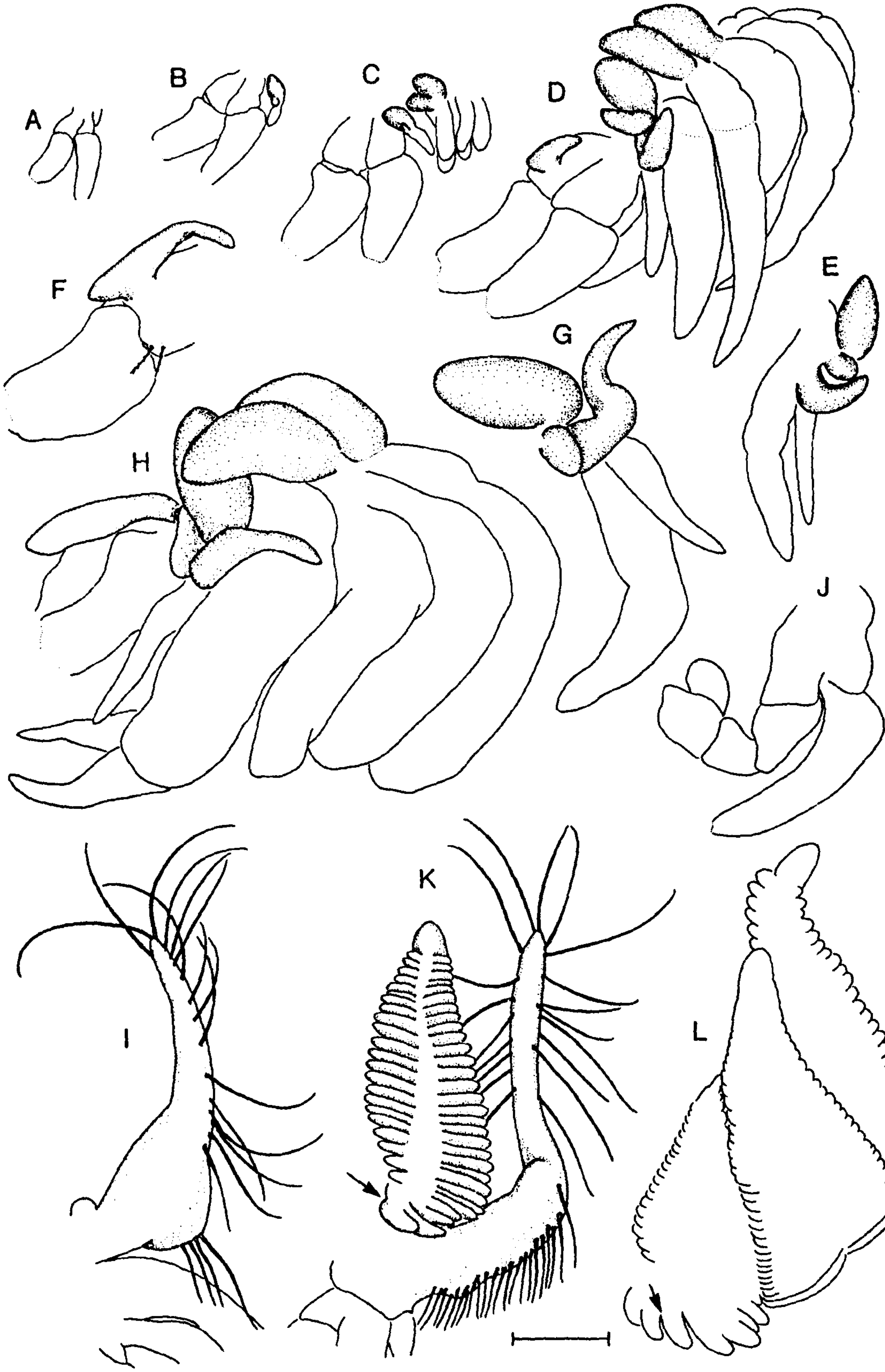
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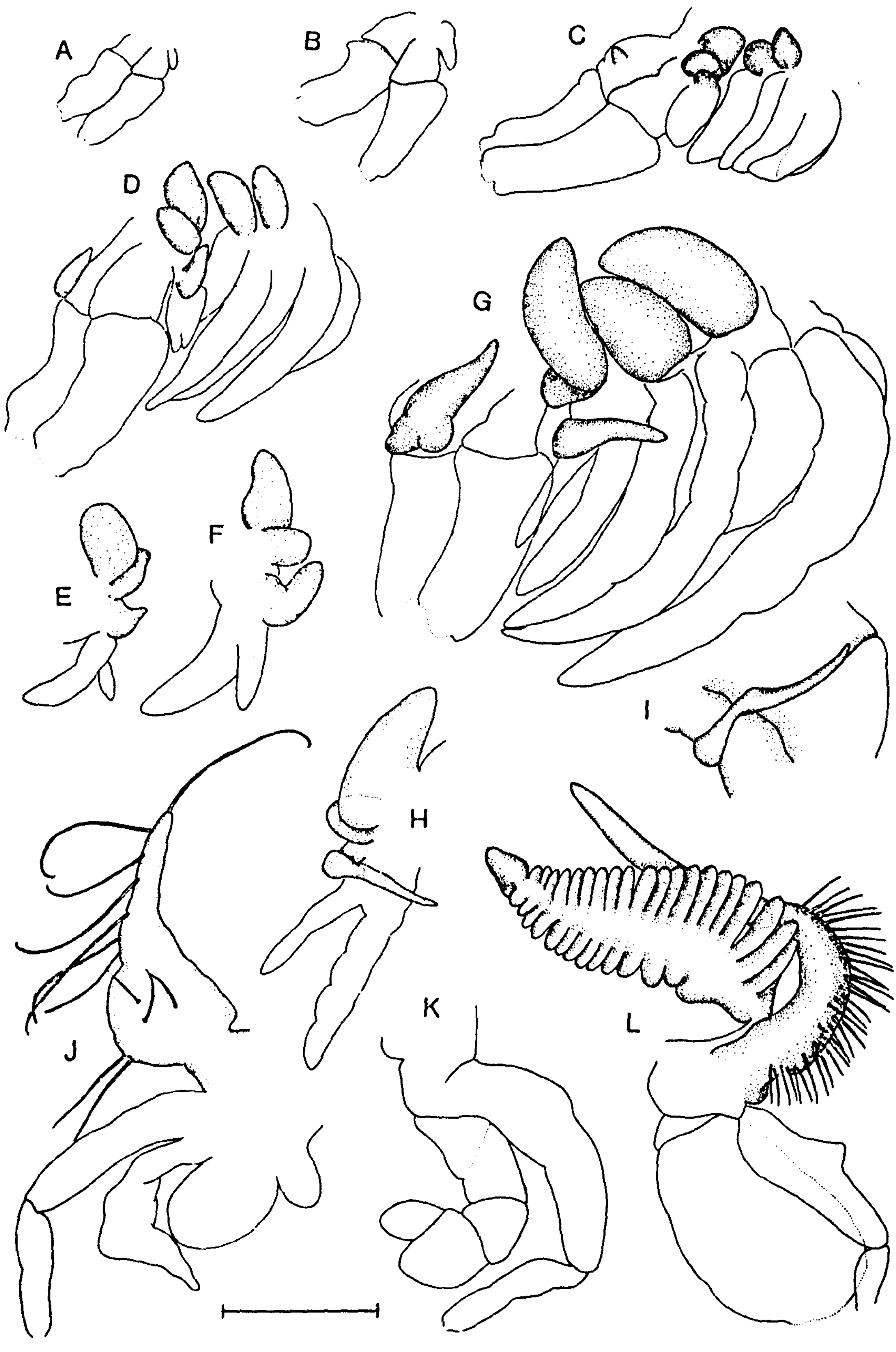
Fig. 39. ***Pinnixa (?)chaetopterana*** Stimpson, Development of gills

A-I, maxillipeds and legs: A, first zoea; B, second zoea; C, third zoea; D, fourth zoea; E-F, third maxillipeds of fourth zoea; G, fifth zoea: H-I, third maxillipeds of fifth zoea; J-L, megalopa: J, first maxilliped; K, second maxilliped; L, third maxilliped. Scale = 0.25 mm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CHAPTER 4

LARVAL DEVELOPMENT OF PETALOMERA JAPONICA (HENDERSON) (DECAPODA: DROMIIDAE) REARED IN THE LABORATORY

(This chapter has been published in Journal of Natural History, 20: 1259-1278.)

INTRODUCTION

Petalomera japonica (Henderson) is occasionally found around the Korean coast, northern China and Japan, from the subtidal region to a depth of about 150 m on mud or sand or rocky bottoms. It carries sponges or shells on its carapace. In Korea and neighbouring waters, more than 30 species of Dromiidae representing 8 genera have been reported (Sakai, 1936, 1976; Takeda and Miyake, 1970; Kim, 1973; Kim and Kim, 1982), but larval development has been described for only two of these species. Sankolli and Shenoy (1967) described the reared larvae of *Conchoecetes artificiosus* from Indian waters, and the larvae of *Petalomera wilsoni* have been described by Wear (1970 a, 1977) based on hatched larvae and plankton samples collected in New Zealand waters.

Montgomery (1922) and Hale (1925) reported direct development of *Petalomera lateralis* from Australia.

The purpose of the present study is to describe the complete larval stages of *P. japonica* reared in the laboratory and to compare these with other known dromiid larvae, particularly those of *P. wilsoni*.

MATERIALS AND METHODS

On 25th September 1984, a local fisherman caught 3 berried female crabs of *Petalomera japonica* in gill nets on a rocky bottom at a depth of 10-20 m in the vicinity of Haewundae (35° 10' Lat. N; 129° 10' Long. E), Korea.

They were brought to the laboratory within 10 minutes, and were kept in a container standing in running sea water. On 5th October more than 230 larvae hatched from 1 female crab. Of these, 70 larvae were individually reared in glass bottles (0.1 litre capacity) which were placed on a tray of running sea water to maintain relatively constant temperature. Some larvae were kept in glass beakers (1 litre) for mass culture. During the rearing experiment sea water temperature in the laboratory fell from 19.5 °C to 15.0 °C (mean 16.4 °C) due to seasonal cooling, and salinity fluctuated between 32.00 ppt and 33.03 ppt (mean 32.58 ppt).

Larvae were fed with newly hatched *Artemia* nauplii. Moulting and mortality were checked daily, and the larvae were transferred to freshly prepared bottles.

Drawings of prezoea were made only with live specimens mounted in sea water; those of later stages were made with live specimens, preserved specimens and exuviae.

Larvae of *Petalomera wilsoni*, for comparison with *P. japonica*, were kindly lent by the National Museum of New Zealand, from the material deposited by Dr. R. G. Wear.

Measurements were based on 10 live specimens. Lateral carapace length (LCL) was measured from anterior margin of forehead to postero-lateral margin of carapace in the prezoea. In other stages LCL was measured from anterior tip of rostrum to postero-lateral margin of carapace; dorsal carapace length (DCL) from anterior tip of rostrum to postero-median margin of carapace. Total length (TL) was measured from anterior tip of rostrum to postero-median margin of telson excluding telson processes.

Specimens for SEM photography were preserved in 7% neutral formalin and cleaned with laboratory detergent solutions. After rinsing in distilled water, they were dehydrated through an alcohol series and critical point dried (POLARON E 3000 critical point drier) using CO_2. The specimens were glued on stubs, sputter coated (POLARON E 5100 sputter coating unit) with 60% Au/Pd, and then viewed with a PHILIPS 501 B Scanning Electron Microscope using an accelerating voltage of 7.2 K.V. or 15 K.V.

RESULTS

Development and duration of the larvae

Petalomera japonica hatched out as a short-lived prezoea, lasting 5-8 minutes, and subsequently passed through 2 zoeal stages and a megalopa (Table 2; Fig. 40). All the prezoeas moulted into 1st zoeas. Of the 70 larvae reared individually, 20 moulted to the megalopa stage. First crab stages were not obtained.

Table 2. Duration of each larval stage of *Petalomera japonica* at 15.0-19.5 °C (mean 16.4 °C) and 32.00-33.03 ppt (mean 32.58 ppt). No megalopa moulted, and 'duration' of megalopa refers to survival times

Larval stages	Duration of larval stages		
	Mean	Range	Number observed
Prezoea	--	5-7 min	20
Zoea 1	7.9 days	6-12 days	63
Zoea 2	9.8 days	9-11 days	20
Megalopa	23 days	9-65 days	20

Descriptions

Prezoea

(Fig. 41)

Size - LCL : 0.95 mm (0.94-0.97 mm)

Carapace (Fig. 41 A) - Newly hatched larvae covered by transparent prezoeal outer membrane. Carapace devoid of processes.

Antennule (Fig. 41 A, B) - Two terminal processes of unequal size with fine hairs; 4 small projections on larger process.

Antenna (Fig. 41 D) - Endopod with 1 small smooth subterminal process and 3 larger terminal processes with fine hairs; exopod with 11 unequal marginal processes with fine hairs.

Maxillule (Fig. 41 E) - A simple bud with slight lobations.

Maxilla (Fig. 41 F) - With 4 inner lobes (endites), 2 distal lobes (endopod) and an outer lobe (scaphognathite).

First Maxilliped (Fig. 41 G-I) - Biramous; endopod and exopod with 4 and 3 processes respectively, processes of exopod longer than those of endopod.

Second Maxilliped (Fig. 41 J-L) - Biramous; endopod and exopod with 3 processes, processes of exopod longer than those of endopod.

Third Maxilliped (Fig. 41 M) - Simple biramous bud.

Legs (Fig. 41 N) - Smooth buds.

Abdomen (Fig. 41 A, B) - No bumps or processes, showing outline of abdominal somites of 1st zoea.

Telson (Fig. 41 A, B) - With 7 pairs of marginal processes: outermost short and naked, all others fringed with marginal sub-processes but inner margin of 7th (innermost) process smooth except near tip; no distinct demarcations at point of attachment between main and sub-processes.

First Zoea

(Figs. 42-44)

Size - DCL : 1.46 mm (1.37-1.50 mm)

LCL : 1.67 mm (1.62-1.72 mm)

DTL : 2.71 mm (2.60-2.87 mm)

Colour - Orange red colour uniformly diffused over whole body surface except antennal exopod, antennal endopod and telson.

Carapace (Figs. 42 A, B; 43 A-C) - Surface ornamented with reticulate striations and some minute pores. Rostrum broad at base, almost parallel-sided for most of the length in lateral view; blunt tip reaching to end of antennular peduncle. Blunt dorso-median projection above eyes and small bump on postero-median margin of carapace. Distinct transverse groove behind eyes; faint transverse groove at about half length of carapace. A pair of dorso-median setae behind anterior groove (Fig. 42 A, B); row of 5 minute dorsal setae on each side in front of anterior groove (not shown in Fig. 42, but 2 inner setae visible in SEM photography, Fig. 43 B).

Eye (Figs. 42 A, B; 43 A) - Sessile, with front of immovable stalk level with middle of rostrum.

Antennule (Fig. 44 C) - Uniramous, with 6 terminal aesthetascs of varying size and 1 subterminal plumose seta.

Antenna (Fig. 45 D) - Endopod with 3 terminal and 1 subterminal plumose setae; exopod with 11, or rarely 12, plumose setae on inner and distal margin; outer margin and proximal part of inner margin with fine hairs.

Mandible (Fig. 44 E) - Left and right almost symmetrical; mandibular palp represented by a small bud.

Maxillule (Fig. 44 F) - Coxal endite with 12 denticulate setae; basial endite with 4 terminal cuspidate setae, 1 fused minute denticle and 3 subterminal setae; endopod 2-segmented: short proximal segment with 2 setae, longer distal segment with 2 subterminal and 4 terminal setae.

Maxilla (Fig. 44 G) - Proximal lobe of coxal endite with 10 denticulate setae, distal lobe with 4; proximal lobe of basial endite with 5 denticulate setae, distal lobe with 5. Endopod 2-segmented; short proximal segment with 3 denticulate setae, longer distal segment with 2 subterminal and 4 terminal setae. Scaphognathite with 30-32 plumose setae.

First Maxilliped (Fig. 44 H) - Coxa with 1 epipod and 3 denticulate setae; basis with 2, 3, 2, 3 medial denticulate setae; endopod 5-segmented with 3+0, 3+0, 1+0, 2+0, 4+1 inner denticulate and outer plumose setae, also fine outer hairs on segments 2 and 3; exopod with 4 plumose natatory setae.

Second Maxilliped (Fig. 44 I) - Coxa with 1 epipod and 1 denticulate seta; basis with 1, 1, 1, 2 medial denticulate setae; endopod 4-segmented with 3+0, 3+0, 2+0, 4+1 inner denticulate and outer plumose setae, also fine outer hairs on segments 2 and 3; exopod with 4 plumose natatory setae.

Third Maxilliped (Fig. 44 J) - Basis with 1 epipod; endopod unsegmented, with 3 terminal denticulate setae; exopod unarmed.

Legs (Fig. 44 K) - Unsegmented; 1st-3rd legs each with 2 gill buds, larger upright and smaller directed downward; 4th-5th legs each with 1 large upright gill bud only.

Abdomen (Figs. 42 A, B; 44 A, B) - Surface ornamented like carapace; 5 somites; 2nd, 3rd and 5th somites with a pair of lateral setae, 4th somite with a pair of dorsal setae.

Pleopods (Fig. 42 A) - Small biramous buds on 3rd to 5th somites.

Telson (Figs. 42 A, B; 43 D; 44 A, B) - Spatuliform with a V-shaped posterior median notch; pairs of plumose setae on posterior dorsal surface; 7 pairs of marginal processes; outermost process a minute articulated spine varying slightly in length between specimens, 2nd a slender plumose seta slightly less than half as long as 3rd and projecting inwardly from ventral margin of telson, 3rd to 7th all long plumose setae.

Second Zoea

(Figs. 42, 45)

Size - DCL : 1.75 mm (1.65-1.80 mm)

LCL : 2.00 mm (1.92-2.07 mm)

DTL : 3.25 mm (3.10-3.35 mm)

Colour - Similar to first stage.

Carapace (Fig. 42 C, D) - Cephalothorax more inflated than in first stage; second groove more distinct. Row of minute setae in front of anterior groove increased to 6 on each side.

Eye (Fig. 42 C, D) - Short movable stalk curves postero-laterally.

Antennule (Fig. 45 D) - Biramous; peduncle with 1 inner and 3 outer setae of varying size and 4 terminal aesthetascs; inner ramus naked and bud-like; outer ramus 2-segmented; proximal segment with 7 aesthetascs, distal segment with 6.

Antenna (Fig. 45 E) - Endopod unarmed and 2-segmented; exopod fringed with 21-24 plumose setae, including about 10 on outer margin (replacing fine hairs of first stage).

Mandible (Fig. 45 F) - Similar in form to first stage, mandibular palp larger.

Maxillule (Fig. 45 G) - Coxal endite with 13 denticulate setae; basial endite with 6 terminal cuspidate setae and 4 subterminal setae; endopod unchanged in form and setation.

Maxilla (Fig. 45 H) - Proximal lobe of coxal endite with 15 setae, distal lobe with 5 setae; proximal and distal lobes of basial endite with 6 setae each. Scaphognathite with 33 plumose setae.

First Maxilliped (Fig. 45 I) - Coxal epipod more elongated but setation unchanged; basis with 2, 3, 3, 3 medial denticulate setae; 5-segmented endopod with 3+1, 3+1, 1+1, 2+0, 4+1 inner denticulate and outer plumose setae; exopod with 7 plumose natatory setae.

Second Maxilliped (Fig. 45 J) - Coxa with 1 epipod and 2 denticulate setae; setation of basis unchanged; endopod now 5-segmented 3+1, 3+1, 0+1, 2+0, 4+1 inner denticulate and outer plumose setae; exopod with 7 plumose natatory setae.

Third Maxilliped (Fig. 45 K) - Coxa with 1 epipod and 2 gill buds; endopod now 5-segmented with 0, 0, 0, 2, 3 denticulate setae; exopod with 8 plumose natatory setae.

Legs (Fig. 45 L-P) - All segmented; 1st with 2 elongate gill buds and 1 epipod, 2nd with 1 small and 1 elongate gill buds, 3rd with 1 small branched and 1 elongate gill buds, 4th with 1 small and 1 elongate gill buds, and 5th with 1 elongate gill bud.

Abdomen (Figs. 42 C, D; 45 A) - Similar in form and setation to first stage.

Pleopods (Figs. 42 C; 45 B, C) - Biramous buds on 2nd to 5th somites, with exopods much larger than endopods; minute curved processes on endopods.

Telson (Figs. 42 C, D; 45 A) - An inner pair of smaller plumose setae added to give 8 pairs of posterior marginal processes.

Megalopa

(Figs. 43, E, F; 46-48)

Size - DCL : 2.00 mm (1.95-2.07 mm)

DTL : 3.11 mm (3.02-3.17 mm)

Colour - Orange red colour uniformly diffused over the whole body surface except antennular rami, antennal endopods, exopods and endopods of pleopods, and telson.

Carapace (Figs. 43 E, F; 46 A, B) - Longer than wide; dorsal surface densely covered with conical spines and bushy plumose setae except near posterior margin; gastric and cardiac region elevated; cervical, branchial and cardiac grooves distinct; rostrum declivated, spiny, with a spiny protuberance on each side; medial tubercles on central part of gastric region and on postero-median margin; posterior margin fringed with plumose setae.

Eye (Fig. 46 A, C) - Stalked with a few short spines and setae and a small tubercle.

Antennule (Fig. 47 D) - Biramous; peduncle 3-segmented; lower ramus 3-segmented with 1, 2, 3 terminal spines; upper ramus 6-segmented, with 0, 7 aesthetascs, 5 aesthetascs, 5 aesthetascs, 0, 1 spine and 1 spine.

Antenna (Fig. 47 E) - Coxa naked; basis with 1 fused spine and 4 setae; fused irregular outer distal projection represents exopod; endopod 9-segmented, with 4, 5, 1, 1, 0, 5, 0, 3, 4 setae.

Mandible (Fig. 47 F) - Cutting edges well-developed, not clearly divided into incisor and molar processes; mandibular palp 3-segmented, with 5 spines on distal segment.

Maxillule (Fig. 47 G) - Coxal endite with 16+3+3 spines, basial endite with 6+4+3+3 spines, outer margin with proximal group of 3 denticulate setae and distal group of 4 plumose setae; endopod with 3 inner and 2 terminal spines.

Maxilla (Fig. 47 H) - Proximal lobe of coxal endite with 8+6+13 spines, distal lobe with 2+3+6 spines; proximal lobe of basial endite with 4+3 spines, distal lobe with 9 spines; scaphognathite fringed with 54-56 plumose setae; endopod with 3 subterminal and 2 terminal setae.

First Maxilliped (Fig. 48 A) - All segments fused. Coxal endite with 10+5 spines; epipod triangular with minute proximal process; basial endite with 17+3+4 spines; endopod with 7 spines; exopod with 5 outer plumose setae, the tip with 3 minute processes.

Second Maxilliped (Fig. 48 B) - Fused coxa and basis with 10 inner spines and a biramous epipod: one branch naked and the other with 1 or more setae and minute tubercles; endopod 5-segmented with 4, 5, 1, 3, 5 denticulate spines; exopod 3-segmented, distal segment with 6 plumose natatory setae.

