UNITED STATES DEPARTMENT OF THE INTERIOR, Stewart L. Udall, *Secretary*
FISH AND WILDLIFE SERVICE, Clarence F. Pautzke, *Commissioner*
BUREAU OF COMMERCIAL FISHERIES, Donald L. McKernan, *Director*

EARLY DEVELOPMENTAL STAGES OF PINK SHRIMP, *PENAEUS DUORARUM* FROM FLORIDA WATERS

By SHELDON DOBKIN

FISHERY BULLETIN 190

From Fishery Bulletin of the Fish and Wildlife Service

VOLUME 61

[Contribution No. 310, Marine Laboratory, University of Miami]

PUBLISHED BY UNITED STATES FISH AND WILDLIFE SERVICE • WASHINGTON • 1961
PRINTED BY UNITED STATES GOVERNMENT PRINTING OFFICE, WASHINGTON, D.C.

For sale by the Superintendent of Documents, U.S. Government Printing Office, Washington 25, D.C.
Price 30 cents

The series, Fishery Bulletin of the Fish and Wildlife Service, is cataloged as follows:

U.S. *Fish and Wildlife Service.*
Fishery bulletin. v. 1–
Washington, U.S. Govt. Print. Off., 1881–19

v. in illus., maps (part fold.) 23–28 cm.

Some vols. issued in the congressional series as Senate or House documents.
Bulletins composing v. 47– also numbered 1–
Title varies: v. 1–49, Bulletin.
Vols. 1–49 issued by Bureau of Fisheries (called Fish Commission, v. 1–23)

1. Fisheries—U.S. 2. Fish-culture—U.S. I. Title.

SH11.A25 639.206173 9—35239*

Library of Congress [59r55b1]

CONTENTS

ABSTRACT

The eggs and the larval and first two postlarval stages of the pink shrimp, *Penaeus duorarum* Burkenroad, from Florida waters are described and illustrated. A series of drawings of the rostra of advanced postlarvae is included.

The first six larval stages through the first protozoea were reared from eggs spawned in the laboratory. The remaining larval and postlarval stages are described from specimens obtained in plankton samples taken in the Florida Bay and Dry Tortugas areas.

The larval and postlarval stages of *P. duorarum* are compared with those of *P. setiferus*. Postlarval stages of *P. aztecus* are compared with those of *P. duorarum*.

EARLY DEVELOPMENTAL STAGES OF PINK SHRIMP, *PENAEUS DUORARUM*, FROM FLORIDA WATERS

By Sheldon Dobkin, Marine Laboratory
University of Miami

Study of the life history of penaeid shrimps has received great impetus in the past 25 years with the increased commercial importance of many of the species. The species of most importance commercially belong to the genus *Penaeus* and the developmental stages of several members of this genus have been described.

Three species of *Penaeus* are fished commercially along the South Atlantic and Gulf coasts of the United States. Of these, *P. setiferus* has received the most study; its early life history has been described by Pearson (1939). The larval development of *P. duorarum* and *P. aztecus* has not been described; however, some information on the postlarval and juvenile phases of their life history is available (Williams, 1953, 1955, 1959).

The pink shrimp, *P. duorarum*, supports a valuable fishery in Florida and accounts for approximately three-quarters of the shrimp landed in the State. The object of this study was to provide detailed descriptions of the egg and larval stages of this shrimp.

The author expresses appreciation to Drs. C. P. Idyll, G. L. Voss, and A. C. Jones, of the Marine Laboratory, University of Miami, for helpful advice during the course of this study and for critical reading of the manuscript; and to T. J. Costello and H. L. Cook, of the Bureau of Commercial Fisheries, and E. S. Iversen, of the Marine Laboratory, for valuable suggestions. The author is indebted to Mrs. D. E. Dimitriou, A. E. Jones, D. I. Dubrow, and J. H. Tweedy for their help in this study, and to Mrs. E. S. Iversen for inking the drawings of the early stages.

Note.—This work was conducted in the Marine Laboratory of the University of Miami, Miami, Fla., for the Bureau of Commercial Fisheries with Saltonstall-Kennedy funds under Contract No. 14–17–008–78.
Approved for publication, July 8, 1960. Fishery Bulletin 190.