Third Maxilliped (Fig. 48 C) - Coxa and basis fused, with 3+5+3 inner spines; lobate gill on outer face directed dorsally and smaller smooth rudiment directed laterally; epipod directed dorsally and bearing 2 setae; 7 outer spines distal to base of epipod; endopod 5-segmented with 10, 15, 8, 10, 6 spines and numerous denticles; exopod 2-segmented, with 3 outer setae on proximal segment and 6 plumose natatory setae on distal.

Legs (Figs. 43 E; 48 D-H) - Robust; outer surface densely covered with conical spines and bushy plumose setae, like carapace; chelipeds (Fig. 48 D) equal in size, with 1 larger and 1 smaller gill buds (future arthrobranchs) and small rod-like epipod on coxa; 2nd and 3rd legs (Fig. 48 E, F) each with lobate developing pleurobranch and small biramous bud representing a future arthrobranch, dactylus with tapered tip; 4th leg (Fig. 48 G) with 1 pleurobranch and minute arthrobranch bud, propodus with distal spine which combines with tapered dactylus to form small chela; 5th leg (Fig. 48 H) subdorsal in position, a little bigger than 4th, with 1 pleurobranch bud, propodus with longer spine than on 4th, 3 long curved setae on dactylus.

Abdomen (Figs. 43 E; 46 A) - Six somites; dorsal surface densely spinous and hairy, like carapace.

Pleopods (Fig. 47 B, C) - Present on 2nd-5th abdominal somites, endopod small with minute curved processes, exopod fringed with 12-18 plumose natatory setae.

Uropod (Fig. 47 A) - Directed posteriorly, lateral to telson; endopod a minute simple bud not separated from protopod, exopod fringed with 14-15 plumose natatory setae.

Telson (Figs. 43 E; 46 A; 47 A, A') - Dorsal surface with some spines and setae; posterior margin strongly concave with a few small spines or rarely a few small plumose setae of varying size.

DISCUSSION

Based on his observations of the 2nd zoeal stage and the megalopa from plankton samples, Wear (1970 a, 1977) was almost certain that *Petalomera wilsoni* would have a 3rd zoea which "possesses characters such as a sixth abdominal segment separated from the telson and unsegmented uropods". However, the expected 3rd zoeal stage was not obtained in his plankton samples. Having found only two zoeal stages of *Petalomera japonica*, some specimens of *P. wilsoni* deposited by Wear (1970 a, 1977) in the National Museum of New Zealand were examined. It was found that the 2nd zoeas of *P. wilsoni* were on the average in intermediate premoult (Stage D_1 as defined by Drach, 1939; Drach and Tchernigovtzeff, 1967). Beginning of setal degeneration was clearly visible, particularly on the antennal scale, and newly growing tissues of the legs showed the formation of dactylar spines, other processes and gill development. Setal growth as a pattern of long stripes was observed in the pleopods. Interestingly, the 2nd zoeas showed the formation of uropods and zoeal telson beneath cuticle, which surely led Wear (1970 a, 1977) to expect another zoeal stage. However, asynchronous processes in different appendages of an individual larva are not uncommon in the decapod moult cycle, and morphogenesis of uropods appears to precede other morphological changes in, for example, *Crangon crangon* and *Galathea intermedia* (K. Anger, personal communication). Based on these examinations, we are of the opinion that Wear's 2nd zoeas of *P. wilsoni* were in the final zoeal stage, and we suggest that there would be later development of the rectangular megalopal telson after complete degeneration of all the major processes of the 2nd zoeal telson. Accordingly, we suggest that *P. wilsoni* has 2 zoeal stages and a megalopa, like *P. japonica*.

Descriptions of prezoeas of Dromiacea are very few. Cano (1893 b) presented a figure of the prezoea of *Dromia personata* (as *Dromia vulgaris*) but detailed descriptions of appendages and telson were lacking. Lebour (1934) described the prezoea of the same species. The antennule has 4 terminal and 1 lateral process, and the antennal scale has 10 processes which bear subprocesses. Based on the embryos detached from a preserved female, Rice (1981) described the larvae of *Acanthodromia erinacea* (Dynomenidae) which were in a pre-zoeal condition. He commented that the larval characters were anomuran, like those of dromiid larvae. Sankolli and Shenoy (1967) described the prezoea of *Conchoecetes artificiosus*, and Wear (1970 a) gave detailed descriptions of the prezoea of *P. wilsoni*. Table 3 includes comparative features of prezoeas of *P. wilsoni* and *P. japonica*.

The subprocesses on the telson processes are broad at base and without distinct demarcations at points of attachment in both *P. wilsoni* and *P. japonica*. In *C. artificiosus* all the telson processes are naked. Prezoeal telsons which bear subprocesses are also found in prezoeas of some true anomuran crabs, including *Porcellana longicornis* (described by Gurney, 1942), *Uroptychus* cf. *politus* (described by Pike and Wear, 1969), *Petrolisthes elongatus* and *Petrolisthes novaezelandiae* (described by Greenwood, 1965), and *Pagurus bernhardus*, *Pagurus prideauxi*, and *Munida rugosa* (Hong, unpublished). In the case of *P. elongatus* and *P. novaezelandiae*, even the processes of the antennule and antenna have such subprocesses, like those of the telson processes (see Chapter 2).

Comparative features of *P. wilsoni* and *P. japonica* are tabulated in Table 3. In the zoeal stages *P. japonica* can be easily distinguished from *P. wilsoni* by the presence of surface striations, by the absence of a dorsal spine and lateral expansions of carapace, and by the presence of paired setae on the dorsal surface of the telson. The larvae of *P. japonica* are smaller than those of *P. wilsoni* in each stage, and even the 2nd stage of *P. japonica* (TL: 3.10-3.35 mm) is smaller than the 1st stage of *P. wilsoni* (TL: 4.0-4.8 mm). Except in size, the megalopas of the two species are more or less similar in general appearance, but some important differences are also found in the telson, endopod of uropod and form of the hairy setae on the body surface. Larval characters would support placing *P. wilsoni* and *P. japonica* in different genera, but any such revision should await a re-examination of the adults.

Table 3. Differences between the larvae of *Petalomera wilsoni* (described by Wear, 1970 a, 1977) and *Petalomera japonica* (present study)

	Petalomera wilsoni	*Petalomera japonica*
General zoeal characters		
Carapace		
Surface	smooth	striated
Dorsal spine	present	absent
Lateral extensions	present	absent
Telson		
Dorsal setae	absent	present
Prezoea		
Antennule	3 plumose + 4 smooth	2 plumose + 4 smooth
Antennal exopod	8 plumose + 1 smooth	11 smooth
Telson	7 plumose	6 plumose + 1 smooth
First Zoea		
Carapace length	2.9-3.3 mm	1.6-1.8 mm
Total length	4.0-4.8 mm	2.6-2.9 mm
Maxillular endopod	2+4 setae	2+6 setae
Mandibular palp	absent	present
Second Zoea		
Carapace length	3.6-4.0 mm	1.9-2.1 mm
Total length	5.0-6.0 mm	3.1-3.4 mm
Second maxilliped endopod setae	3+1,3+1,1+1,2+1,4+1	3+1,3+1,0+1,2+0,4+1
Third maxilliped		
endopod setae	0,0,0,2,4	0,0,0,2,3
exopod setae	7	8
Megalopa		
Carapace length	3.5 (3.3-3.7)* mm	2.0 (1.9-2.1) mm
Total length	6.7* (6.5-6.9)* mm	3.1 (3.0-3.2) mm
Telson		
posterior margin	slightly concave	strongly concave
marginal processes	absent	present
Mandibular palp	0,0,8(or 9) setae	0,0,5 setae
First maxilliped epipod	fringed with long setae	naked

* Measured by the present author

A further important character in which our zoeal material of *P. japonica* differs from Wear's description of zoeas of *P. wilsoni* is the presence or absence of an outer seta on the maxillule. Such a seta is absent in both zoeal stages of *P. japonica*, but a large plumose seta was illustrated in the 2nd zoea but not 1st zoea of *P. wilsoni*. The condition in *P. japonica* agrees with that in all known dromiid larvae of other genera and in all known anomuran larvae, while the presence of a setae in the 2nd zoea and any subsequent zoeal stages but not in 1st zoea is typical of brachyuran larvae (Rice, 1980; Williamson, 1982). This apparent brachyuran character in the zoeal stages of *P. wilsoni* has been noted by several authors, but a re-examination of larvae of this species in the present work has failed to find the seta in question. It can only be suggested that the drawing of the maxillule of the 2nd zoea of *P. wilsoni* published by Wear (1970 a) is incorrect in this respect.

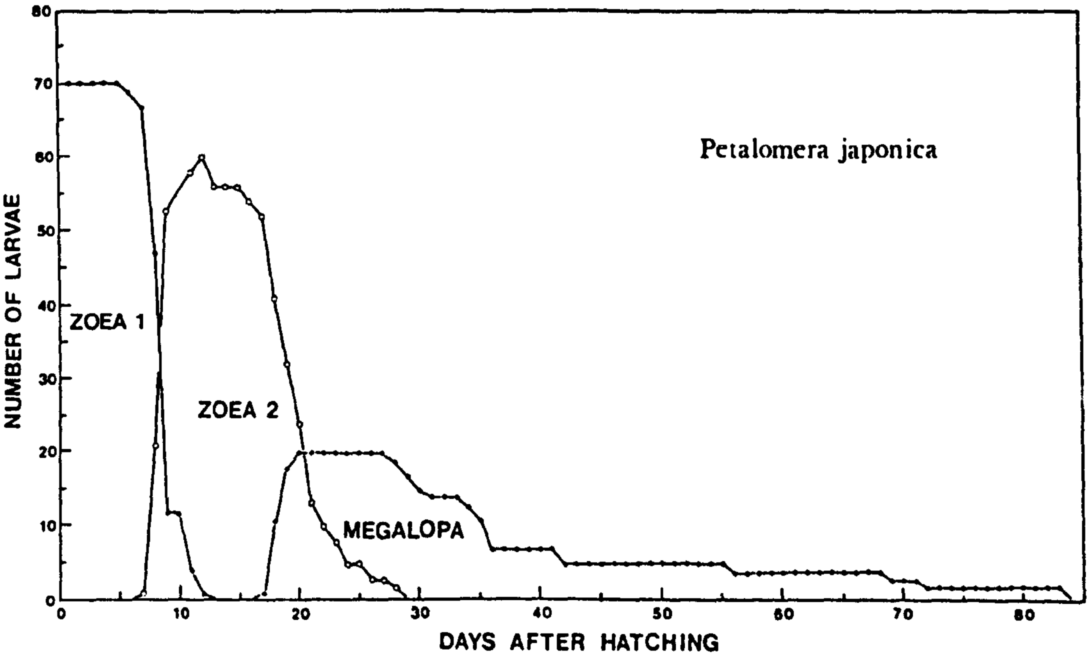
Unidentified larvae of 3 species of Dromiidae have been described from East Asian waters, but none of these belong to *P. japonica* or *P. wilsoni*. Boas (1880) described a late stage zoea and megalopa from the western part of the Yellow Sea, and he attributed them, probably correctly, to *Dromia*. Yokoya (1935) reported 2 specimens (TL: 4.0 mm, 5.5 mm) of zoeal stages of Dromiidae from southern Japan. These larvae have a minute dorsal spine and lateral extensions on the carapace, and they thus show some affinity with larvae of *P. wilsoni* and may represent another species of the same genus. They also have a pair of minute tubercles on the postero-lateral part of carapace. Gamo and Muraoka (1977) described a megalopa (CL: 2.08 mm) from plankton samples collected off southern Japan, and they attributed it to "*Petalomera* ? sp.". It is of similar size to the megalopa of *P. japonica*, but there are conspicuous differences in the form of the rostral region, and the armature of the legs is also different.

Based on the general resemblance of dromioid to anomuran larvae, many authors have suggested separation of the Dromioidea from the Homoloidea, Raninoidea and higher Brachyura, and linked them with the Anomura and Thalassinidea (Gurney, 1924 b, 1942; Kircher, 1970; Lebour, 1934; Pike and Williamson, 1960; Rice, 1980, 1983; Williamson, 1965, 1976, 1982). Of the common shared characters of Dromioidea and Anomura, Williamson (1965, 1976) attached particular importance to the reduced 2nd telson process in dromiid larvae. In the majority of known dromiid larvae in the 1st stage, this process is a plumose setae, about half the length and less than half the thickness of the 3rd process (Rice and Provenzano, 1966: *Dromidia antillensis;* Sankolli and Shenoy, 1967: *C. artificiosus;* Wear, 1970 a: *P. wilsoni;* present study: *P. japonica;* Lang and Young, 1980: *Hypoconcha sabulosa*). It is a naked hairlike process in *Dromia personata* (described by Rice, Ingle and Allen, 1970) and *Dromia erythropus* (by Laughlin, Rodríguez and Marval, 1982). In *Hypoconcha arcuata*, however, it is an unarmed hair in the 1st stage but a plumose seta in the 2nd stage (Kircher, 1970), and in *Cryptodromia pileifera* it is a minute vestigial knob (Tan, Lim and Ng, 1986). The 2nd process is reduced to varying degrees in larvae of the Thalassinidea and markedly reduced in larvae of the Stenopodidea and Anomura *(sensu stricto)*. In larvae of all the forementioned groups this process is typically in the form of a reduced setae or fine hair, in contrast to the condition in the Homoloidea and other Brachyura, in which it is a short spine or absent. Williamson (1965, 1976, 1982) and Rice (1980) suggested that the hair-like condition is a derived character, but Burkenroad (1981) argued that it is "a relic from the stem-form of the three incubatory suborders", Euzygida (Stenopodidea), Eukyphida (Caridea) and Reptantia. On this view, Rice (1983) questioned "why such a primitive feature should have become altered independently, and in much the same way, in several quite distinct groups". In relation to this, it is worthwhile to note that the 2nd telson process of dromiid prezoeas (Lebour, 1934; Wear, 1970 a; present study) are not modified in size and shape when compared to the inner telson processes. If prezoeal features reflect more primitive states than the zoea, then the reduced 2nd telson process of zoeal stages in the Dromiidae and Anomura would appear to be a derived character.

The anomuran affinities of dromiid zoeas and the brachyuran affinities of the corresponding adults leaves the true phylogeny of the group an unsolved paradox.

Fig. 40. ***Petalomera japonica***, (Henderson),

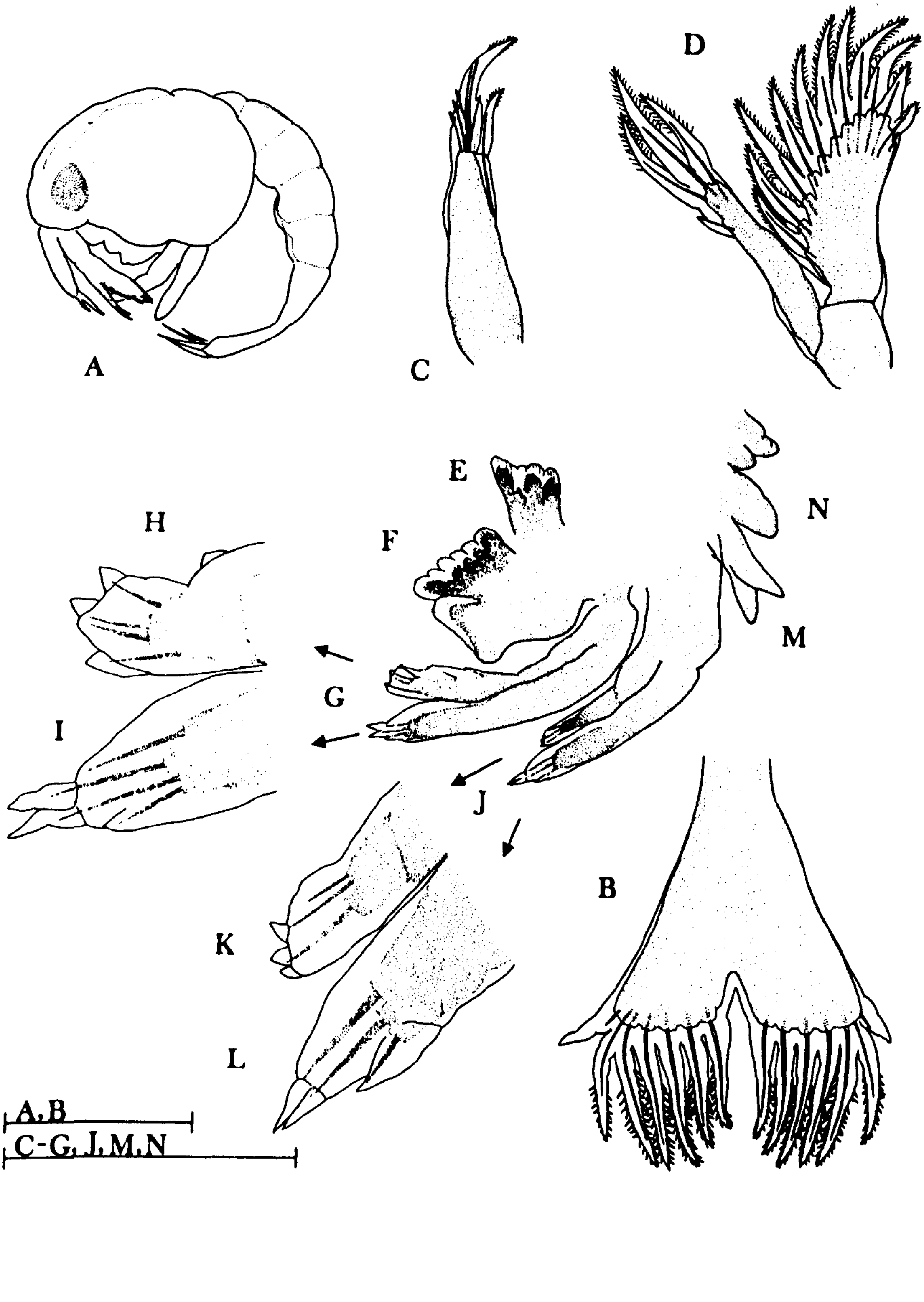
Survival and duration in stages of larvae reared under laboratory conditions of 15.0-19.5 °C (mean 16.4 °C) and 32.00-33.03 ppt (mean 32.58 ppt).



Petalomera japonica
NUMBER OF LARVAE
DAYS AFTER HATCHING
ZOEA 1
ZOEA 2
MEGALOPA
0
10
20
30
40
50
60
70
80

Fig. 41. *Petalomera japonica* (Henderson), Prezoea

A, lateral view; B, telson; C, antennule; D, antenna; E, maxillule; F, maxilla; G-I, first maxilliped, J-L, second maxilliped, M, third maxilliped; N, leg buds. Scales = 0.5 mm



A
B
C
D
E
F
G
H
I
J
K
L
M
N
A,B
C-G, J, M, N

Fig. 42. ***Petalomera japonica*** (Henderson), Zoeal stages

A, laterla view of first zoea; B, dorsal view of first zoea; C, lateral view of second zoea; D, dorsal view of second zoea. Scale = 0.5 mm

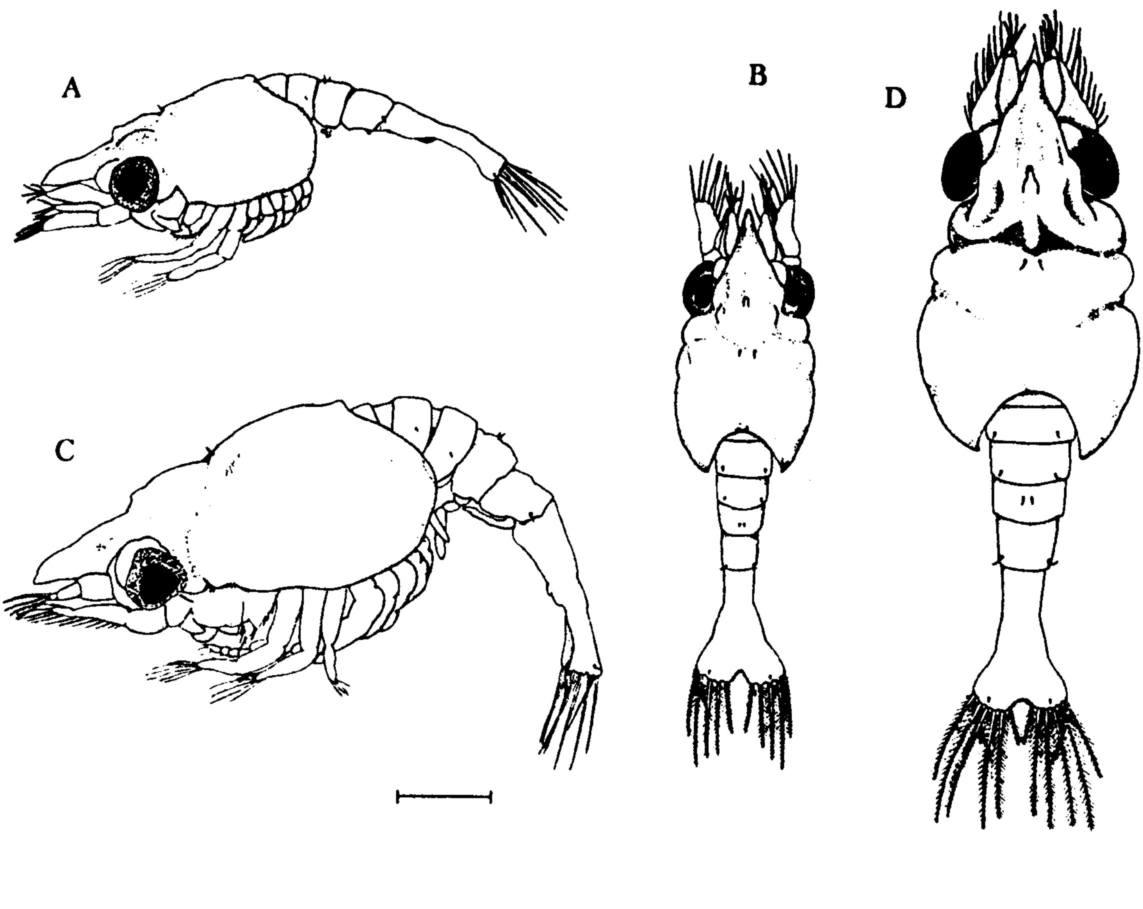

A
B
C
D

Fig. 43. *Petalomera japonica* (Henderson),

First zoea and Megalopa

A, dorsal view of carapace of first zoea (scale = 250 µm); B, dorso-median part of carapace of first zoea showing a median projection and 2 minute setae (scale = 50 µm); C, reticulate striations on the lateral surface of carapace of first zoea (scale = 5 µm); D, ventral view of the tip of telson of first zoea showing a minute outermost process and a slender plumose 2nd process (scale = 25 µm); E, lateral view of megalopa (scale = 500 µm); F, median tubercle on carapace of megalopa bearing conical spines and bushy plumose setae (scale = 50 µm).