METHODS AND MATERIALS

PLANKTON COLLECTIONS

To obtain the eggs and larvae of penaeid shrimps, which are planktonic, more than 500 plankton samples were taken between January and December, 1959, in Florida Bay and in the Dry Tortugas areas and adjacent waters. These collections were made from research vessels of the University of Miami Marine Laboratory and from commercial trawlers. Tows were made at all times of day and night and at several water depths (see table 1). The depth at which the nets were fished was determined by applying the wire angle measured by an inclinometer to the known amount of wire out. Three-quarter meter (mouth diameter) "Discovery"-type nets were used in most instances with either a No. 10 mesh silk bolting or a No. 2 mesh nylon cod end. A 1-foot (mouth diameter) "Turtox" net of No. 6 mesh silk bolting cloth was also used.

Plankton tows were generally of 30 minutes' duration except when other considerations, such as the necessity for making hydrographic observations, caused the net to be brought up sooner. A towing speed of approximately 3½ knots was maintained in most cases. The plankton was preserved in 3-percent formalin buffered with hexamethylenamine and stored in 16-ounce jars.

REARING EXPERIMENTS

Four rearing experiments were conducted from late March through July 1959. In these experiments, large females (approximately 120 to 170 mm. total length) with opaque ova were removed from the regular commercial hauls of a shrimp trawler on the Dry Tortugas fishing grounds and taken to the laboratory. The shrimp were kept

TABLE 1.—*Station data for 161 larvae and postlarvae of* Penaeus duorarum *taken from the plankton, 1959*

Station	Date	Time	Location	Depth (m.)	Number and stage of specimens
ELH 79	Mar. 14	0510	25°39′ N., 81°41′ W.	6	2 (second postlarvae).
ELH 104	June 2	0315	24°50′ N., 82°11′ W.	0	22 (first, second, and third postlarvae).
ELH 111	3	0040	24°56′ N., 82°27′ W.	0	1 (second mysis).
ELH 112	3	0205	24°58′ N., 82°31′ W.	30	1 (first mysis).
ELH 169	July 16	2045	24°55′ N., 82°03′ W.	0	46 (all stages from first protozoea through third postlarva).
ELH 172	16	0320	24°50′ N., 82°17′ W.	0	1 (first mysis).
ELH 175	17	2152	24°51′ N., 82°09′ W.	0	4 (third protozoea and first mysis).
ELH 179	18	0150	24°54′ N., 82°05′ W.	0	1 (third mysis).
ELH 185 [1]	18	0940	24°35′ N., 82°09′ W.	2	4 (advanced postlarvae).
ELH 197	18	2125	25°05′ N., 82°08′ W.	0	1 (third mysis).
ELH 221	Sept. 10	0025	24°43′ N., 82°36′ W.	28	4 (first and second protozoea).
ELH 229	10	0905	24°43′ N., 82°36′ W.	28	2 (second and third protozoea).
ELH 233	10	1300	24°43′ N., 82°36′ W.	28	25 (all stages from first protozoea through third mysis).
ELH 240	10	2105	24°43′ N., 82°36′ W.	0	18 (first and second mysis).
ELH 283	Oct. 5	2100	25°10′ N., 82°14′ W.	0	1 (second mysis).
ELH 317	10	0345	24°43′ N., 82°35′ W.	0	1 (advanced postlarva).
ELH 334a	Nov. 3	1830	Flamingo Canal	0	27 (advanced post larvae).

[1] One-minute trawl with seine.

alive in transit in plastic 20-gallon trash cans containing sea water circulated by a 12-volt pump. About 1 dozen shrimp were held successfully in each container for the duration of the 160-mile trip. The water was changed midway of the trip.

At the laboratory three to six shrimp were placed in 15-gallon aquariums, and circulation was maintained by filtering sea water through No. 6 silk bolting cloth (fig. 1). The small size of the apertures (0.24 mm.) made it certain that all eggs found in an aquarium were spawned by the shrimp being held. The runoff from each tank was drained through a section of plankton netting fitted to a collecting jar. During the course of each experiment the collecting jars and aquariums were examined for eggs and larvae, which were removed and studied microscopically. Periodically, each tank was drained and its entire contents examined.