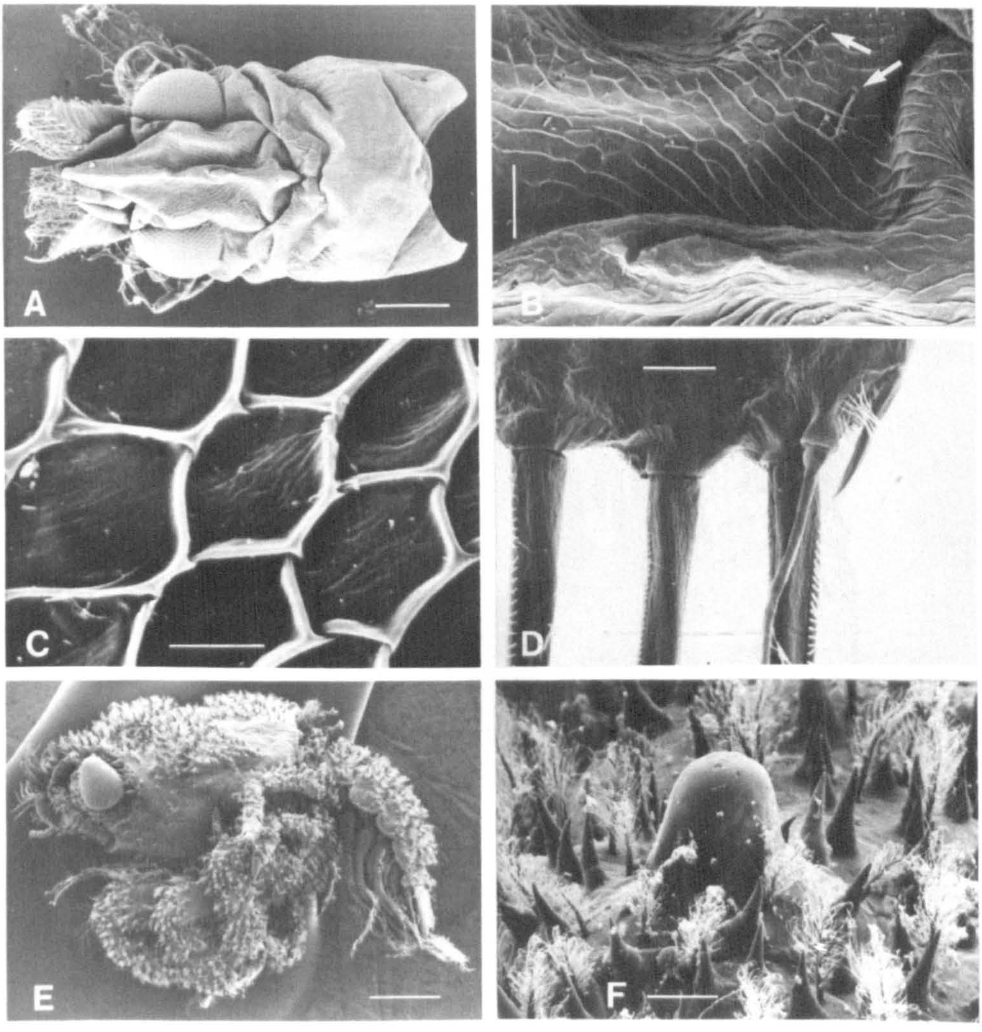
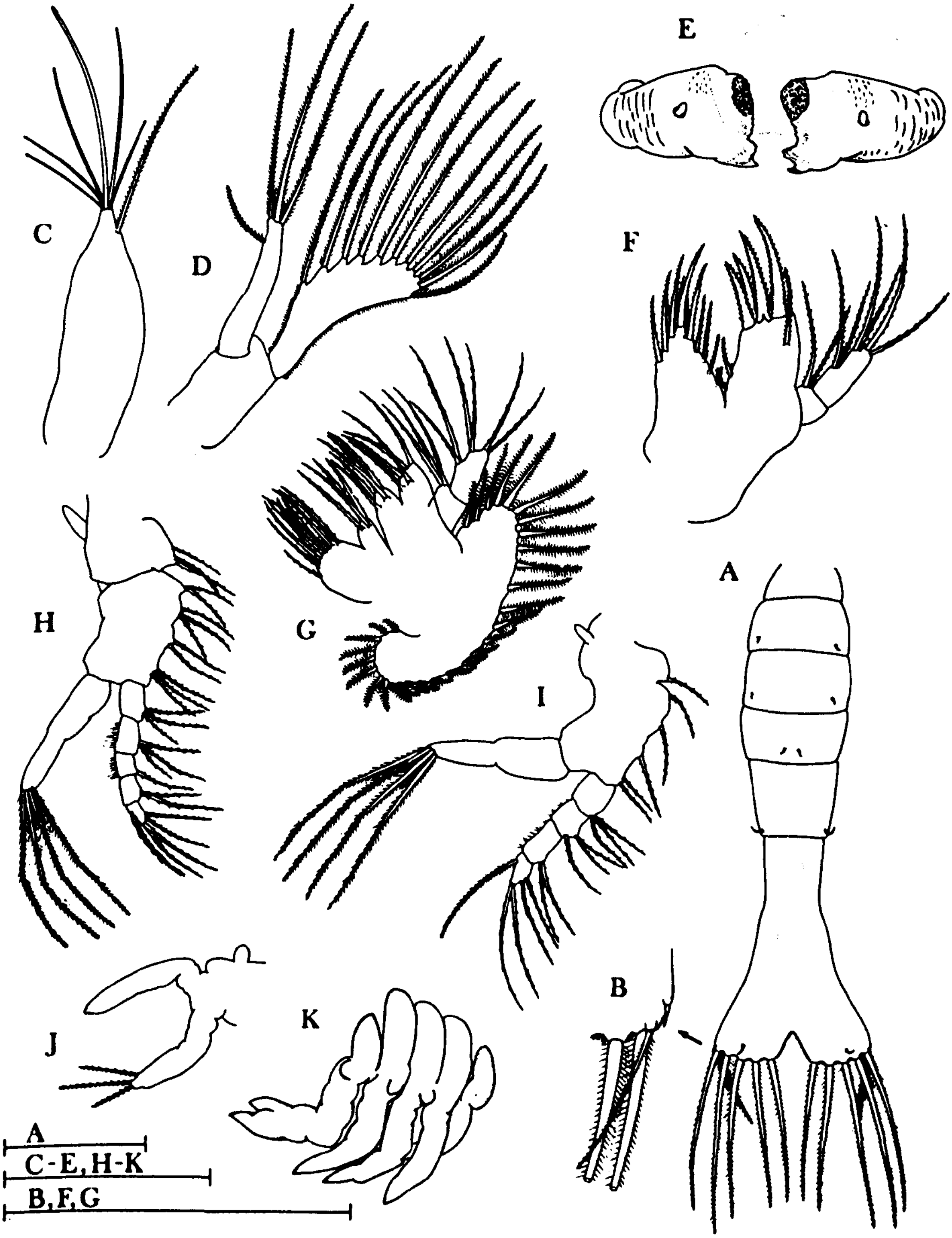

A
B
C
D
E
F

Fig. 44. ***Petalomera japonica*** (Henderson), First zoea

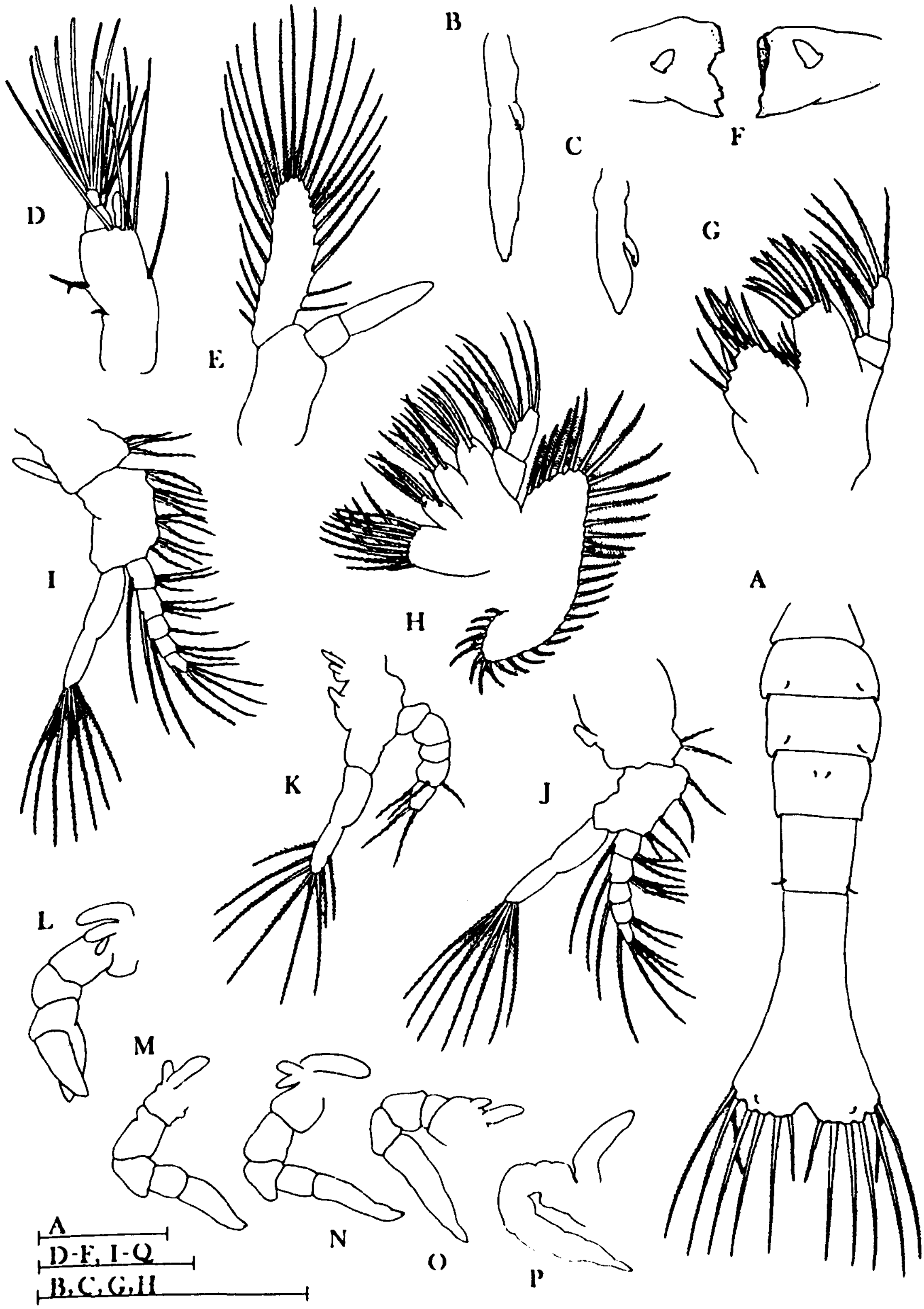
A, abdomen and telson, dorsal view; B, angle of telson, enlarged, ventral view; C, antennule; D, antenna; E, mandible; F, maxillure; G, maxilla; H, first maxilliped; I, second maxilliped; J, third maxilliped; K, legs and gill buds. Scale = 0.5 mm



A
B
C
D
E
F
G
H
I
J
K
A
C-E, H-K
B, F, G

Fig. 45. ***Petalomera japonica*** (Henderson), Second Zaoea

A, abdomen and telson; B, pleopod on 2nd somite; C, pleopod on 5th somite; D, antennule; E, antenna; F, mandible, G, maxillule; H, maxilla; I, first maxilliped; J, second maxilliped; K, third maxilliped; L-P, first to fifth legs. Scales = 0.5 mm



A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
A
D-F, I-Q
B, C, G, H

Fig. 46. *Petalomera japonica* (Henderson), Megalopa

A, dorsal view; B, lateral view of carapace; C, dorsal view of eye. Scale = 0.5 mm

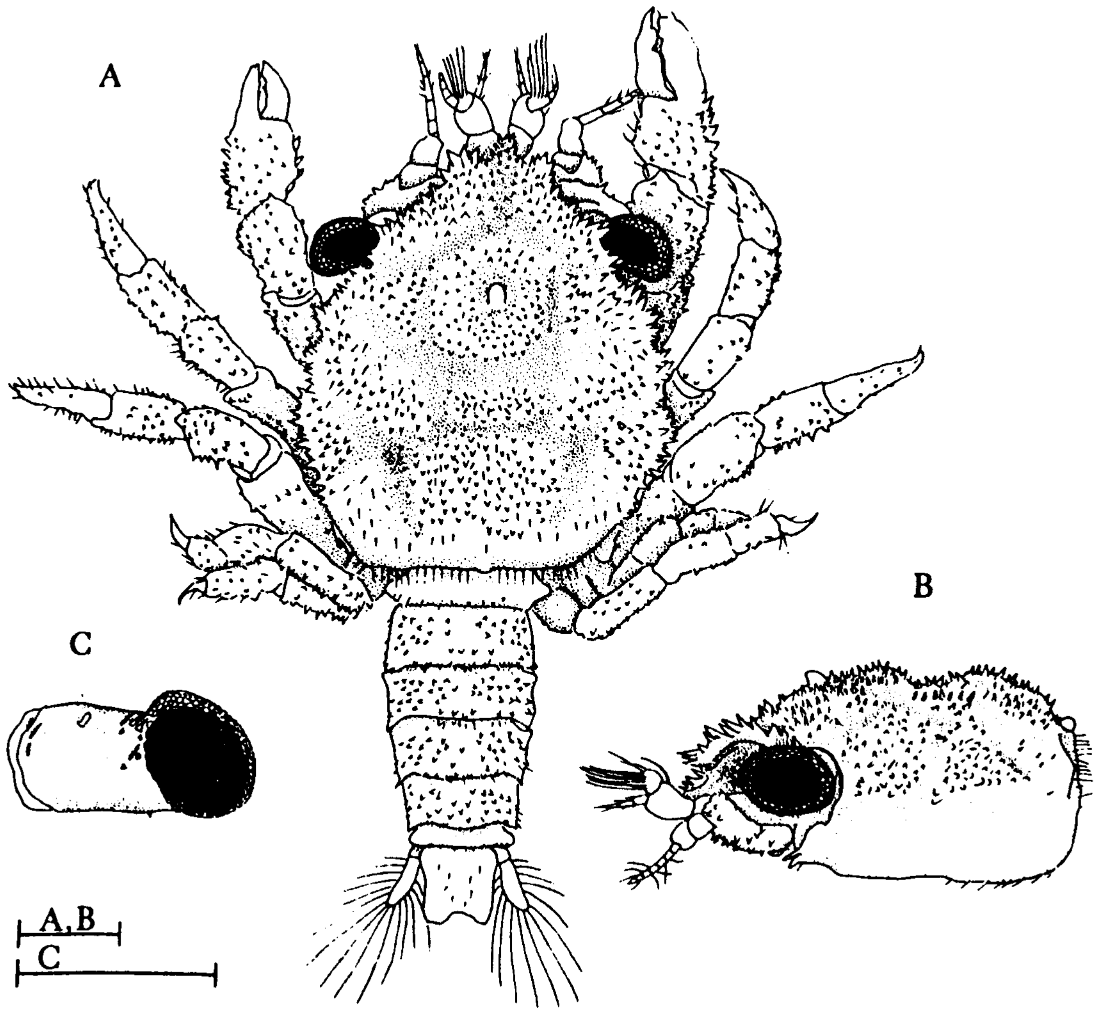

A
B
C
A, B
C

Fig. 47. ***Petalomera japonica*** (Henderson), Megalopa

A and A', telson; B, first pleopod; C, fourth pleopod;D, antennule; E, antenna; F, mandible; G, maxillule; H, maxilla. Scales = 0.5 mm

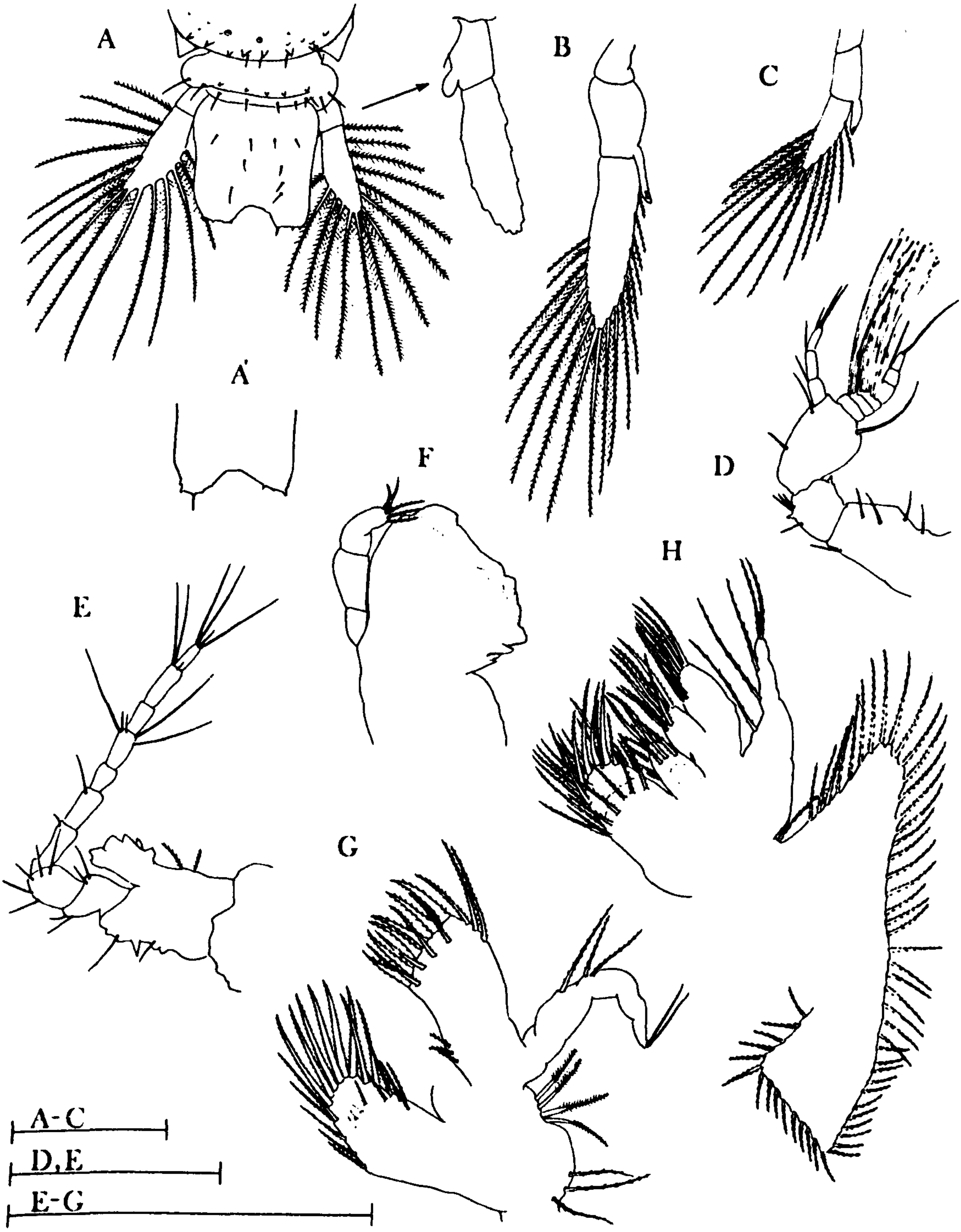
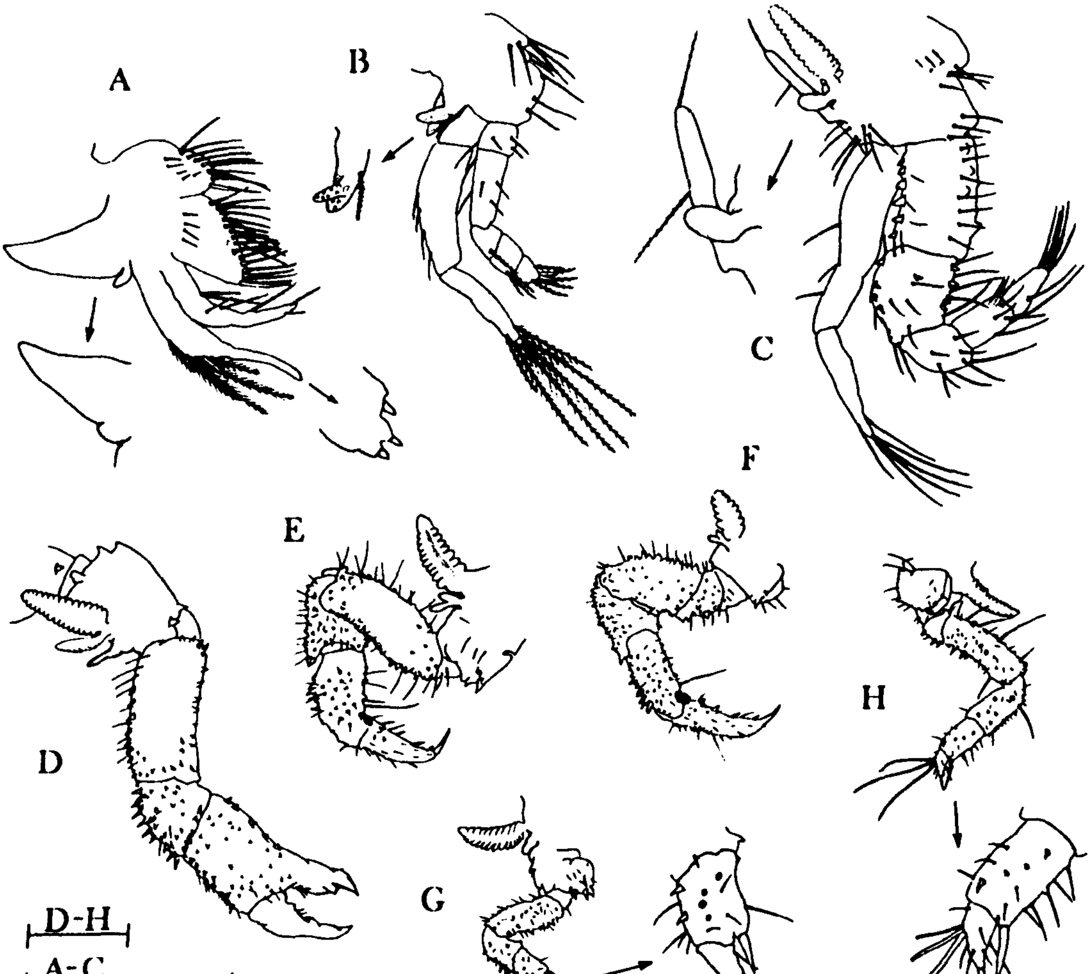

A
A'
B
C
D
E
F
G
H
A-C
D,E
E-G

Fig. 48. *Petalomera japonica* (Henderson), Megalopa

A, first maxilliped, also showing form of epipod in another specimen; B, second maxilliped; C, third maxilliped; D-H, first to fifth legs. Scales = 0.5 mm


A
B
C
D
E
F
G
H
D-H
A-C

CHAPTER 5

LARVAL DEVELOPMENT OF EURYNOME SPINOSA HAILSTONE

AND

RE-EXAMINATION OF THE ZOEA LARVAE OF

EURYNOME ASPERA (PENNANT) (DECAPODA: BRACHYURA: MAJIDAE)

REARED IN THE LABORATORY

INTRODUCTION

Eurynome spinosa has been reported from the west coast of Norway and Sweden, the British Isles including the English Channel and the northwestern coast of Spain; it also occurs in the Mediterranean (Sicily, Gulf of Naples and the Adriatic Sea) (Hartnoll, 1961; Zariquiey Alvarez, 1968; Christiansen, 1969; Ingle, 1980).

Previous descriptions of larvae of the genus *Eurynome* are limited to *Eurynome aspera* (Kinahan, 1860; Gurney, 1924 a; Lebour, 1928 b; Bourdillon-Casanova, 1960; Salman, 1982), but larval descriptions of *E. spinosa* are not available.

The present study aims to describe the complete larval stages of *E. spinosa* and redescribe the zoeal stages of *E. aspera* for comparison.

MATERIALS AND METHODS

On 2nd May, 1985 a berried female of ***Eurynome spinosa*** was collected from the ***Modiolus*** bed off south of the Isle of Man. On 18th May more than 60 larvae hatched. On 6th July, 1986 a berried female of ***Eurynome aspera*** was collected from the same place. On 17th July more than 80 larvae hatched.

Fifty larvae were reared individually in compartmented plastic trays, and mass cultures were made in a glass beaker (1 litre) in water of 34.37 ppt (34.01-34.56 ppt) at 15 °C in a temperature controlled room. Larvae were fed with newly hatched ***Artemia*** nauplii. Moulting and mortality were checked daily, when the larvae were transferred to freshly prepared trays and beakers.

Measurements taken were: a) distance between tips of dorsal and rostral spines (TT); b) carapace length, from between eyes to postero-lateral carapace margin for zoea, from rostral tip to postero-median carapace margin for megalopa (CL); c) total length of megalopa, from tip of rostrum to postero-median margin of telson (TL). Measurements were based on at least 5 specimens.

RESULTS

Development and duration of the larvae

In the complete larval development of *Eurynome spinosa* and *Eurynome aspera* there were each 2 zoeal and 1 megalopal stages. At the end of the rearing experiment 2 individuals of *E. spinosa* in the 2nd crab stage were obtained. Durations of each larval stage and survivals of *E. spinosa* from an initial 50 larvae are given in Table 4.

Table 4. Duration of larval stages and survival of 50 hatched larvae of *Eurynome spinosa* individually reared at 34.37 ppt and 15 °C.

Larval Stages	Duration (days)	Survivors at end of stage
Z-1	8.4 (6-10)	37
Z-2	11.6 (8-13)	21
Megalopa	20.5 (17-26)	9
First crab	15	2

Both species hatch as a prezoea, but a description of this stage is given for *E. spinosa* only. Zoeal features of *E. aspera* are almost identical to those described by Salman (1982). Therefore, only some additional characters are described for the 2 zoeal stages of this species. Gill developments of zoea and megalopa were given in Chapter 3.

Descriptions

Eurynome spinosa Hailstone

Prezoea
(Fig. 49)

Duration : 3-23 min

Size - CL : 0.75-0.83 mm

Carapace and Abdomen (Fig. 49 A) - Newly hatched larvae covered by transparent outer membrane. Carapace devoid of processes. Abdomen without processes and showing outline of abdominal somites of first zoea.

Antennule (Fig. 49 B) - With 2 unequal plumose terminal processes, smaller ca. 2/3 length and width of larger: 2 minute projections, each occupied by aesthetasc of first zoea, at base of larger process.

Antenna (Fig. 49 C) - With 4 terminal plumose processes, with processes of exopod of first zoea projecting towards or into the 3 outer processes; two smooth subterminal processes, almost filled by spinous process and endopod of first zoea.

Mandible (Fig. 49 A) - Not clearly separated from epistome and labrum, bulbous in lateral view.

Maxillule and Maxilla (Fig. 49 A) - A smooth bud with slight lobations.

First and Second Maxillipeds (Fig. 49 A) - Biramous; endopod and exopod with 2-4 terminal minute projections respectively.

Telson (Fig. 49 H) - Bilobed, with 7 pairs of marginal processes: 4th much the shortest, smooth; others plumose; lengths in ratio 3 : 3.5 : 4.2 : 1 : 4.8 : 4.5 : 2.4. Developing telson of first zoea clearly visible within prezoeal membrane; processes of first zoea protrude into proximal parts of all prezoeal processes except 2nd. The shortest (4th) process occupied by protuding telson fork of first zoea.

First Zoea

(Fig. 50)

Size - CL : 0.67 mm (0.66-0.70 mm)

DS : 0.49 mm (0.48-0.51 mm)

RS : 0.33 mm (0.30-0.37 mm)

TT : 1.39 mm (1.36-1.48 mm)

Colour - Yellowish-brown chromatophores on: posterior base of dorsal spine of carapace; antero-ventral part, postero-ventral part and postero-lateral part of carapace; labrum; mandible; basis of first and second maxillipeds; postero-lateral parts of 1st-5th abdominal somites.

Carapace (Fig. 50 A, B) - With dorsal and rostral spines; dorsal spine slightly curved posteriorly; rostral spine shorter than dorsal spine and distal half slightly curved posteriorly; pair of antero-median and pair of postero-dorsal setae; postero-lateral margin fringed with 4 submarginal setae.

Eyes (Fig. 50 A, B) - Partially fused to carapace; a minute pointed process on the basal part of each eye-stalk.

Antennule (Fig. 50 C) - With 1 setae and 4 aesthetascs.

Antenna (Fig. 50 D) - Endopod a simple bud about 1/3 length of exopod; exopod with 1+2 or 1+3 naked processes, and (excluding spines) ca. 1/2 length of spinous process; spinous process with 2 rows of spinules on distal 2/3.

Mandible (Fig. 50 E) - Incisor and molar processes well developed, palp absent.

Maxillule (Fig. 50 F) - Coxal and basial endites each with 7 denticulate setae. Endopod 2-segmented with 1, 2+4 setae.

Maxilla (Fig. 50 G) - Proximal and distal lobes of coxal endite with 5 and 4 denticulate setae respectively. Proximal and distal lobes of basial endite with 4 setae each. Endopod with 5 denticulate setae. Scaphognathite with 8-9 bushy plumose setae and 1 long and thick plumose posterior projection.

First Maxilliped (Fig. 50 H) - Coxa with 1 denticulate seta; basis with 2, 2, 3, 3 medial denticulate setae; endopod 5-segmented with 3, 2, 1, 2, 1+4 denticulate setae; exopod with 4 plumose natatory setae.

Second Maxilliped (Fig. 50 I) - Basis with 1, 1, 1 medial denticulate setae; endopod 3-segmented with 1, 1, 3+2 denticulate setae; exopod with 4 plumose natatory setae.

Legs - Simple buds under carapace.

Abdomen (Fig. 50 A, J) - Five somites; each somite with pair of minute hairs on postero-dorsal margins; 2nd somite with pair of dorso-lateral knobs; postero-lateral margins of 1st and 2nd somites with obtuse angle, and that of 3rd-5th somites with acute processes.

Telson (Fig. 50 A, J-M) - Telson fork spinulated only on ventral surface (Fig. 50 L, M), with 1 fused lateral spine, 2 minute secondary dorso-lateral spines (less than ca. 0.15 times length of the fused lateral spine; rarely as large as the fused lateral spine, shown in Fig. 50 K) and 1 articulate dorsal spine. Median posterior notch round, flanked by 3 pairs of spinnate spines: innermost pair with 2-3 long exterior and 4-6 long interior spinules located on proximal 1/4 of spines.

Second Zoea

(Fig. 51)

Size - CL : 0.80 - 0.83 mm

DS : 0.52 - 0.54 mm

RS : 0.38 - 0.40 mm

TT : 1.52 mm

Colour - Similar to first stage.

Carapace (Fig. 51 A, B) - General shape unchanged, but 2 pairs of anterio-median setae added between eyes and 5 or 6 submarginal setae on posterio-lateral margin.

Eyes (Fig. 51 A, B) - Stalked and movable.

Antennule (Fig. 51 C) - Endopod developed as small bud, with 1 terminal seta and 5 aesthetascs.

Antenna (Fig. 51 D) - Endopod bud equal to exopod in length; exopod with 1+2 processes; spinous process similar to first stage.

Mandible (Fig. 51 E) - Similar to first stage, but mandibular palp developed as small bud.

Maxillule (Fig. 51 F) - Coxal and basial endites with 7 and 9 setae respectively. Endopod setation unchanged. One plumose seta on outer margin.

Maxilla (Fig. 51 G) - Setation of proximal and distal lobes of coxal endite unchanged. Proximal and distal lobes of basial endite with 5 setae each. Setation of endopod unchanged. Scaphognathite fringed with 16 plumose setae.

First Maxilliped (Fig. 51 H) - Setation of basis and endopod unchanged; exopod with 6 plumose natatory setae.

Second Maxilliped (Fig. 51 I) - Setation of basis and endopod unchanged; exopod with 6 plumose natatory setae.

Legs (Fig. 51 A) - Well-developed and protruding from carapace.

Abdomen (Fig. 51 A, J) - Six somites; 1st somite with 3 minute hairs and 2nd-5th somites with a pair of fine hairs on postero-dorsal margin; postero-lateral process of 3rd-5th somites more acute than in first stage.

Telson (Fig. 51 A, J-L) - Setation of telson fork unchanged (Fig. 51 L), but rarely one or both dorso-lateral spines as large as fused lateral spine (Fig. 51 K); 4 pairs of telson processes on posterior margin, innermost pair much smaller than others.

Megalopa

(Figs. 52-53)

Size - CL : 1.05 mm (1.01 - 1.09 mm)

TL : 1.94 mm

Colour - Black chromatophores on dorsal surface of 1st-6th abdominal somites; red chromatophores on stermum and mouth parts; orange-red chromatophores on legs; yellow tinge on carapace and eye-stalks.

Carapace (Fig. 52 A-B) - Longer than wide; rostrum down-turned and directed antero-ventrally; prominent protuberances above eyes; hepatic region inflated, with a seta; dorsal surface of carapace with longituninal ridge and groove, with 2 small low, rounded protuberances on gastric and cardiac regions, followed by a tubercle-like swelling on posterior margin; pair of setae on gastric region.

Antennule (Fig. 52 C) - Peduncle 3-segmented: first segment bulbous with a notch, 2nd with 2 setae and 3rd with 2 setae. Endopod 2-segmented with 4 terminal setae on distal segment. Exopod 3-segmented with 0, 4, 3 aesthetascs.

Antenna (Fig. 52 D) - Peduncle 3-segmented with 2, 2, 3 setae. Flagellum 4-segmented with 1, 0, 3, 4 setae.

Mandible (Fig. 52 E) - Cutting edges well-developed, not clearly divided in incisor and molar processes; palp incipiently 3-segmented but 2 proximal segments partially fused, with 6 setae on the distal segment.

Maxillule (Fig. 52 F) - Coxal and basial endites with 5+5 setae and 2+6+7 setae respectively. Endopod not clearly segmented, with 1 terminal seta.

Maxilla (Fig. 52 G) - Proximal and distal lobes of coxal endite with 4+2 and 2+1 setae respectively. Proximal and distal lobes of basial endite with 3 and 5 setae respectively. Endopod bilobed and naked. Scaphognathite fringed with 30-31 plumose setae.

First Maxilliped (Fig. 53 A) - Coxal and basial endites with 7 and 9 setae respectively. Endopod not distinctly segmented, distal part flattened, with convex outer margin, with a subterminal seta. Exopod 2-segmented, distal segment with 4 plumose setae.

Second Maxilliped (Fig. 53 B) - Endopod 5-segmented with 0, 0, 1, 3, 1+4 setae. Exopod 2-segmented, distal segment with 4 plumose setae.

Third Maxilliped (Fig. 53 C) - Coxa with 1 epipod and 5 setae. Coxa with an epipod and 5-6 setae, basis/ischium with 2/10-12 spines, merus with 5 spines, carpus with 2 spines, propodus with 5 spines, dactylus with 5 spines. Exopod 2-segmented, distal segment with 4 plumose setae.

Pereiopods (Fig. 53 D-H) - All segmented and sparsely spinous without coxal or ischial spines; dactyli of 2nd to 4th pereiopods with 3 spinulated spines on lower margin.

Abdomen (Fig. 52 A, B, H, I) - Six somites, with 4, 2, 2, 2, 2 pairs of surface setae; postero-lateral margin of 2nd-5th somites broadly truncate.

Pleopods (Fig. 52 A, H, J, K) - Present on 2nd-5th abdominal somites. Endopod with 2-3 minute curved processes. Exopod fringed with 11, 11, 10, 8 plumose natatory setae on 1st to 4th pairs respectively.

Uropods (=pleopod on 6th somite) (Fig. 52 H, L) - Uniramous with 3 plumose natatory setae.

Telson (Fig. 52 A, B, H, I, L) - Broader than long, in some specimens distally rounded. A pair of median dorsal setae.

First Crab

(Fig. 54)

Size - CL (including rostrum) : 1.56 mm

CL (excluding rostrum) : 1.20 mm

Carapace (Fig. 54 A) - Longer than broad; dorsal surface covered by setae and 4-5 acute spines on antero-lateral margin; a minute tubercle on gastric and cardiac regions; frontal region produced as a broad rostrum with widely separated processes, slightly pointing downward, with long curved setae and 3 or 4 acute spines on outer margin; pre-orbital and post-orbital spines acute. Pereiopod and abdomen covered by setae; carpus of chela with an acute spine.

Abdomen (Fig. 54 B) - Six somites, with 10, 9, 8, 6, 4, 2 setae on dorsal surface; telson with an obtuse tip, with a pair of minute setae on dorsal surface.

Eurynome aspera (Pennant)

First Zoea

(Fig. 55 A-D)

Duration : 6-9 days

Size - CL : 0.72-0.74 mm

DS : 0.55 mm

RS : 0.32 mm

TT : 1.36-1.40 mm

Colour - Yellowish-brown chromatophores on: antero-ventral part of 3rd-5th abdominal somite; postero-lateral part of 1st-5th abdominal somite; basis of 1st-2nd maxillipeds; base of 3rd maxilliped bud. Reddish-brown chromatophores on: antero-ventral part, postero-ventral part and postero-lateral part of carapace; antero-ventral part of telson; basis of 1st maxilliped; posterior base of dorsal spine of carapace; frontal base of rostral spine between eyes. Tinged with light red on: mandible; labrum; base of antennule and antenna; ventral part of 3th-5th abdominal somite; antero-ventral part of telson.

All morphological features similar to *E. spinosa*. Features of carapace, abdomen, telson and 1st maxilliped illustrated in Fig. 55 A-D.

Second Zoea

(Fig. 55, E-H)

Duration : 6-8 days

Size - CL : 0.80 mm

DS : 0.58 mm

RS : 0.35 mm

TT : 1.47 mm

Colour - Reddish-brown chromatophores disappeared from ventral part of 1st-5th abdominal somites and replaced by light yellow tinges. Other parts similar to first stage.

Carapace (Fig. 55 E) - General shape unchanged, but 2 pairs of antero-median setae added between eyes and 5 or 6 submarginal setae on postero-lateral margin.

Appendages and telson (Fig. 55 F-H) similar to those of *E. spinosa*.

DISCUSSION

Gurney (1924 a) described the prezoeal stage of *Eurynome aspera*. Plumose processes on the antennule and antenna are very similar in prezoeas of *Eurynome aspera* and *Eurynome spinosa*. A minor difference occurs in the processes of the antennule: those of the former species (Gurney, 1924 a, Fig. 1) are almost equal in size, while those of the latter species (present study) are not equal; the smaller being ca. 2/3 the length and width of the larger.

It appears that Salman (1982) overlooked the following features of *E. aspera*: First zoea; (1) a minute pointed keel on basal part of eye-stalk. (2) a seta on coxa of 1st maxilliped, (3) 1 or 2 secondary minute dorso-lateral spines on telson fork. Second zoea (including the above-mentioned 3 features of first zoea); (1) 3 pairs of antero-median setae on carapace, (2) mandibular palp bud, (3) a plumose seta on outer margin of maxillule.

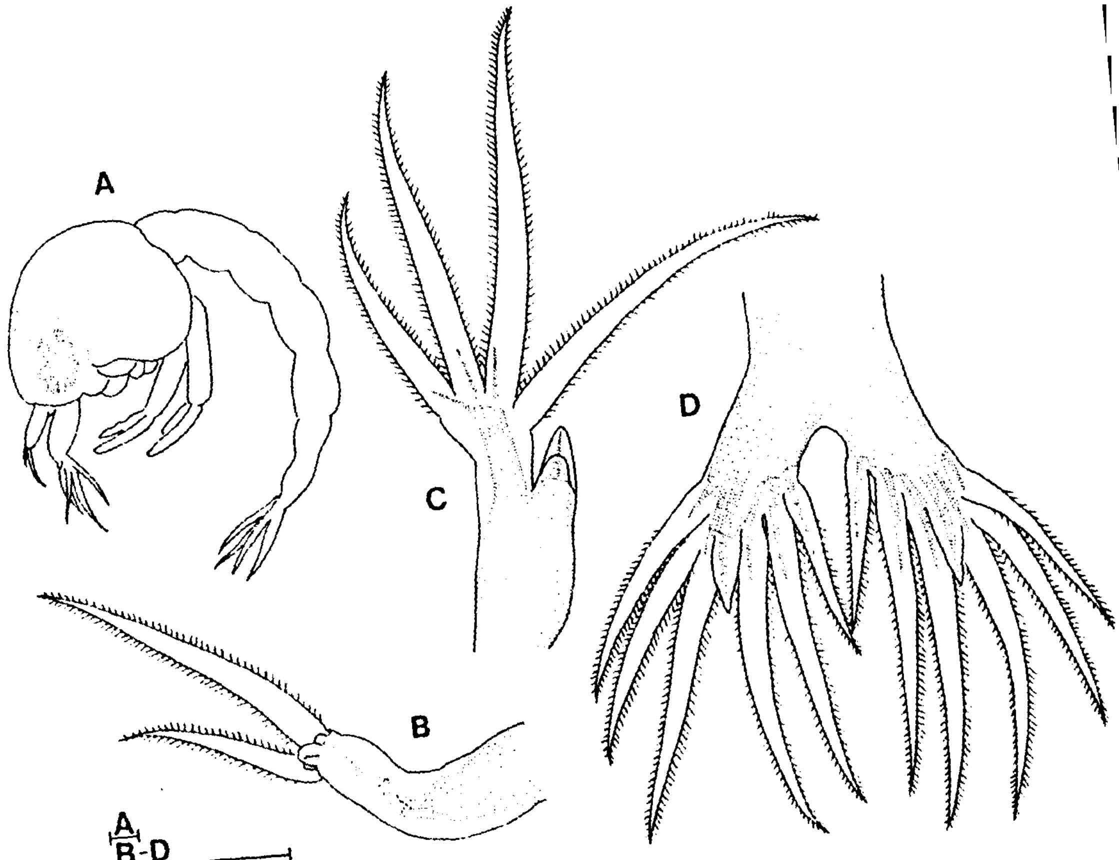
Apart from some slight differences in the colour of the larvae, the zoeal stages of *E. spinosa* and *E. aspera* are very similar to each other. Consequently, as indicated by Williamson (1982), it is very hard to distinguish the preserved specimens of these two species.

Salman (1982) distinguished the zoeas of these *E. aspera* and *E. spinosa* by the relative sizes of exopod and spinous process of the antenna, and the configuration of the median notch of the telson. In the present study on the two species, no significant differences were found in these features. On the other hand, some minor differences were found in the relative sizes of lateral spines of the telson fork. Both species have 3 lateral spines on the telson fork. Of these, the distal 2 spines are usually very minute. Both spines are less than 0.2 times the length of the outermost lateral spine in *E. spinosa*, whereas they are ca. 0.2 times in *E. aspera*.

Ingle and Clark (1980) compared the larval feature of 3 species of British Pisinae: *Pisa armata, E. aspera* and *Rochinia carpenteri*. Salman (1982) presented a taxonomic key to identify the first zoeas of 13 species of Pisinae. Based on the present study, zoeas of *E. aspera* and *E. spinosa* are distinguished from those of other Pisininae by the following common characters: (1) a minute pointed process on base of eye-stalk, (2) a seta on coxa of 1st maxilliped, (3) 3 pairs of lateral processes on telson fork, (4) exopod (excluding spines) of antenna ca. 1/2 length of spinous process.

Fig. 49. *Eurynome spinosa* Hailstone, Prezoea

A, lateral view; B, antennule; C, antenna; D, telson. Scales = 0.10 mm.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B
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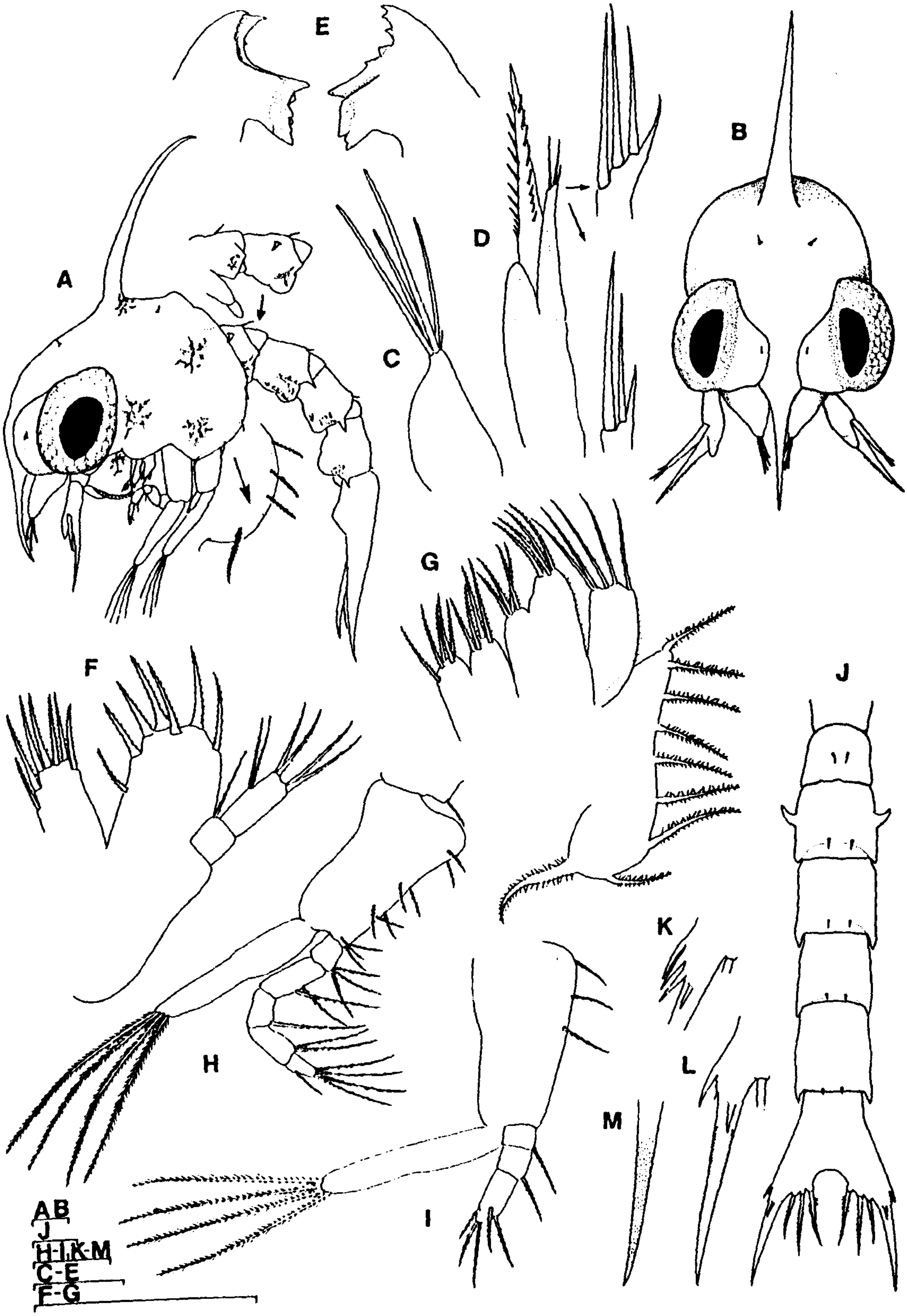
A
B-D