Eggs and nauplii removed from the aquariums were held in a variety of containers ranging from petri dishes to a 4-gallon bell jar. The sea water in the smaller containers was changed frequently. In the larger vessels it was generally not renewed during the course of an experiment, but in several instances was aerated by means of an air pump. On one occasion a glass plunger provided mechanical agitation of the water in the bell jar.

Several types of food were introduced into the containers when the larvae in them reached the first protozoeal stage. The first of these was "Liquifry," a food intended for fish fry and made up of particles the size of ciliate protozoans. In subsequent experiments, cultures of the unicellular green algae, *Chlamydomonas* sp. and *Dunaliella* sp., were fed to the larvae.

In the last two experiments, an attempt was made to minimize bacterial contamination by adding antibiotics to the water in which larvae were being held. In one instance, approximately 400,000 units of penicillin were added to each of several of the gallon jars; in another, several milliliters of a broad-spectrum antibiotic (10 milligrams/milliliter aureomycin, 2 mg./ml. chloramphenicol, 2 mg./ml. streptomycin) were used.

First Experiment

The first rearing experiment took place from March 26 to April 2. Six ripe female shrimp were brought to the laboratory on March 30; three shrimp were placed in a 15-gallon aquarium, and the other three in a large concrete holding tank. Eggs were found in the collecting jar of the aquarium the following morning, and the entire aquarium was drained and the eggs gathered. The eggs were placed in a variety of containers (in 32-, 16-, and 10-ounce jars and in petri dishes) and by early afternoon they were beginning to hatch. The water in which the larvae were held was changed approximately twice daily. Within 2 days the larvae that had not succumbed in the nauplius stage, approximately 10 in number, had developed to the first protozoea. They were fed on Liquifry, approximately 1 milliliter being added per 32 ounces of water, and examination of the gut of the protozoea showed that feeding had taken place. Despite this, all the remaining larvae died in the first protozoeal stage within 5 days of the time the eggs were found. Because the number of eggs spawned was relatively small and

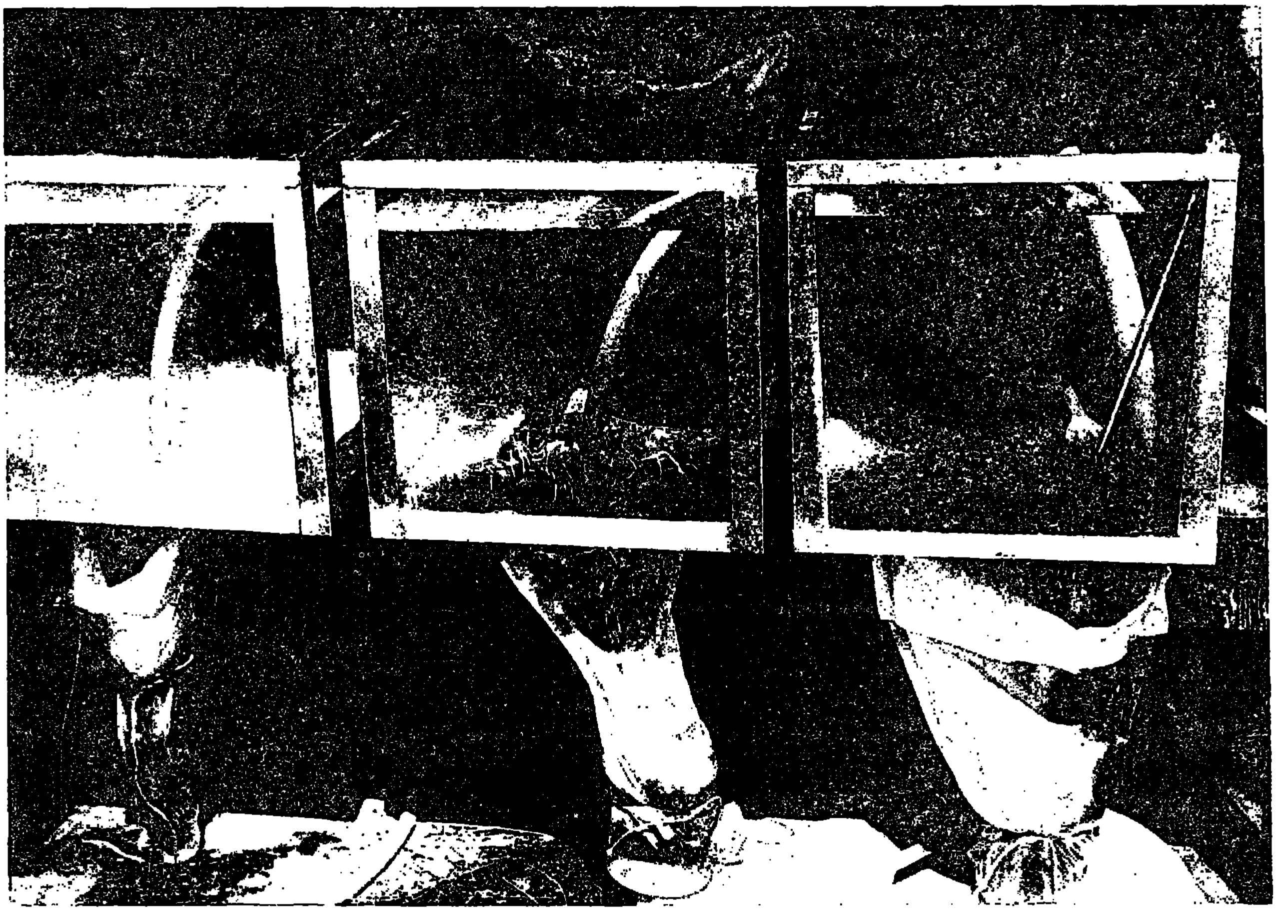

FIGURE 1.—Aquariums used in rearing experiments, showing plankton netting attached to collecting jar to catch larvae and eggs in runoff.

mortality was high, insufficient larvae were obtained to be certain of the number of naupliial stages.

Second Experiment

In the second rearing experiment, April 8 to 17, 17 shrimp were brought to the laboratory and divided among 3 aquariums. On the morning of April 13, viable eggs and both newly hatched and advanced nauplii were observed in the runoff from one aquarium. This aquarium was drained and the eggs and larvae collected and placed in 16- and 32-ounce jars as well as in a 5-gallon aquarium, the bottom of which was covered with sand and equipped with a subsand filter. Individual eggs were isolated in petri dishes in an attempt to determine the number of molts undergone by the nauplii and the interval between molts. The developing eggs and nauplii were observed continuously for 36 hours, in order to preserve specimens of each developmental stage.

The eggs isolated in petri dishes failed to develop past the first nauplius. The larvae in the 5-gallon aquarium did not survive the molt into the first protozoeal stage. Of the approximately 40 first protozoea that did develop in the 16- and 32-ounce jars, only 1 larva passed through the next molt. This high mortality in the first protozoeal stage was probably due to a combination of factors, one of which was that the larva must now seek food for the first time, having been supplied by its own yolk in the nauplial stages (Pearson, 1939; Hudinaga, 1942). During the experiment a culture of *Chlamydomonas* sp. was fed to the first protozoea in the 16- and 32-ounce jars by adding approximately one medicine dropper full of the culture per 32 ounces of water per day, and although the digestive tracts of many of the larvae were colored green, this food appeared to be inadequate. Another factor that caused high mortality was entanglement of the setae of the larvae by algae, by the shrimp's own excrement, which is emitted in long strands, and by other particles that are found in the water. The larvae so entangled settled to the bottom where they could not feed.

Eggs, the five nauplial stages, and the first protozoea were preserved in sufficient quantity during this experiment to describe these stages.

Third Experiment

The third rearing experiment took place from June 3 to June 6. Twenty-two shrimp were brought to the laboratory on June 3, and were placed in three 15-gallon aquariums. Eggs were found in two of the aquariums on the morning of June 6 and were removed and placed in 12 1-gallon jars. Approximately 400,000 units of penicillin were added to six of these jars, and the water in one was agitated mechanically. A number of the eggs developed, and two newly hatched nauplii were seen. Several hours later, however, eggs removed from the jars were not viable, and no additional nauplii were found.