Fig. 50. *Eurynome spinosa* Hailstone, First zoea

A, lateral view; B, frontal view; C, antennule; D, antenna; E, mandibles; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped; J, abdomen and telson; K-L, spines of telson fork; M, ventral view of telson fork. Scales = 0.10 mm



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H-I,K-M
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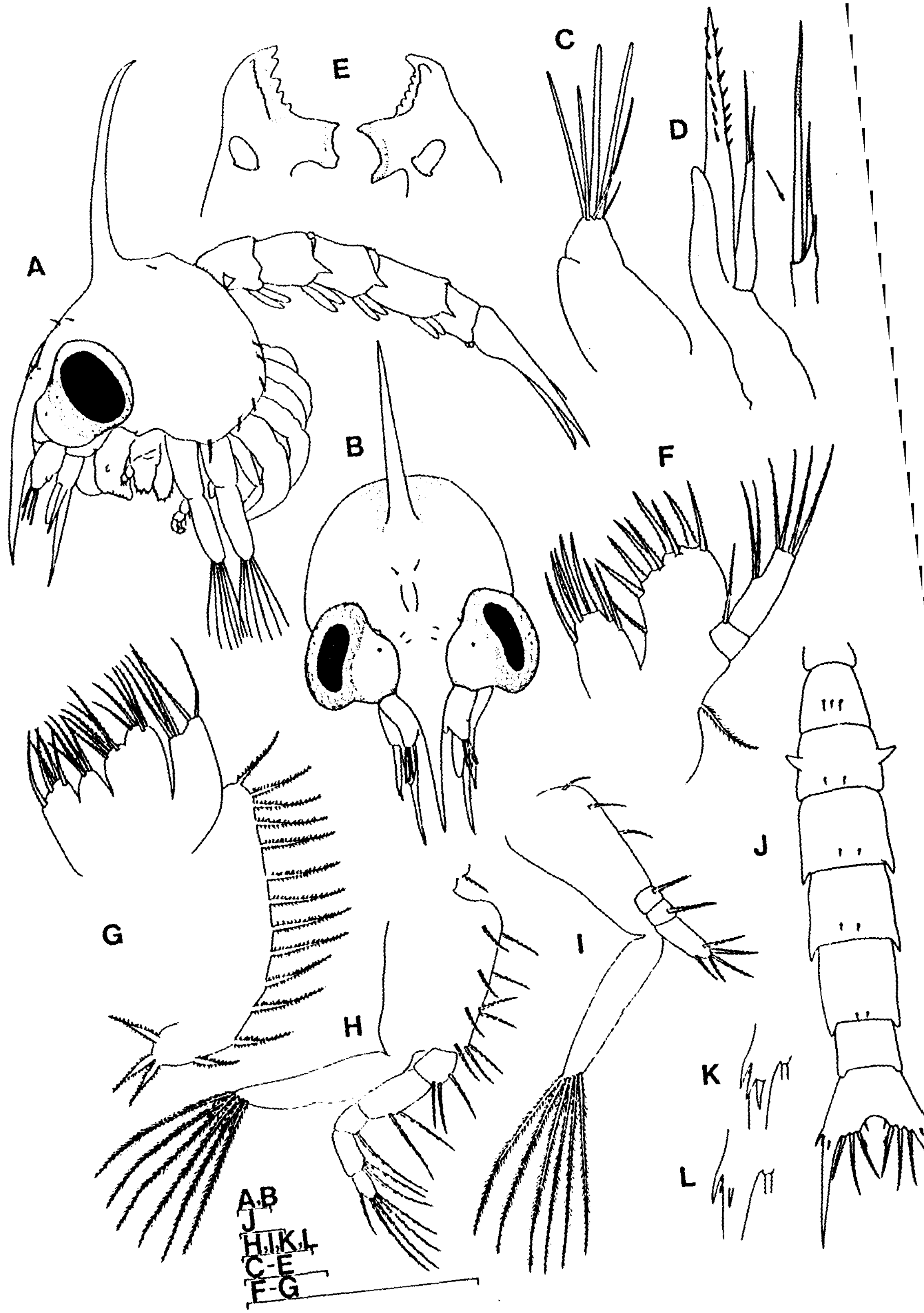
F-G

Fig. 51. *Eurynome spinosa* Hailstone, Second zoea

A, lateral view; B; frontal view; C, antennule; D, antenna; E, mandibles; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped; J, abdomen and telson; K, spines of telson fork. Scale = 0.10 mm



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H,I,K,L
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F-G

Fig. 52. *Eurynome spinosa* Hailstone, Megalopa

A, lateral view, B, dorsal view; C, antennule; D, antenna; E, mandibles; F, maxillule; G, maxilla; H, lateral view of abdomen; I, dorsal view of abdomen; J, pleopod of 2nd somite; K, pleopod of 5th somite.

Scale = 0.50 mm

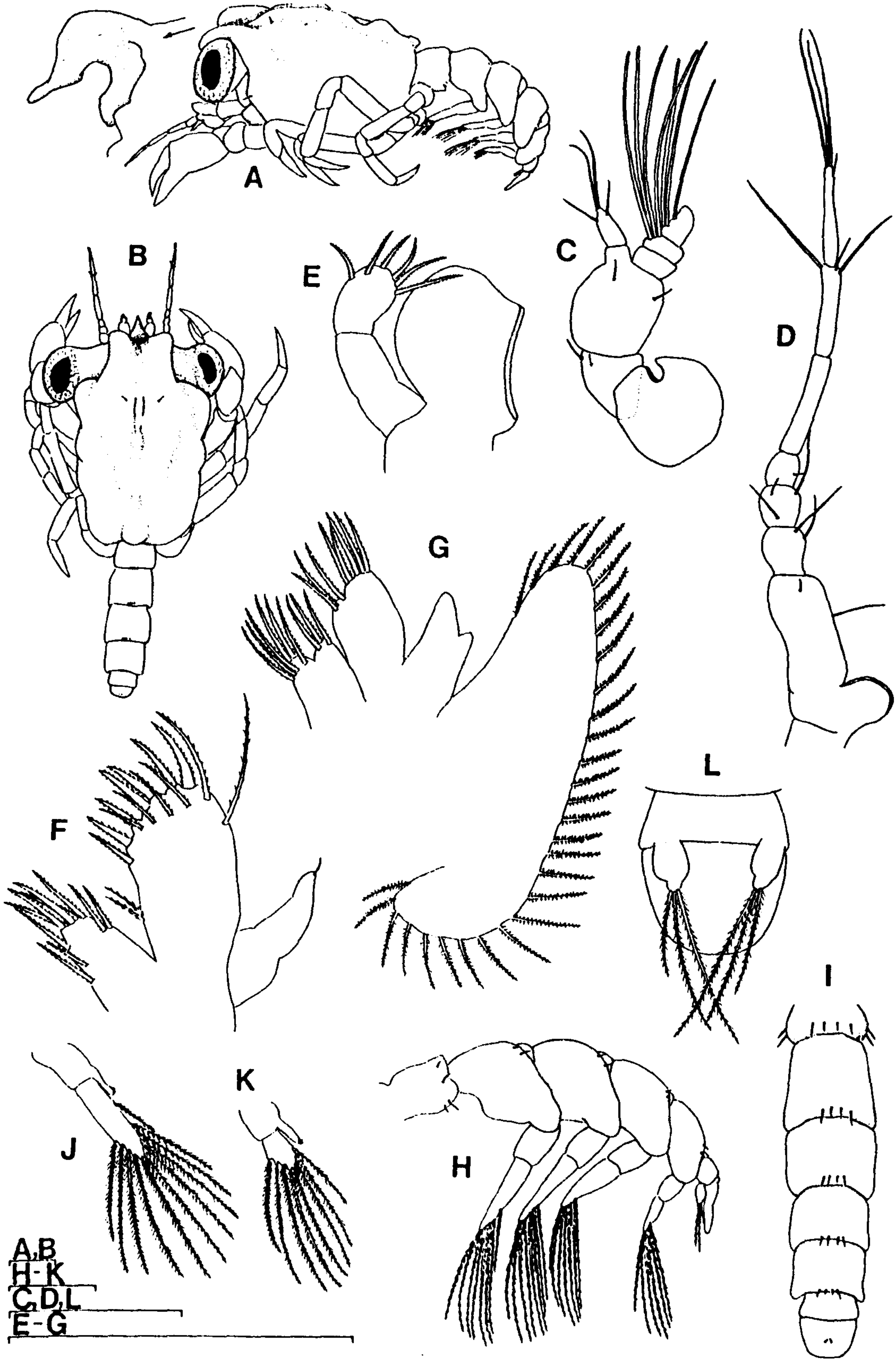
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Fig. 53. *Eurynome spinosa* Hailstone, Megalopa

A, first maxilliped; B, second maxilliped; C, third maxilliped; D, D-H, 1st-5th legs. Scale = 0.10 mm

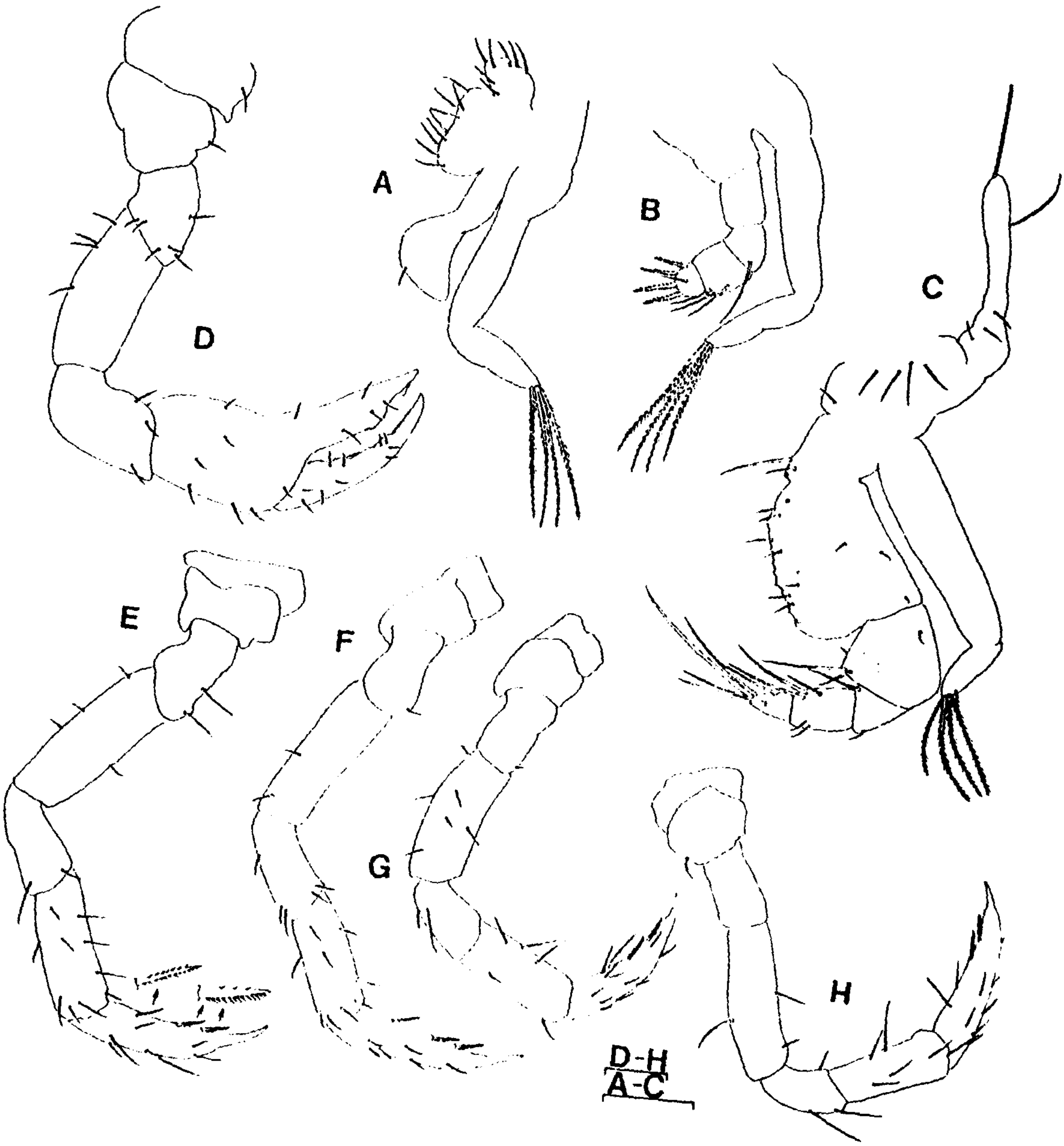
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Fig. 54. *Eurynome spinosa* Hailstone, First crab

A, dorsal view; B, abdomen and telson. Scale = 0.25 mm

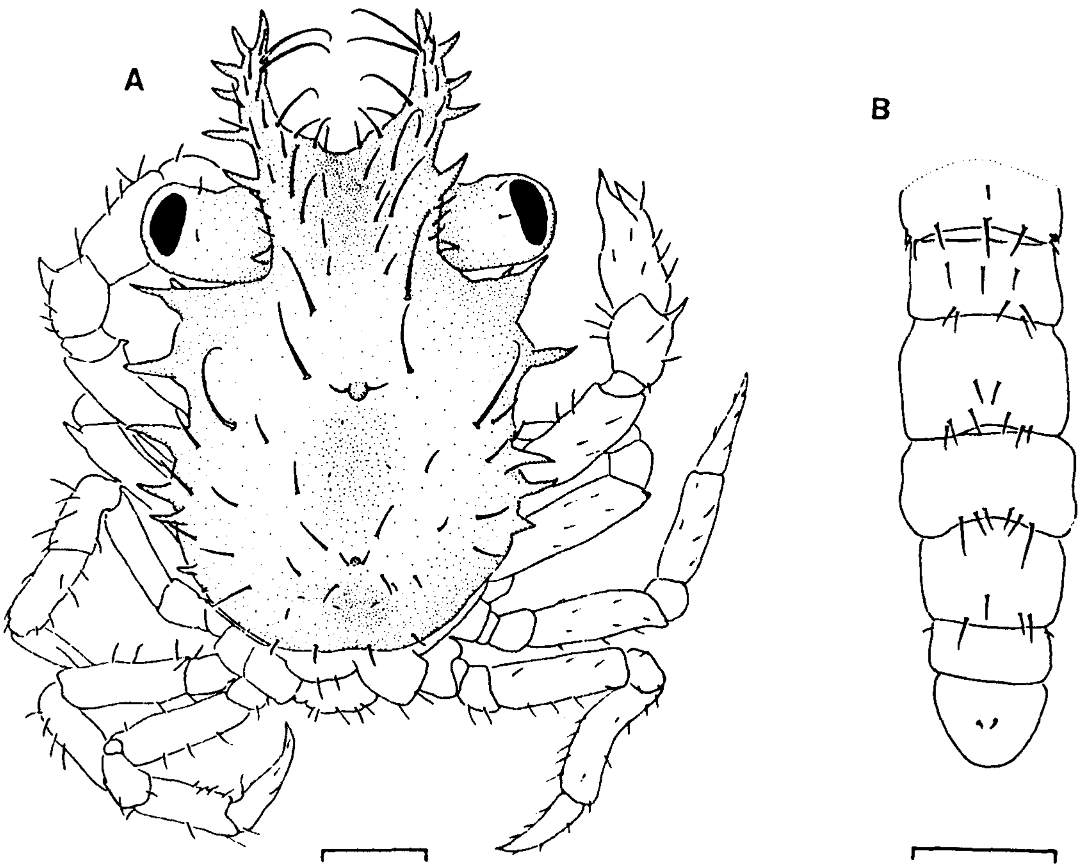
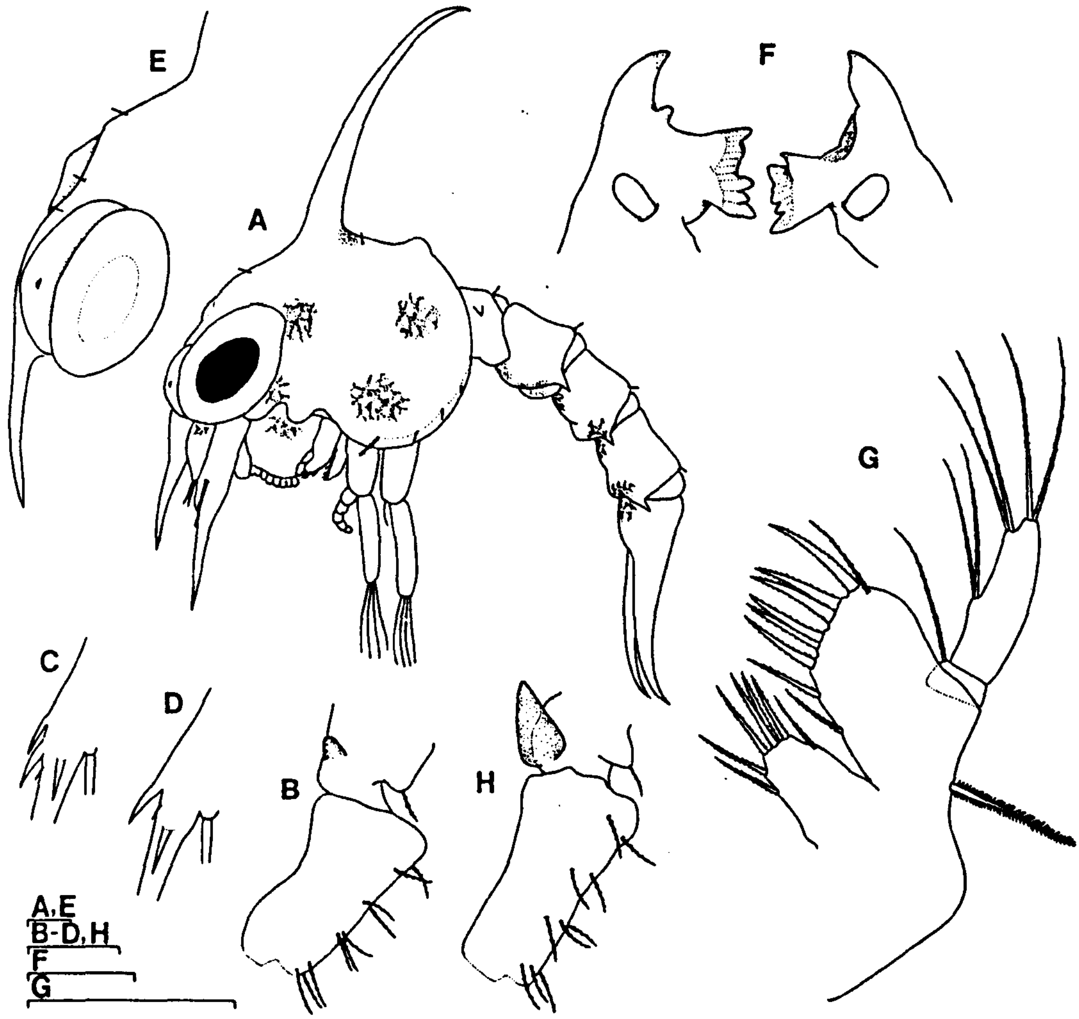

A
B

Fig. 55. *Eurynome aspera* (Pennant), First and second zoea A-D, First zoea: A, lateral view; B, first maxilliped; C-D, spines of telson fork: E-H, Second zoea: E, lateral view of front of carapace; F, mandibles; G, maxillule; H, first maxilliped. Scale = 0.10 mm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CHAPTER 6

LARVAL DEVELOPMENT OF THE CIRCULAR CRAB ATELECYCLUS ROTUNDATUS (OLIVI) (CRUSTACEA: BRACHYURA: ATELECYCLIDAE) REARED IN THE LABORATORY

(This chapter is in press in Journal of Natural History, 1987)

INTRODUCTION

The Circular or Face Crab, ***Atelecyclus rotundatus*** (Olivi) has been reported northward as far as Grip (on the west coast of Norway), and as far south as Port Elizabeth (South Africa); it also occurs in the Mediterranean (Christiansen, 1969; Ingle, 1980; Kensley, 1981; Manning and Holthuis, 1981; Zariquiey Alvarez, 1968).

Lebour (1928 b) first described the larval stages of ***A. rotundatus*** (as ***A. septemdentatus***) from material obtained in the Plymouth region of Devon. Her account of the pre- and first zoeal stages was based upon laboratory hatched specimens, later stages were described from plankton collected larvae which metamorphosed in captivity. Bourdillon-Casanova (1960) figured the telson of a fourth stage zoea obtained from plankton in the Marseille region, and Paula (in press) tentatively assigned to this species plankton-caught first and second stage zoeae from the Portuguese coast. In 1985 the author and Dr. R. W. Ingle independently reared the larvae of ***A. rotundatus*** to megalopal stage from laboratory-hatched eggs thus making available sufficient material for a detailed description of the complete larval morphology of this species and a brief review of features distinguishing ***A. rotundatus*** larvae from other N.E. Atlantic brachyrhynchs. The opportunity is also taken to elaborate on the discussion by Rice (1980) of the larval features of the Atelecyclidae.

MATERIALS AND METHODS

The larvae forming the basis of this study were hatched and reared from 3 female crabs collected in the following regions. Two from 5 miles west of Port Erin, Isle of Man on 15. 2. 1985 and 26. 3. 1985; one crab from Millport region, Isle of Cumbrae on 13. 6. 1985. The crab obtained on 15. 2. 1985 hatched her eggs on 10. 3. 1985 and these were reared in a salinity of 34.37 ppt (34.01-34.56 ppt) at 15 °C. The larvae of the crab caught on 26. 3. 1985 hatched on 15. 4. 1985 and were reared in 34.40 ppt (33.86-34.60 ppt) at 10 °C. Both rearings were carried out in a laboratory of the Marine Biological Station, Port Erin. Fifty larvae of each hatching were reared individually in compartmented plastic trays, and mass cultures were made in glass beakers (1 litre). Larvae were fed with newly hatched *Artemia* nauplii. Moulting and mortality were checked daily, when the larvae were transferred to freshly prepared trays and beakers. The crab collected at Millport on 13. 6. 1985 hatched her eggs over the period of 22-23. 6. 1985 in the larval rearing laboratory of the Zoology Department, British Museum (Natural History), London. This crab and her larvae were maintained by Dr. R. W. Ingle at 15-18 °C in a salinity of approximately 34.00 ppt and the larvae were reared on a diet of newly hatched *Artemia* nauplii, chiefly in mass culture units of the type described by Rice and Ingle (1975) and using seawater treated with Streptomycin sulphate (0.02 mg/ml).

Measurements taken were: a) distance between tips of dorsal and rostral spines (TT); b) carapace length, from between eyes to posterio-lateral carapace margin for zoea, from rostral tip to posterio-lateral carapace margin for megalopa (CL); c) total length of megalopa, from tip of rostrum to posterio-median margin of telson (TL).

The female crabs and the reared larvae have been deposited in the British Museum (Natural History) under the accession numbers 1986: 333, 334.

RESULTS

Development and duration of the larvae

The larvae hatched as free swimming prezoeas. The majority of these shed the prezoeal cuticle 4-12 minutes after hatching, but a few did not moult and sank to the bottom.

There were 5 zoeal and one megalopal stages. For the Port Erin hatchings the duration of each larval stage and survivals from an initial 50 larvae, reared individually in each of two temperature regimes, are given in Table 5. No megalopa moulted to the first crab stage. Survival was good up to the 4th zoeal stage in both temperature regimes, but high mortality occurred during moulting to the 5th stage. A similar mortality pattern was evident in the cultures reared at the British Museum (Natural History).

Table 5. Duration of larval stages and survival of 50 hatched larvae reared at Port Erin, in each of two temperature regimes at similar salinities. 'Duration' of megalopa stage refers to survival time.

Larval Stages	Duration (days)	Survivors at end of stage
10 °C; 34.40 ppt. (33.86-34.60 ppt.)		
Z-1	14.4 (14-17)	50
Z-2	11.6 (8-14)	47
Z-3	13.1 (11-16)	47
Z-4	15.2 (10-20)	47
Z-5	20.5 (19-23)	10
Megalopa	20-46 (survival)	0
15 °C; 34.37 ppt. (34.01-34.56 ppt.)		
Z-1	9.5 (9-13)	45
Z-2	7.2 (6- 9)	42
Z-3	8.6 (6-13)	36
Z-4	12.5 (11-13)	25
Z-5	14.8 (12-16)	8
Megalopa	4-25 (survival)	0

Atelecyclus rotundatus (Olivi, 1792)

Larval references:

Atelecyclus septemdentatus; -- Lebour, 1928 b. 474-476, 524-525, Fig. 1. (5, 10), Fig. 4 (1-5, 24, 26, 27), Fig. 5 (13-14), Pl. II (Fig. 1), Pl. IX (Figs. 1-6), Pl. X (Figs. 1-2) (pre-zoea, 1st-5th zoea, megalopa); *Atelecyclus rotundatus* -- Bourdillon-Cassanova, 1960: 167, Fig. 52 (4th zoea); ? *A. rotundatus* -- Paula, in press: Fig. 7 (1st, 2nd zoea).

Descriptions

Specimens used for these descriptions are from the Port Erin material reared at 15°C, except where mentioned.

Prezoea

(Fig. 56)

Size - CL : 0.56 mm (0.55-0.59 mm)

Carapace (Fig. 56 A) - Newly hatched larvae covered by transparent outer membrane. Carapace devoid of processes.

Antennule (Fig. 56 B) - With 2 unequal plumose terminal processes, smaller less than 1/3 length and less than 1/2 width of larger; 2 minute projections at base of larger process.

Antenna (Fig. 56 C) - With 4 terminal plumose processes, outermost much the smallest, with processes of exopod of 1st zoea projecting towards or into the three larger; one smooth subterminal process, almost filled by spinous process of 1st zoea.

Mandible (Fig. 56 A) - Not clearly separated from epistome and labrum, bulbous in lateral view.

Maxillule (Fig. 56 D) - A smooth bud with slight lobations.

Maxilla (Fig. 1 56 E) - With smooth inner lobes containing developing endites and endopod; smooth outer lobe containing developing scaphognathite.

First Maxilliped (Fig. 56 F) - Biramous; endopod and exopod each with 3 terminal processes, those on endopod minute.

Second Maxilliped (Fig. 56 G) - Biramous; tip of endopod obtuse, exopod with 3 terminal processes.

Abdomen (Fig. 56 A) - Without processes and showing outline of abdominal somites of 1st zoea.

Telson (Fig. 56 H) - Bilobed, with 7 pairs of marginal processes: 4th much the shortest, smooth; others plumose; lengths in ratio 2.5 : 4 : 5 : 1 : 7 : 6 : 4. Developing telson of 1st zoea clearly visible within prezoeal membrane; processes of 1st zoea protrude into proximal parts of all prezoeal processes except 2nd; lengths of zoeal processes (to same base as prezoeal processes) in ratio 0.5 : 0 : 0.6 : 0.7 : 1.5 : 1.7 : 1.7.

First Zoea

(Fig. 57)

Size - TT : 1.75 mm (1.70-1.85 mm)

CL : 0.65 mm (0.63-0.67 mm)

Colour - Reddish-black chromatophores on each side on the posterio-ventral part of carapace; reddish chromatophore just above the base of each lateral spine; spines tinged with yellow; black chromatophores on dorsal surface of fore-gut (under carapace); paired black chromatophores on posterio-lateral part of 2nd-5th abdominal somites; telson tinged with red, with 2 pairs of red chromatophores on ventral surface; reddish-black chromatophores on ventro-basal part of rostral spine, frontal surface of labrum and ventral surface of mandible; red chromatophores on ventro-basal part of antenna and distal part of basis of 1st and 2nd maxillipeds; minute red chromatophore on inner coxal region of 2nd maxilliped.

Carapace (Fig. 57 A, B) - Dorsal spine stout, slightly convex anteriorly, strongly curved near tip; rostral spine slightly concave anteriorly; a pair of prominent lateral spines, about 1/2 carapace length in Millport specimens, rather shorter in Port Erin specimens; rostrum about 3/4 length of carapace and dorsal spine about 1.6 times length of rostrum; anterio-median tubercle very inconspicuous; no anterio-median setules; pair of posterio-dorsal setules present; 5-6 minute teeth on posterio-lateral margin.

Eyes (Fig. 57 A, B) - Partially sessile.

Antennule (Fig. 57 C) - Unsegmented with 4 aesthetascs and 1 short seta.

Antenna (Fig. 57 D) - Spinous process about 2.5 times length of exopod, with 2 rows of spinules on distal half. Exopod with 3 unequal terminal spines, showing considerable variation between specimens (but no noticeable variation in Millport specimens).

Mandible (Fig. 57 E) - Incisor and molar processes well developed, palp absent.

Maxillule (Fig. 57 F) - Coxal and basial endites with 7 and 1+4 denticulate setae respectively. Endopod 2-segmented with 1 and 1+4 denticulate setae.

Maxilla (Fig. 57 G) - Proximal and distal lobes of coxal endite with 1+2 and 1+1 denticulate setae respectively. Proximal and distal lobes of basial endite with 1+4 and 1+3 denticulate setae respectively. Smaller proximal lobe and larger distal lobe of endopod with 3 and 4 denticulate setae respectively. Scaphognathite with 4 densely plumose setae and 1 long and thick plumose posterior projection.

First Maxilliped (Fig. 57 H) - Basis with 2, 2, 3, 3 medial denticulate setae; endopod 5-segmented with 2, 2, 1, 2, 1+4 denticulate setae; exopod with 4 plumose natatory setae.

Second Maxilliped (Fig. 57 I) - Basis with 1, 1, 1, 1 medial denticulate setae; endopod 3-segmented with 1, 1, 1+4 denticulate setae; exopod with 4 plumose natatory setae.

Third Maxilliped - Not developed.

Pereiopods - Not developed.

Abdomen (Fig. 57 A, J) - Five somites; 2nd with pair of dorso-lateral processes; posterio-lateral margin of 2nd-5th with obtuse angle bearing 3 or 4 minute teeth; pair of minute setae on posterio-dorsal margin of 2nd-5th somites.

Telson (Fig. 57 A, J) - Telson fork with 1 lateral fused spine, a minute secondary spine (very minute in Millport specimens) and

1 dorsal articulated spine; lateral and dorsal spines equal in size. Median posterior margin concave, armed with 3 pairs of spines: distal half of inner margin of outermost pair with strong serrations; innermost pair with 0-5 long exterior and 4-10 long interior spinules located on the proximal 1/4 of spine.

Second Zoea

(Fig. 58)

Size - TT : 2.14 mm (2.10-2.19 mm)

1.95 mm average (Millport specimens)

CL : 0.81 mm (0.79-0.82 mm)

Colour - Similar to 1st stage.

Carapace (Fig. 58 A, B) - General shape unchanged, but rostrum now as long as carapace and dorsal spine about 1.2 times length of rostrum. Tip of dorsal spine almost straight. Anterio-median region with 3 pairs of setae present in Millport specimens; 4-5 setae on posterio-lateral margin (average of 3 setae in Millport specimens).

Eyes (Fig. 58 A, B) - Stalked and movable.

Antennule (Fig. 58 C) - With 6 terminal aesthetascs.

Antenna (Fig. 58 D) - Similar to 1st zoea.

Mandible (Fig. 58 E) - Similar to 1st zoea.

Maxillule (Fig. 58 F) - Coxal and basial endites each with 2+5 setae. Endopod setation unchanged. One plumose seta on outer margin.

Maxilla (Fig. 58 G) - Proximal and distal lobes of coxal endite with 2+1 and 1+3 setae respectively. Setation of proximal and distal lobes of basial endite unchanged. Setation of endopod unchanged. Scaphognathite fringed with 11 (10 only in Millport specimens) plumose setae.

First Maxilliped (Fig. 58 H) - Basis and endopod setation unchanged; exopod with 6 plumose natatory setae.

Second Maxilliped (Fig. 58 I) - Basis and endopod setation unchanged; exopod with 6 plumose natatory setae.

Third Maxilliped (Fig. 58 J) - Each consisting of 2 minute buds.

Pereiopods (Fig. 58 J) - Five minute buds.

Abdomen (Fig. 58 A, K) - Posterio-lateral margin of 3rd-5th somites with processes more acute than in 1st stage.

Telson (Fig. 58 A, K) - Four pairs of spines on posterior margin; innermost pair much smaller than others (innermost pair not present in Millport specimens). The minute secondary spine on each telson fork absent in some of Port Erin specimens, when present much reduced in size and located near the base of dorsal spine.

Third Zoea

(Fig. 59)

Size - TT : 2.64 mm (2.43-2.76 mm)

2.55 mm average (Millport specimens)

CL : 0.89 mm (0.82-0.91 mm)

Colour - Similar to 2nd stage, but red chromatophores on posterio-ventral surface of 5th abdominal somite and on ventral surface of 6th abdominal somite.

Carapace (Fig. 59 A) - General shape similar to 2nd stage, but dorsal and rostral spines almost equal in size, and 6 (8 in Millport specimens) setae on posterio-lateral margin.

Antennule (Fig. 59 B) - Similar in shape and armature to 2nd stage.

Antenna (Fig. 59 C) - Spinous process about 3 times length of exopod. Endopod bud developed.

Mandible (Fig. 59 D) - Similar in shape and armature to 2nd stage.

Maxillule (Fig. 59 E) - Setation of coxal endite and endopod unchanged; basial endite with 4+5 setae.

Maxilla (Fig. 59 F) - Setation of coxal endite unchanged. Proximal and distal lobes of basial endite with 1+5 (1+4 in Millport specimens) and 1+4 setae respectively. Setation of endopod unchanged. Scaphognathite with 19 (18 in Millport specimens) plumose setae.

First Maxilliped (Fig. 59 G) - Coxa with 1 epipod bud; basis and endopod setation unchanged. Exopod with 8 plumose natatory setae.

Second Maxilliped (Fig. 59 H) - Coxa with 1 epipod bud; basis and endopod setation unchanged. Exopod with 8 plumose natatory setae.

Third Maxilliped (Fig. 59 I) - Biramous with distinct endopod and exopod buds; 1 epipod and 1 gill bud (future arthrobranch) on protopodal part.

Pereiopods (Fig. 59 J) - Small buds; 2nd and 4th comparatively smaller than others; 1st with 2 gill buds (future arthrobranchs); 2nd and 3rd each with 1 gill bud (future pleurobranch).

Abdomen (Fig. 59 A, K) - Six somites; a dorso-median seta on 1st somite. Processes on posterio-lateral margin of 3rd-5th somites longer than those of 2nd zoea.

Telson (Fig. 59 A, K) - Apparent length reduced by formation of 6th somite. Lateral spine on each fork now articulated. The minute spine present on the inner side of lateral spine on each fork is now very reduced and absent in some specimens from Millport.

Fourth Zoea

(Fig. 60)

Size - TT : 3.34 mm (3.17-3.51 mm)
3.20 mm average (Millport specimens)
CL : 1.12 mm (1.01-1.23 mm)

Colour - Similar to 3rd stage.

Carapace (Fig. 60 A) - Similar to 3rd stage, but 3 pairs of anterio-median setae now recognisable in Isle of Man specimens, and 9-10 (12-13 in Millport specimens) setae on the posterio-lateral margin.

Antennule (Fig. 60 B) - With 2 subterminal and 4 terminal aesthetascs.

Antenna (Fig. 60 C) - Endopod developed as elongate bud, about 0.7 times length of exopod; exopod with 2 terminal spines of unequal size.

Mandible (Fig. 60 D) - Similar to 3rd stage.

Maxillule (Fig. 60 E) - Coxal endite with 5+3 setae; basial endite with 5+6 setae. Setation of endopod unchanged. One naked seta added at the proximal end of outer margin.

Maxilla (Fig. 60 F) - Proximal and distal lobes of coxal endite with 4 setae each (distal lobe sometimes has 5 setae in Millport specimens). Proximal and distal lobes of basial endite with 6 setae each (proximal lobe with 5 setae in Millport specimens). Setation of endopod unchanged. (One Millport specimen has 5 setae on distal lobe on one side.) Scaphognathite fringed with 22-29 setae.

First Maxilliped (Fig. 60 G) - Coxa with 1 epipod bud; basial setation unchanged. Endopod with 2, 2, 1, 2, 2+4 setae; exopod with 10 plumose natatory setae.

Second Maxilliped (Fig. 60 H) - Coxa with 1 biramous epipod bud (future epipod and podobranch); basis and endopod setation unchanged. Exopod with 10 plumose natatory setae.

Third Maxilliped (Fig. 60 I, J) - Endopod and exopod buds elongate, with 1 epipod bud and 2 gill buds (future arthrobranchs) on basal part.

Pereiopods (Fig. 60 J) - Segmented buds, gill formula unchanged.

Abdomen (Fig. 60 A, K) - First somite with 2 dorso-median setae. Processes on posterio-lateral margin of 3rd-5th somites prominently elongate.

Pleopods (Fig. 60 A) - Simple buds on 2nd-6th abdominal somites.

Telson (Fig. 60 A, K) - Median length increased compared with 3rd zoea, with 5 pairs of marginal spines, innermost 2 pairs smaller than others.

Fifth Zoea

(Fig. 61)

Size - TT : 4.36 mm (only 1 measured)

3.75-4.10 mm (Millport specimens)

CL : 1.41 mm (1.37-1.44 mm)

Colour - Similar to 4th stage.

Carapace (Fig. 61 A) - Similar to 4th stage, but anterio-median margin with 4 pairs of setae; 14 (15 in Millport specimens) setae on the posterio-lateral margin

Antennule (Fig. 61 B) - With 2 small setae on proximal part. Endopod present as small bud; exopod with 12 aesthetascs.

Antenna (Fig. 61 C) - Endopod elongate, more than 1.5 times length of exopod; spinous process about 2 times length of exopod. Setation of exopod unchanged.

Mandible (Fig. 61 D) - Mandibular palp present as small bud.

Maxillule (Fig. 61 E) - Coxal endite with 3+6 setae; basial endite with 10+6 setae. Setation of endopod and outer margin unchanged.

Maxilla (Fig. 61 F) - Proximal and distal lobes of coxal endite with 2+3 and 3+1 setae respectively. Proximal and distal lobes of basial endites with 4+3 and 3+4 setae respectively. Setation of endopod unchanged. Scaphognathite with 38-42 (34-38 in Millport specimens) setae.

First Maxilliped (Fig. 61 G) - Epipod on coxa elongate. Setation of basis and endopod unchanged. Exopod with 11 plumose natatory setae.

Second Maxilliped (Fig. 61 H) - Biramous epipod bud (future epipod and podobranch) on coxa unchanged. Setation of basis and endopod unchanged. Exopod with 12 plumose natatory setae.

Third Maxilliped (Fig. 61 I) - Epipod and gill buds (future arthrobranchs) elongate. Endopod bud larger than exopod bud.

Pereiopods (Fig. 61 J) - Similar to 4th stage. Gill formula unchanged.

Abdomen (Fig. 61 A, K) - Shape similar to 4th zoea. First somite with 3 dorsal setae.

Pleopods (Fig. 61 A) - Elongate biramous buds on 2nd-6th abdominal somites.

Telson (Fig. 61 K) - Median length increased compared with 4th stage; 5+5 or rarely 6+5 (6+6 in Millport specimens) marginal spines. Dorsal spine on telson fork smaller than lateral spine.

Megalopa

(Figs. 62, 63)

Size - TT : 3.64 mm (3.47-4.02 mm)

CL : 2.82 mm (2.67-3.00 mm)

2.60-2.65 mm (Millport specimens)

TL : 4.73 mm (4.67-5.00 mm)

Colour - Red chromatophores on ventral and on posterio-lateral part of carapace, on midgut (under carapace), on ventro-basal part of rostrum, and on proximal part of basis of 3rd maxilliped. Posterior spine of carapace tinged with light yellow. Pereiopods tinged with light yellow, but proximal parts of dactyli and outer surface of coxae of 2nd-5th legs tinged with red. Blackish chromatophores on ventro-lateral corners of 2nd-5th abdominal somites. Red chromatophores on anterio-ventral part of telson.

Carapace (Fig. 62 A-C) - Longer than broad; rostrum long and horizontally directed; a median ventral conical process at base of rostrum; gastric region with 2 median shallow furrows;

branchial region with well-defined carina; posterior region with a posteriorly directed horizontal spine.

Antennule (Fig. 62 D) - Peduncle 3-segmented: 1st segment bulbous, 2nd with 3 setae and 3rd with 1 or 2 setae. Endopod 2-segmented with 4 terminal setae on distal segment (sometimes an additional subterminal seta in Millport specimens). Exopod 4-segmented with 0, 5, 6, 4+3 (0, 8, 8, 6 in Millport specimens) aesthetascs/setae.

Antenna (Fig. 62 E) - Peduncle 3-segmented with 1, 1, 5 setae (5, 2, 4 setae in Millport specimens). Flagellum 8-segmented with 0, 1, 4, 0, 4, 0, 4, 5 setae (0, 2, 4, 0, 4, 1, 4, 5 in Millport specimens).

Mandible (Fig. 62 F) - Cutting edges well-developed, not clearly divided in incisor and molar processes; palp incipiently 3-segmented, with 1+8 setae on the distal segment.

Maxillule (Fig. 62 G) - Coxal and basial endites with 1+9 (11-12 in Millport specimens) setae and 13+7 (25 in Millport specimens) setae respectively. Endopod 2-segmented with 1, 2+2 setae.

Maxilla (Fig. 62 H) - Proximal and distal lobes of coxal endite with 6 (5 in Millport specimens) and 4 setae respectively. Proximal and distal lobes of basial endite with 1+9 and 1+7 (9 and

8 in Millport specimens) setae respectively. Endopod a simple lobe with minute marginal teeth and 4 setae on outer margin. Scaphognathite fringed with 61-63 (72 average in Millport specimens) plumose setae.

First Maxilliped (Fig. 63 A) - Epipod a well-developed process with 2+9 long setae. Coxal and basial endites with 11 and 20 setae respectively. Endopod not distinctly segmented, distal part flattened, with convex outer margin, with subterminal group of 5 setae and terminal group of 2+2 setae. Exopod 2-segmented, proximal segment with 1 seta and distal segment with 1+1+5 plumose setae.

Second Maxilliped (Fig. 63 B) - Coxa with 1 epipod and 1 gill bud (future podobranch). Endopod 5-segmented with 0, 2, 0, 5, 9 setae. Exopod 2-segmented, distal segment with 5 plumose setae.

Third Maxilliped (Fig. 63 C) - Coxa with 2 gill buds (future arthrobranchs), 1 epipod and 1 small gill bud (future podobranch) at base of epipod. Exopod 2-segmented, distal segment with 4 plumose setae.

Pereiopods (Fig. 63 D-H, E'-G') - All segmented and sparsely spinous. First pereiopod with 2 gill buds (future arthrobranchs) at base of coxa; 2nd with 1 gill bud (future arthrobranch) on coxa; 3rd with 1 gill bud (future pleurobranch) on coxa; 4th and

5th devoid of gill buds. First pereiopod without a coxal or an ischial spine; 2nd with a coxal and an ischial spine, 3rd to 5th pereiopods without coxal or ischial spine. Dactyls of 2nd to 5th pereiopods stout, slightly curved distally, lower margins of 2nd to 4th pereiopods with 5 stout spines, conspicuously spinulate on 2nd and 3rd. Upper inner surface of 2nd and 3rd dactyls with at least 4 and 3 stout setae near their respective margins. Dactylus of 5th with 1 long straight seta and 2 long curved setae, one of them highly pectinate on distal part.

Abdomen (Fig. 62 A, C, I, J) - Six somites, with 6, 6, 5, 5, 3 pairs of surface setae; posterio-lateral margin of 2nd-5th somites broadly truncate.

Pleopods (Fig. 62 A, J-L) - Endopod small with minute curved processes. Exopod fringed with 17-19 plumose natatory setae (1st to 4th pairs respectively with 18-20, 18-20, 17-18, 18 setae in Millport specimens).

Uropods (=pleopod on 6th somite) (Fig. 62 J, M, M') - Uniramous with 10 plumose natatory setae. In Millport specimens 1 seta on proximal segment and 9 setae on the distal segment (One specimen with abnormal setation on telson has total of 11 setae.).

Telson (Fig. 62 I, J, M, M') - Broader than long, subquadrate with 2 pairs of median dorsal setae. In Millport specimens telson

(Fig. 62 M') broader than long in all specimens and distally rounded.

DISCUSSION

Variability of laboratory reared larvae belonging to the same species but from separated localities has received little study, but the available evidence suggests that there is considerable variation of some characters used to identify brachyuran larvae. The best documented reported to date is, perhaps, the absence of the setae on the outer margin of the maxillule basial endite in some populations of majid zoeae (Ingle, 1982; Clark, 1983), but other differences have been noted when laboratory reared larvae of the same species from widely separated localities were compared (Ingle, 1977). In the present study the parent females were collected from adjacent sea areas (Irish Sea and Firth of Clyde), but the larvae show a number of differences when compared, particularly in the later stages of development. These differences are chiefly in setal armature of the carapace posterio-lateral margin, scaphognathite, and telson spines of the zoeae, and setation of the antennular exopod, antennal flagellum, maxillule and maxilla and telson shapes of the megalopas. It is not known whether this reflects genotypic variability or is the result of dissimilar environmental regimes during rearing.

Two species of *Atelecyclus* occur in the N.E. Atlantic, *Atelecyclus rotundatus* (Olivi) and *Atelecyclus undecimdentatus* (Herbst), but nothing is known about the larval stages of the latter species. At present the larvae of *A. rotundatus* can be recognised by having the following combined features:

Zoea

1. Distal segment of maxillule endopod with 5 setae.
2. Maxilla endopod with 3+4 setae (very rarely with 3+5 in fourth stage zoea).
3. Maxilla coxal endite in first stage zoea with total of only 5 setae.
4. Endopod basial segment of first maxilliped with 2 setae.
5. Third segment of abdomen without dorso-lateral processes.
6. Only one well developed lateral spine on telson furca.
7. Outermost spine on telson posterior margin prominently serrate.
8. Innermost spine on telson posterior margin with long setules. on inner proximal margin.

Megalopa

1. Cardiac spine present.
2. Antennal flagellum 8-segmented, setal formula 0, 1-2, 4, 0, 4, 0-1, 4, 5.
3. Scaphognathite of maxilla with 61-72 setae.
4. Only coxa and ischium of second pereiopod with spines.
5. Dactyls of pereiopods 2 and 3 with 5 spines on lower and at least 3 stout setae on upper margins.
6. Exopods of first to fourth pleopods with 18-20, 18-20, 17-18, 18 setae.
7. Proximal segment of uropod with a seta.

Bigot (1979: 8) listed features for distinguishing the larvae of *A. rotundatus* from those of *Cancer pagurus* and *Liocarcinus puber*, larvae of the two last mentioned being frequently present in the plankton hauls. These combined features are: (1) tip of rostral to tip of dorsal spine length is equal to the total body length in zoeae I, II, and slightly more in later stages. (2) dorsal and rostral spines curved in stages I-II and rarely straight in last stage. (3) two lateral spines on telson furcae. (4) abdomen broad and "thickset" in all stages. (5) one pair of dorso-lateral processes on second segment of abdomen. (6) telson furcae "thickset", particularly in stages I-III. (7) telson cleft broadly arched. (8) in zoeae IV-V length of innermost seta on telson margin less than 1.5x length of longest lateral spine; two (?larger) telson spines close together (it is not certain whether Bigot observed the minute second lateral spine).

Rice (1980: 336) discussed zoeal features of the Subfamily Atelecyclinae and remarked that *Erimacrus* and *Telmessus* are "... quite distinct from those of any other brachyuran family ...". He was unable to comment further about larval affinities of species within this subfamily due to lack of evidence. The larval development of *Peltarion spinosulum* (see Iorio, 1983) and of *A. rotundatus* (present paper) are now known, and that of *Thia scutellata* (see Ingle, 1984) and of *Pirimela denticulata* (Paula, in press and pers. comm.) have been described in more detail. These accounts now enable further comments to be made on relationships of atelecyclinid genera and on the integrity of the Corystoidea (=Cancridea Glaessner, 1969: R508 and others).

Balss (1957: 1634-1636) accepted the Atelecyclidae as being composed of three subfamilies, Atelecyclinae, Acanthocyclinae and Thiinae, but the status of these subfamilies has been variously interpreted. Lebour (1928 b: 528), for example, had raised the Thiinae to family level ("Thiidae fam. n."), Balss (1957: 1635) maintained it as a subfamily and Allen (1967: 35) disregarded either status and assigned the monotypic genus *Thia* to the Atelecyclidae. Similarly, Guinot (1978: 280) elevated the Acanthocyclinae to family level under the name of Bellidae recognising this taxon as the only representative of the Superfamily Bellioidea. Rice (1980: 334) drew attention to the unusual larval features known for two of the four genera belonging to this family (*Corystoides* and *Heterozius*), evidence which supports Guinot's reappraisment.

Of the seven genera assigned to the Atelecyclinae by Balss (1957) the zoeal stages of *Erimacrus* and *Telmessus* have such unusual features that Rice (1980) suggested "... that these genera should be separated from the rest of the Atelecyclidae and perhaps also from the remaining cyclometopes." The megalopas of these genera (as described by Kurata, 1963), however, do not show any features which significantly distinguish them from the megalopas of other brachyrhynch families, except perhaps in the spination of the pereiopods. *Erimacrus isenbeckii* is reported as having spines on the coxa of pereiopod 5 and on the ischium of 1-4, whereas in *Telmessus cheiragonus* coxal spines are present on all the pereiopods and on the ischium of 1-3; in *Telmessus acutidens* these spines are confined to the coxa of pereiopod 5 and to the ischium of the first pereiopod. A comparison of larval features of *Atelecyclus* with those of *Peltarion* (see Table 6) reveals that they do not share characters that we regard here as of possible significance for expressing phylogenetic relationships of brachyuran larvae (Rice, 1980: 378). For example, in the zoeae: uniform setation of the distal segment of the endopod of maxillule, of the coxal endite and of the basial endopod segment of the first maxilliped and of the distal endopod segment of the second maxilliped; development of lateral spines on the telson furcae, and the number of zoeal stages. In the megalopa: the presence of a cardiac spine; segmentation and armature of the antennular endopod and of the antennal peduncle first segment (with spines in *Peltarion*, none in *Atelecyclus*), and the number of segments and setae composing the flagellum. Details of pereiopod armature were not described for *Peltarion* but may be found to differ from *Atelecyclus*. Thus, the larval evidence does not support the retention of *Atelecyclus* and *Peltarion* in the same subfamily, although there would seem little point in dismembering this subfamily until larval information is available for the remaining genera.

The tribe Corystoidea was established by Bouvier (1940: 215) for the families Atelecyclidae, Thiidae, Corystidae, Cancridae and

Table 6. Larval features of seven cancridean species based upon material examined except for --- 1 Iorio, 1983; 2 Bourdillon-Casanova, 1960; 3 Paula, in press; 4 Anderson, 1978; Iwata and Konishi, 1981. At least three zoeal groupings for eight *Cancer* species were recognised by Iwata and Konishi (1981). *C. pagurus* belong to their *C. irroratus/borealis* group in having the combined zoeal features listed by them on p. 390. Megalopas of *Cancer* appear to have been less well described than the zoea. *Cancer* zoeae show considerable diversity (a species from each of two groups proposed by Iwata and Konishi is included here). For example, *C. edwardsi* is unusual in having an outer seta on the maxillule basis in the first stage (see Quintana, 1983 Fig. 4 E) and *C. magister* retains a five-segmented abdomen throughout all stages (see Iwata and Konishi, 1981 p.382).

This is to certify that the thesis submitted

CHARACTER OF ZOEA I (except where stated)	*Atelecyclus rotundatus*	*Peltarion spinosulum*[1]	*Thia scutellata*	*Pirimela denticulata*[2,3]	*Cancer pagurus*	*Cancer anthonyi*[4,5]	*Corystes cassivelaunus*
Antenna:spinous process/exopod length	about 3x	less than 2x	about 2½x	about 2x	about 3½x	about 3x	about 2x
Antenna:exopod,number of terminal setae	3	3	2	2-3	3	2	2
Maxillule:endopod setation	I,5	I,6	I,6	I,6	I,6	I,5	I,6
Maxillule:coxal setation	7	8	7	6-7	7	6	6-7
Maxilla:endopod setation	3 + 4	3 + 5	3 + 5	3 + 5	3 + 5	2 + 4 or 3 + 3	3 + 5
Maxilla:basial setation	5 + 4	6 + 5 (5 + 5 in fig.)	5 + 4	5 + 4	5 + 4	4 + 4	5 + 4
Maxilla:coxal setation	3 + 2 or 2 + 3	5 + 4	3 + 4	3 + 4	3 + 3	3 + 3	4 + 4
First maxilliped:basial setation	2,2,3,3	2,2,3,3	2,2,3,3	2,2,3,3	2,2,3,3	2,2,2,2	2,2,3,3
First maxilliped:endopod setation	2,2,I,2,4+I	3,2,I,2,4+I	2,2,I,2,4+I	2,2,I,2,4+I	3,2,I,2,4+I	2,2,I,2,4+I	3,2,I,2,4+I.
Second maxilliped:basial setation	4	4	4	4	5	prob.4	5
Second maxilliped:endopod setation	I,I,4+I	I,I,5+I	I,I,3+I	I,I,3+I	I,I,4+I	I,I,4+I	I,I,4+I
Abdomen:segments 3-4,posterio-lateral margins	rounded	rounded	rounded	subtruncate	rounded	?subacute	subacute
Abdomen:separation of 6th segment at	stage III	stage III	stage III	stage III	stage IV	stage III	stage III
Abdomen:setules appear on dorsal surface of first segment at	stage III,	stage II,	stage II	stage II	stage V	not recorded	stage V
Telson: lateral spines	one large + one setule	two	one large + one setule	one small + one setule	one large + one setule	? one	absent
Telson:one lateral spine (or setule) absent from	stage III or IV	never absent	stage IV	sometimes stage IV	stage II	not recorded	stage I
Telson:dorsal setules appear at	stage V	no setules	stage IV	stage IV	stage V	not recorded	stage V
Telson:posterior margin,outermost spine	serrulate	prob. spinulate	spinulate	spinulate	serrulate	not recorded	spinulate
Telson:posterior margin additional seta acquired at	stage II	stage II	stage II	stage II	stage III	stage III	stage II
Telson:posterior margin, proximal part of innermost spine	with setules	with setules	without setules	with setules	without setules	without setules	with setules
Telson:spinules on furcae	present	not recorded	*absent*	*absent*	present	*not recorded*	present
Abdomen:bud of 5th pleopods appear at	stage V	stage IV	stage IV	stage III	stage V	stage IV	stage IV
Number of zoeal stages	V	IV	IV	IV	V	V	V
CHARACTERS OF MEGALOPA							
Carapace:cardiac spine	present	absent	absent	absent	present	present	present
Antennule:*endopod segment number* and setation	2,0-I + 4	I,2 + 5	I,I + 4	I, 2 + 4	2, 2 + 4	I,2 + 5	I,2 + 4-5
Antenna:flagellum segment number and setation	8:0,2,4,0,4,I,4,5	6:0,6,4,I,4,2	7:0,2,0,4,0,3,4	6:0,4,0,4,I,5	8:0,0,4,0, 4,0,4,5	not recorded	I7 segments +
Maxilla:scaphognathite setae, maximum number	72	approx I00	42	43	49	53	82+
Pereiopods:I,2,3,4,5,coxal spines	0,I,0,0,0	first with numerous spinules	*0,0,0,0,0*	*0,I,0,0,0*	0,I,0,0,0	not recorded	0,I,I,0,0
Pereiopods:I,2,3,4,5,ischial spines	0,I,0,0,0	not recorded	0,0,0,0,0	I,0,0,0,0	I,I,0,0,0	not recorded	I,I,I,0,0
Pereiopods:dactyls of 2,3,spines on lower margin	5,5	not recorded	5,5	4,4	4,4	not recorded	7-I0,7-I0
Abdomen:posterio-lateral process on segments 2-4	absent	on 3-4	absent	absent	absent	not recorded	on 4
Abdomen:pleopods I,2,3,4,exopod setation	I8-20,I8-20,I7-I8,I8	20,20,I7,I4	I3,I5,I3,II-I2	I6,I6,I6,I3	I6-I7,I5-I6, I5-I7,I4-I5	I6-I7,I7,I8, I6-I7,I5-I6	20,20,2I,I8
Abdomen:uropods,exopod setation	I,9-I0	0,4	0,9	0,8	0,8	0,9-I0	0,9

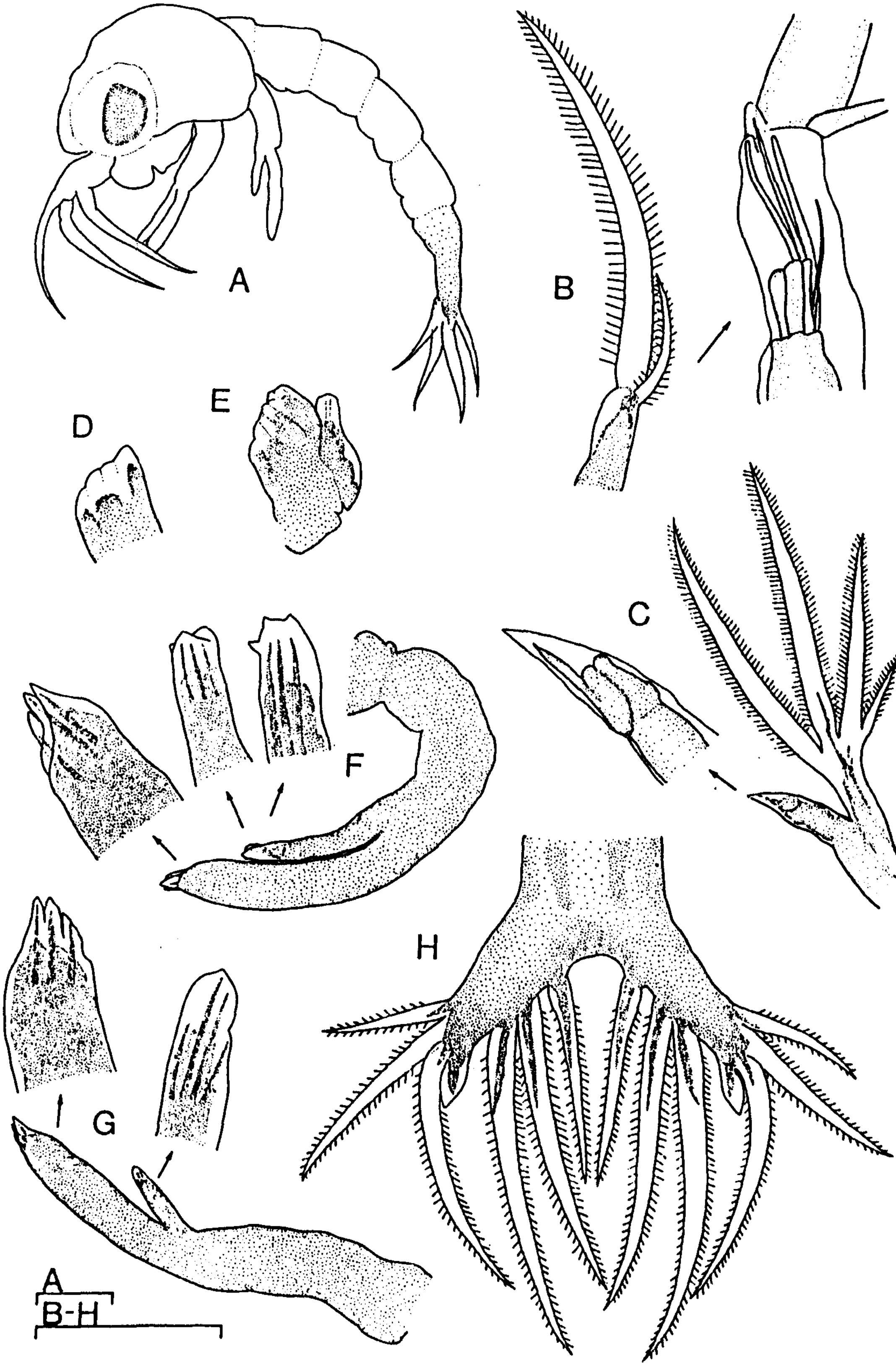
Pirimelidae. Bouvier recognised two series within the tribe, one with a longitudinally ovoid carapace (*Corystes*) and the other with a subcircular, marginally toothed carapace (*Atelecyclus, Thia*) that attains its maximum development as a transversely oval shape with blunt lobes (*Cancer*). The grouping of these families seems to have found general acceptance, and in a recent classification (Bowman and Abele, 1982: 24) they form the Section Cancridea of the Infraorder Brachyura. However, it is apparent that there is considerable variation between larvae of species assigned to the Cancridea and almost as much variability within one of the genera (*i.e. Cancer*, although this may partly reflect descriptive errors).

Within the Cancridea, the noticeable lack of shared larval features is apparent. In particular, the reduced number of setae (from the normal 1+6 to 1+5) on the distal segment of the zoeal maxillule endopod, the spine investment of the megalopal pereiopod segments, and the presence of a cardiac spine on carapace. These combined features at least remove *Atelecyclus* from this Section. Similar incongruencies are apparent when the setation of the first and second maxillipeds, spination of the telson furcae and posterior margins, and the number of zoeal stages are compared in these genera. Furthermore, the megalopas show variability with respect to the presence or absence of a cardiac spine, the number and setae of the segments of the antennal flagellum, the scaphognathite and the pleopod exopod and the spination of the pereiopods.

The present larval evidence therefore suggests that taxonomic reappraisal is needed of the Subfamily Atelecyclinae and also indicates that there is little support for the maintaining the present concept of the Cancridea.

Fig. 56. *Atelecyclus rotundatus* (Olivi), Prezoea

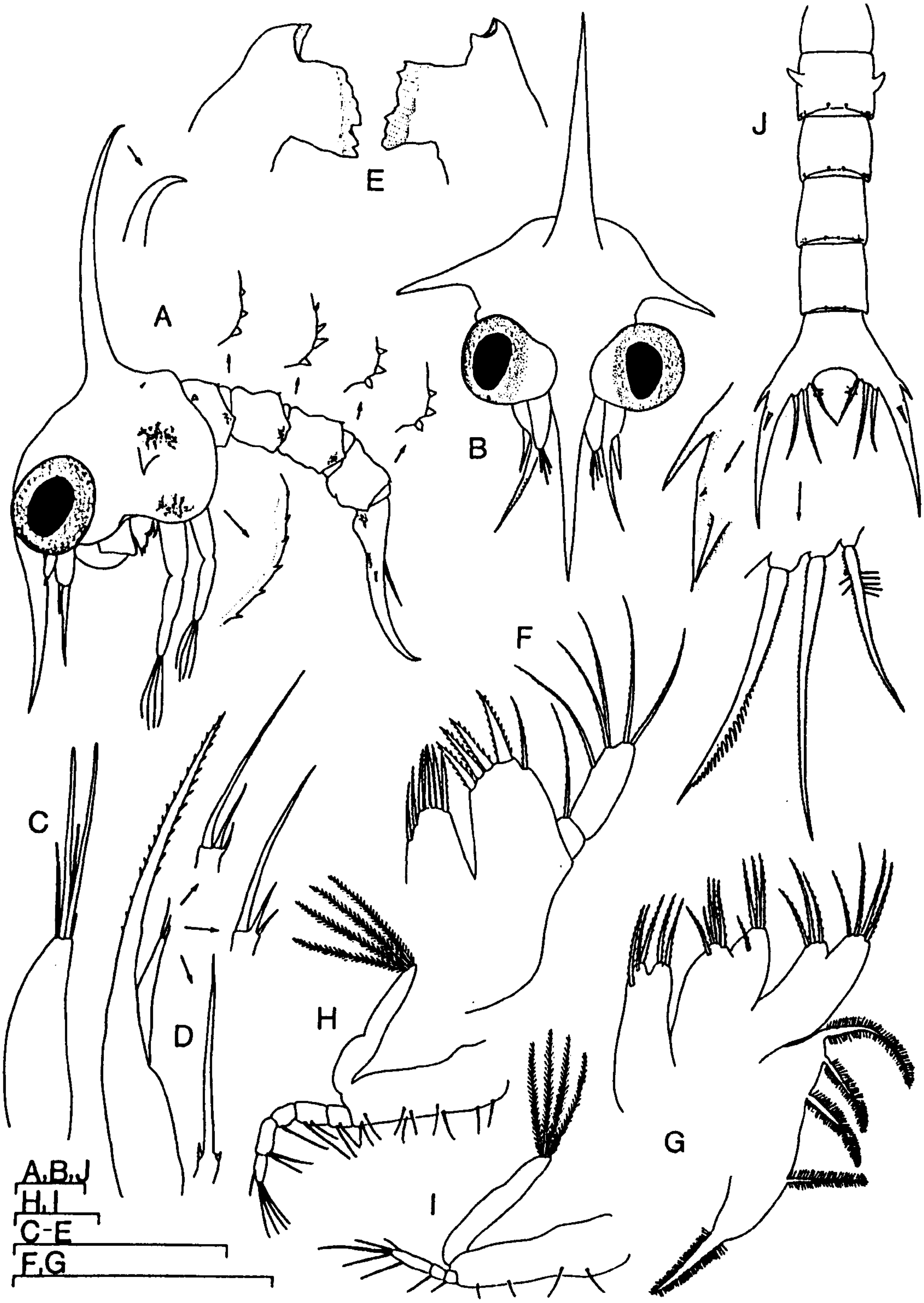
A, lateral view; B, antennule; C, antenna; D, maxillule; E, maxilla; F, first maxilliped, G, second maxilliped, H, telson. Scales = 0.2 mm



A
B
C
D
E
F
G
H
A
B-H

Fig. 57. ***Atelecyclus rotundatus*** (Olivi), First Zoea

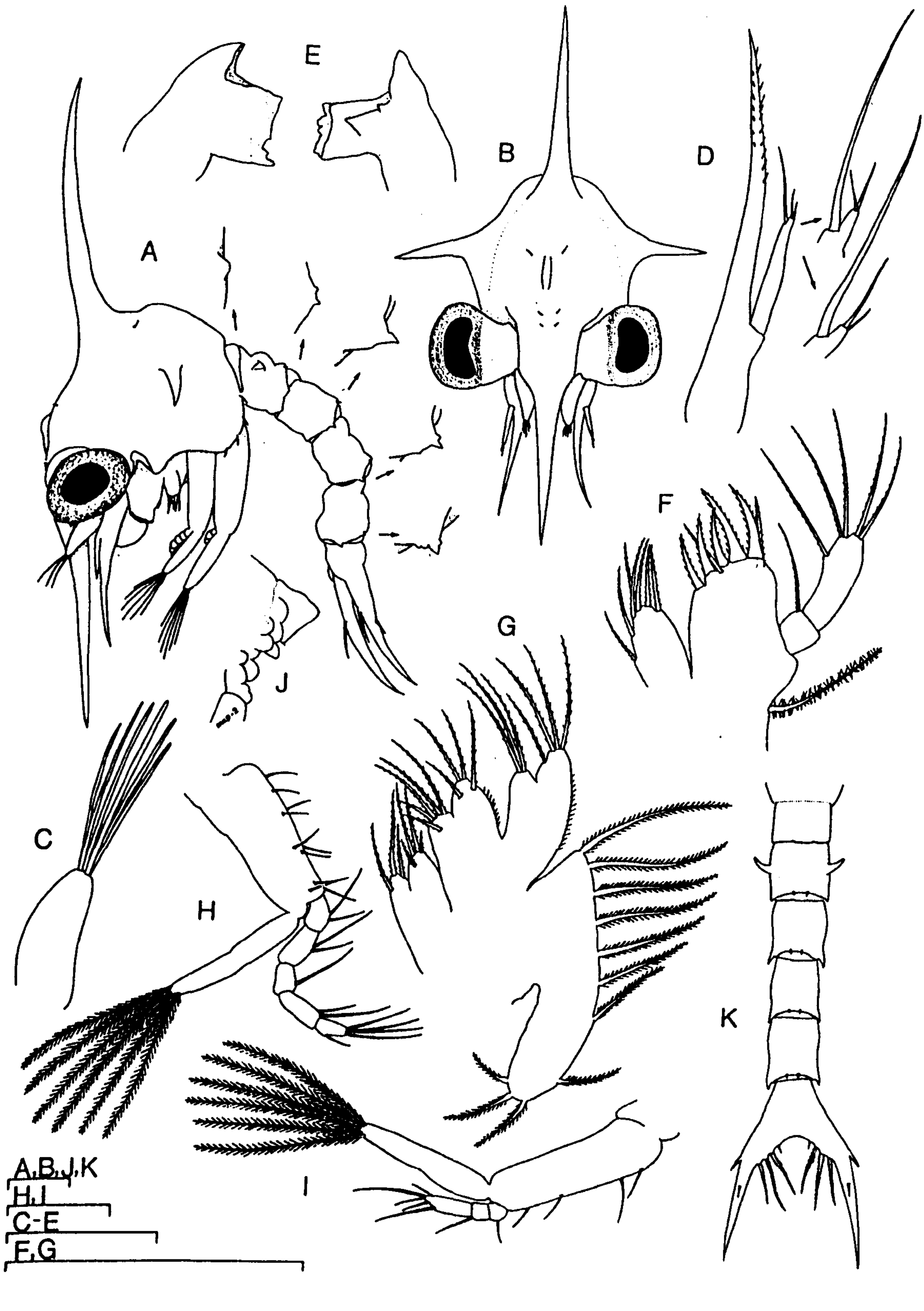
A, lateral view; B, frontal view; C, antennule; D, antenna, Inset shows variation of setal armature; E, mandible; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped; J, abdomen and telson. Scales = 0.2 mm



A
B
C
D
E
F
G
H
I
J
A,B,J
H,I
C-E
F,G

Fig. 58. ***Atelecyclus rotundatus*** **(Olivi), Second Zoea**

A, lateral view; B, frontal view; C, antennule; D, antenna, Inset shows variation of setal armature; E, mandible; F, maxillule; G, maxilla; H, first maxilliped; I, second maxilliped; J, third maxilliped and pereiopod buds; K, abdomen and telson. Scales = 0.2 mm



E
B
D
A
F
G
J
C
H
K
I
A,B,J,K
H,I
C-E
F,G

Fig. 59. ***Atelecyclus rotundatus*** (Olivi), Third Zoea

A, lateral view; B, antennule; C, antenna; D, mandible;, E, maxillule; F, maxilla; G, first maxilliped; H, second maxilliped; I, third maxilliped; J, pereiopod buds; K, abdomen and telson. Scales = 0.2 mm

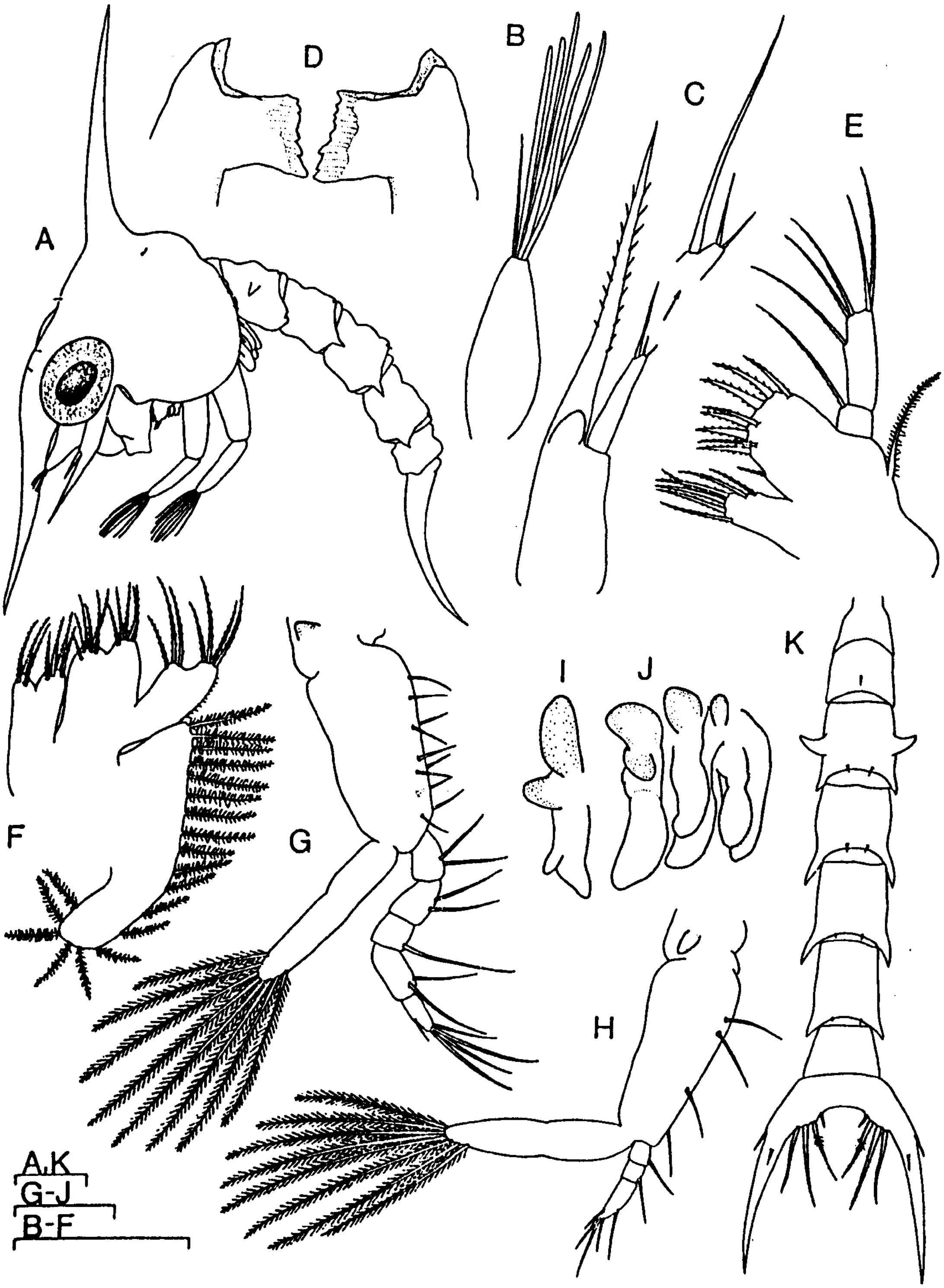

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Fig. 60. ***Atelecyclus rotundatus*** (Olivi), Fourth Zoea

A, lateral view; B, antennule; C, antenna; D, mandible; E, maxillule; F, maxilla; G, first maxilliped; H, second maxilliped; I, third maxilliped; J, third maxilliped and pereiopod buds; K, abdomen and telson. Scales = 0.5 mm

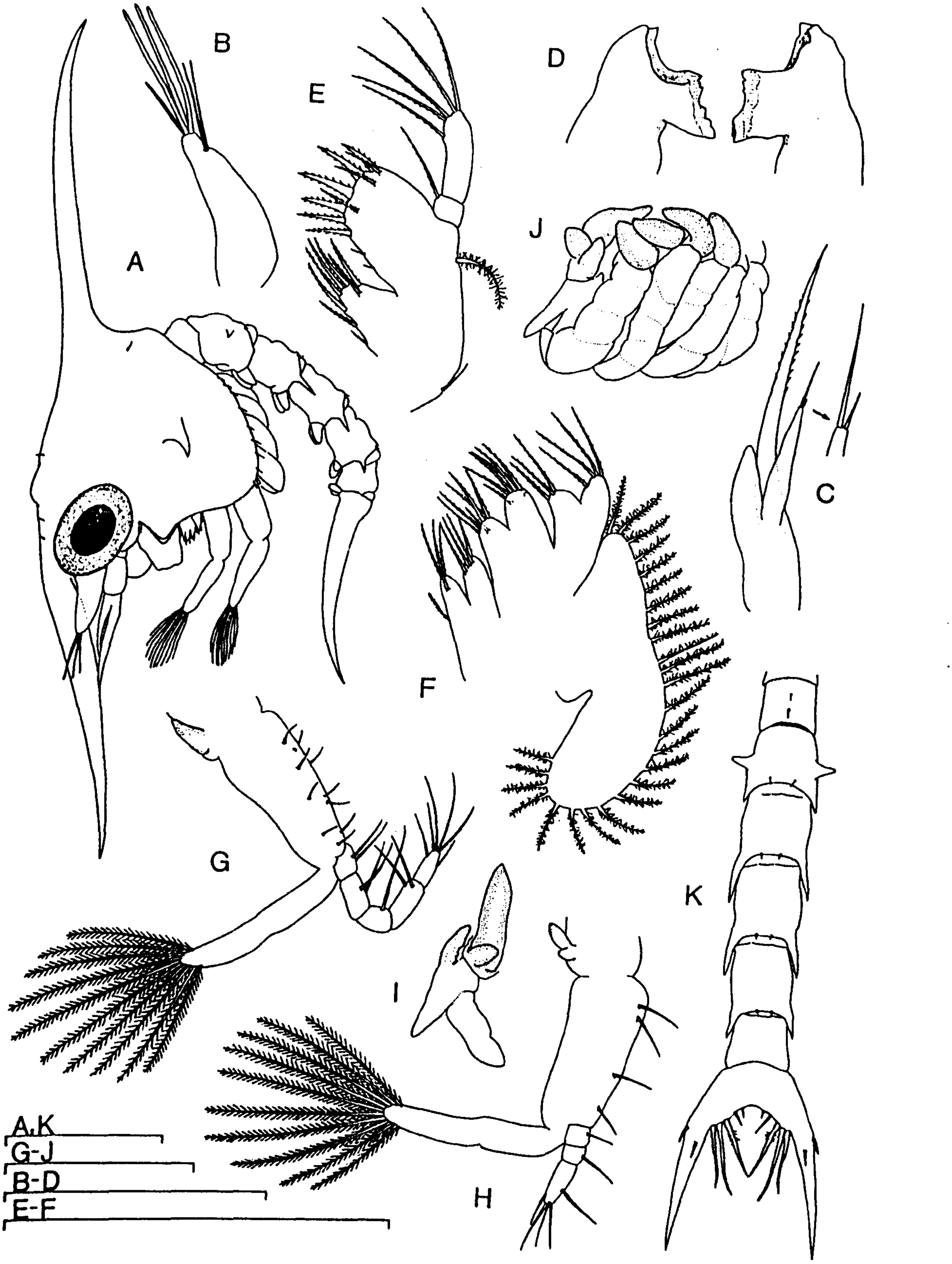
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Fig. 61. ***Atelecyclus rotundatus*** (Olivi), Fifth Zoea

A, lateral view; B, antennule; C, antenna; D, mandible; E, maxillule; F, maxilla; G, first maxilliped; H, second maxilliped; I, third maxilliped; J, pereiopods; K, abdomen and telson. Scales = 0.5 mm

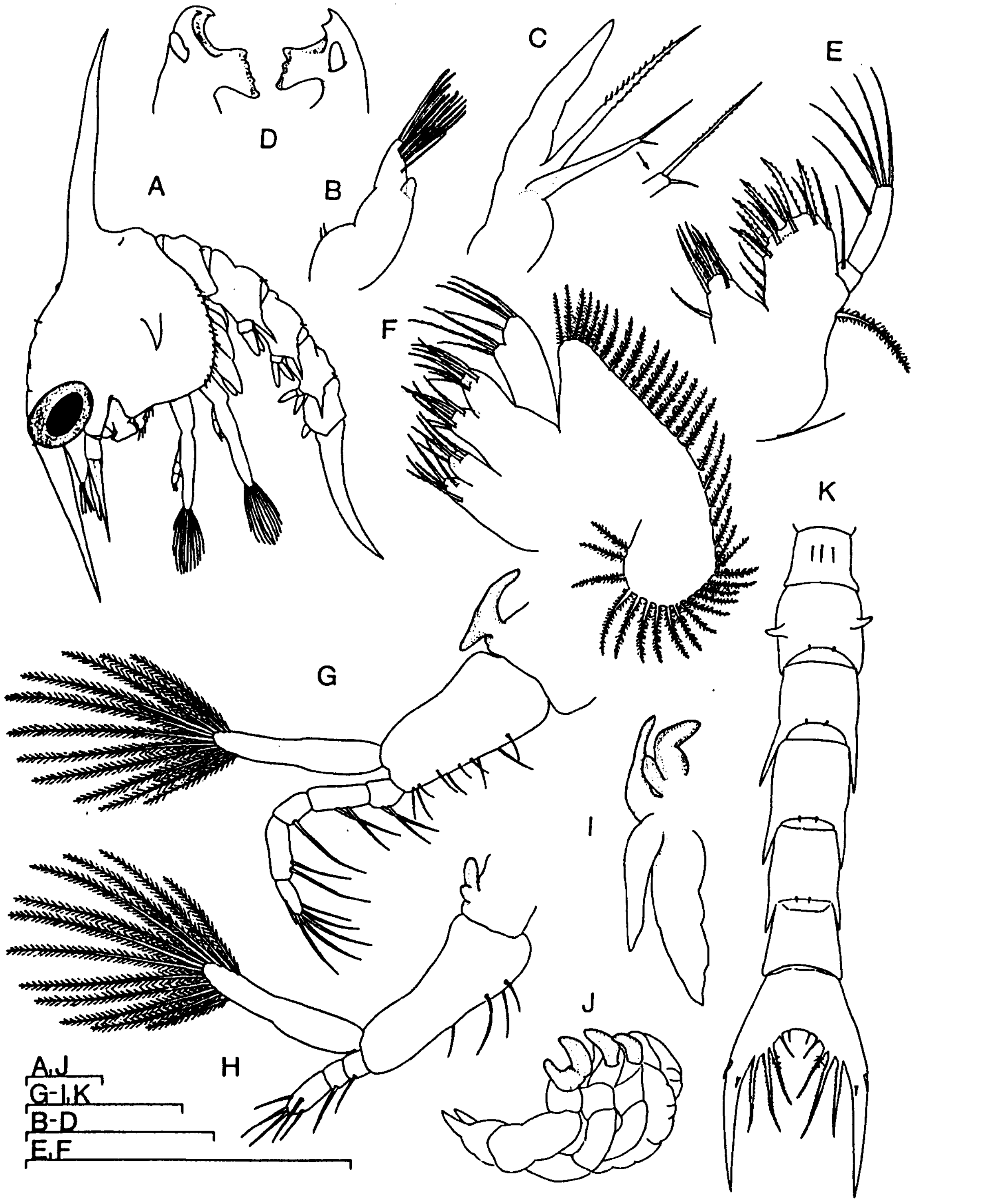
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Fig. 62. *Atelecyclus rotundatus* (Olivi), Megalopa

A, lateral view; B, lateral view of carapace; C, dorsal view; D, antennule; E, antenna; F, mandible; G, maxillule; H, maxilla; I, dorsal view of abdomen and telson; J, lateral view of abdomen and telson; K, pleopod on 2nd somite; L, pleopod on 5th somite; M, uropod and telson; M', uropod and telson of Millport specimens. Scales = 0.5 mm

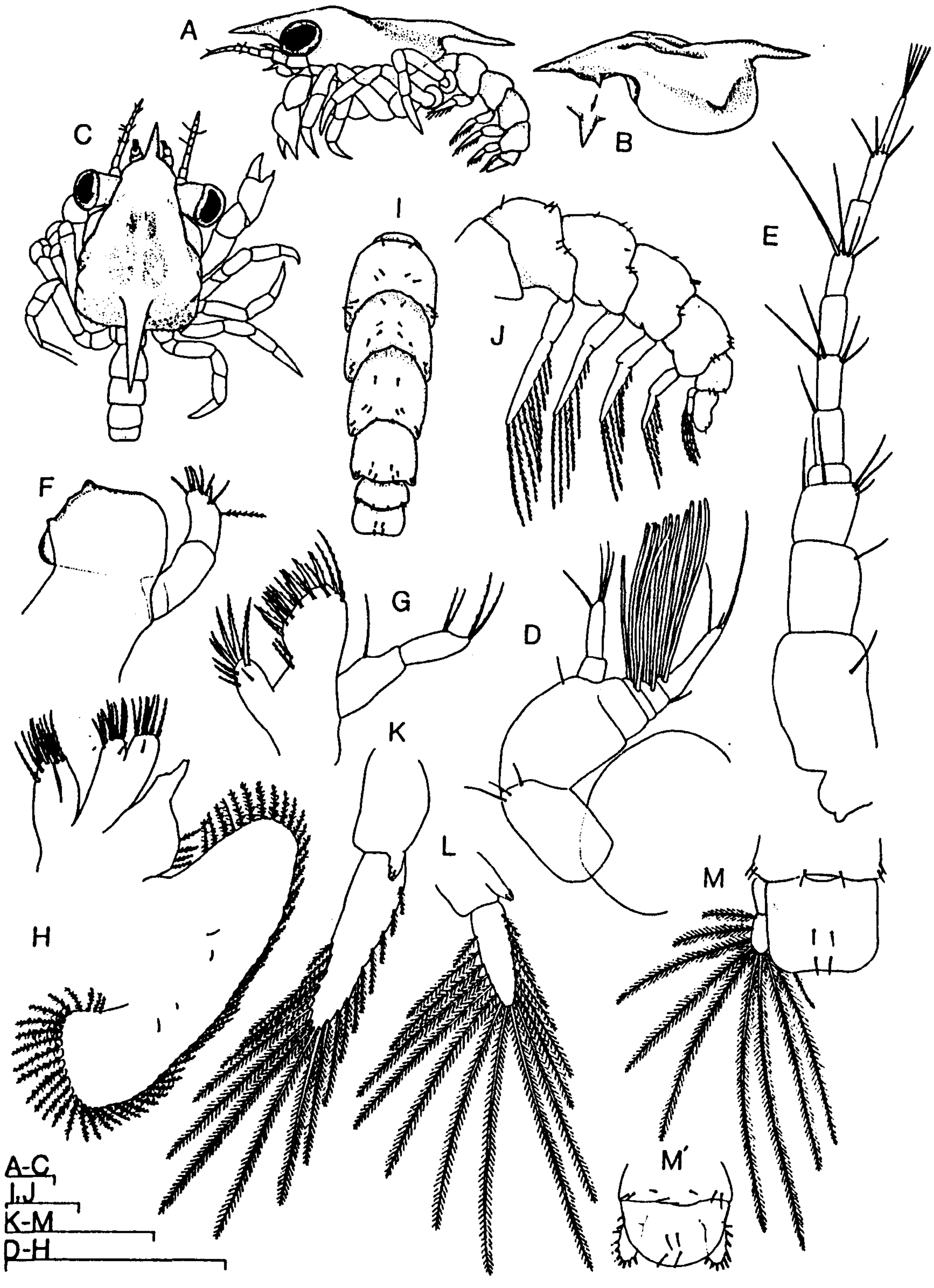
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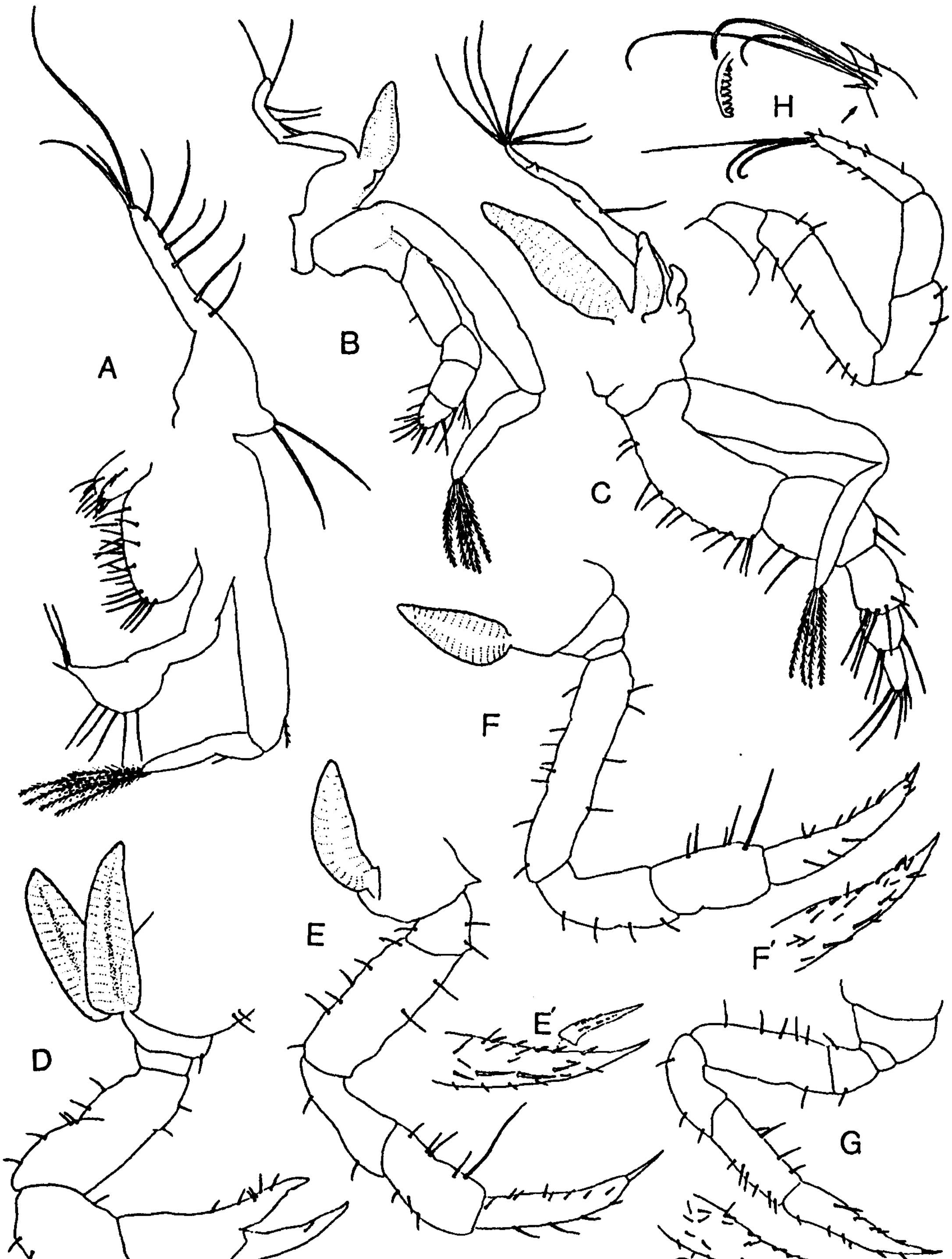
Fig. 63. ***Atelecyclus rotundatus*** (Olivi), Megalopa

A, first maxilliped; B, second maxilliped; C, third maxilliped; D-H, first to fifth pereiopods; E'-G', dactyls of second to fourth pereiopods (Millport specimens). Scale = 0.5 mm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CHAPTER 7

GENERAL DISCUSSION

In the prezoeas of decapod crustaceans, there is a gradual trend towards better development of processes on the antennule, antenna and telson from carideans to anomurans, and a gradual reduction from majids through cyclometopous species to pinnotherids. These features of development and reduction of prezoeal processes can be intepreted in terms of swimming ability and the duration of the prezoea. A prezoea provided with well-developed processes seems to be a more efficient swimmer than one with reduced processes. In majids, for example, processes on the antennule, antenna and telson are densely plumose and articulated at the proximal end, like the setae of the zoeal stage.

The present work shows that those species with well developed prezoeal processes have a prezoeal phase of comparatively longer duration. It is assumed that the well developed prezoea results in primitive condition and that reduction in the prezoeal processes has occurred independently in several evolutionary lines. The functional significance of the prezoea remains unclear.

In the present study, data on the duration of prezoeas are not sufficient to establish this opinion. Studies on the relationships between the development of processes and duration of the prezoeal stages are recommended for further research.

Rice (1980) assumed that "well developed spines and highly setose conditions and highly segmented appendages are plesiomorphous features, whereas reduced spination, setation and segmentation represent the derived conditions" in evolution of brachyuran larvae. The evident reduction of prezoeal processes in various decapod groups indicates that, in overall view, similar processes have occurred in the evolution of prezoeas. It appears that the evolutionary pattern is simpler to interpret in the prezoeal phase than in the zoeal phase, and that phylogenetic relationships of prezoeas are clearer in the higher taxa, above the family level. More information on the prezoeas of all the brachyuran families, including Dromiidae, Homolidae, Raninidae, Tymolidae and Pinnotheridae, are desirable for the further understanding of brachyuran evolution.

Burkenroad (1981: 258) stated that there is "a total lack of podobranchs in all Anomala" and "a total loss of arthrobranchs posterior to the first leg in Brachyura". Development of gills in two Pagurus species shows no exceptions in these features of Anomala (=Anomura). However, in brachyurn larvae, we need more information to support his opinion. Burkenroad (1981) was convinced that the Brachyura are characterized by the delayed appearance of posterior arthrobranchs (relative to posterior pleurobranchs) during development. But his conclusion was based on the observations by Gurney (1924 b) on the larval gills of an uncertain Dromia species, and it is suggested that this evidence is not sufficient to be regarded as a feature of the whole Brachyura. Studies on the gill development of macrurans, anomurans, primitive brachyurans and pinnotherids are desirable. The Pinnotheridae are particularly interesting because of the wide range of zoeal characters shown by different members of the family and because they provide the first known instance of gills which appear as rudiments in the larvae and then disappear as the crab develops further.

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