Fourth Experiment

In the fourth rearing experiment, July 20–27, approximately 20 female shrimp were placed in three 15-gallon aquariums at the laboratory in the early afternoon of July 20. The following morning eggs and newly hatched nauplii were found in each aquarium and were removed to six 1-gallon jars and a 4-gallon bell jar. Approximately 5 milliliters of the broad-spectrum antibiotic were added to three of the 1-gallon jars and about 20 milliliters were added to the bell jar. The latter was agitated mechanically by a glass plunger. The water was not changed in these containers during the course of this experiment.

The larvae had advanced to the fifth nauplial stage by the late afternoon of July 22, and the following morning all the jars were found to contain first protozoea. They were fed a culture of *Dunaliella* sp. (which was used as food for oyster and clam larvae by Davis and Guillard, 1958), by adding approximately 4 milliliters to each 1-gallon jar and 10 milliliters to the bell jar daily.

High mortality again occurred in the first protozoeal stage. The larvae held in the jars to which no antibiotic was added were all dead by the afternoon of July 24, and by the morning of July 27 all of the larvae in the other jars had died. None of the larvae molted into the second protozoea despite the fact that feeding had taken place.

During this experiment, photomicrographs of the egg in various stages of development and of the nauplial and first protozoeal stages were taken.

Conclusions

To rear *Penaeus duorarum* successfully, suitable food and the prevention of crowding of the larvae are necessary. Hudinaga (1942) was successful in raising larvae of *Penaeus japonicus* through the critical protozoeal stage by feeding them the diatom *Skeletonema costatum*. He reported that the mysis stage could be raised on that diatom alone, although good results were obtained by mixing the nauplius of *P. japonicus* with the diatoms. Heldt (1938) found that the protozoea of several species of penaeids prospered on small copepods if the individual larva was isolated and the debris and excrement removed from the water.

Broad (1957) reported that caridean larvae fed on algae did no better than those that were not fed. He reared larvae to the young adult stage by feeding them *Artemia* nauplii, and limited the number of larvae placed in each 4-inch finger bowl to 10. Costlow and Bookhout (1959) were successful in rearing zoeae of the blue crab, *Callinectes sapidus*, by placing them in plastic compartmented boxes with one zoea per compartment and feeding them *Arbacia* eggs and *Artemia* nauplii. The author (unpublished data) succeeded in rearing the larvae of several species of carideans by placing from 1 to 10 larvae in each compartment of plastic compartmented boxes and feeding them on *Artemia* nauplii. Each compartment contained from 50 to 75 ml. of sea water, and the water was changed each morning.

EGG AND LARVAL STAGES

ABBREVIATIONS USED IN ILLUSTRATIONS

a1—first antenna
a2—second antenna
ab—abdomen
c—carapace
ch—chela
dt—digestive tract
e—eye
en—endopod
ex—exopod
fr—frontal organs
fu—furca
gp—gill plate
la—labium
lm—labrum
md—mandible
mp—mastigobranchial plate
mx1—first maxilla
mx2—second maxilla
mxp1—first maxilliped
mxp2—second maxilliped
mxp3—third maxilliped
o—ocellus
ped—peduncle
per—pereiopods
pl—pleopods
pr—protopod
r—rostrum
sc—scaphognathite
st—statocyst
su—supraorbital spine
th—thorax
u—uropods

EGG

Several hundred eggs were obtained from the spawning of mature female pink shrimp in the laboratory. Fifty-three viable eggs measured from 0.31 to 0.33 millimeters in diameter. The viable eggs are yellow brown in color and opaque, although when light is reflected in a certain way, the chorion shows the blue hue reported by Pearson (1939) for the eggs of *P. setiferus*.

The complete development of the fertilized egg was not observed, since the eggs were already in an advanced state when found. The development of eggs of *Penaeus japonicus* is adequately described by Hudinaga as summarized by Pearson (1939). Development in *P. duorarum* may be similar, since conditions under which the eggs of the two species of shrimp were reared and development subsequent to hatching are comparable. Photomicrographs of several stages of viable eggs were made (fig. 2).

Hatching was observed by the author in the laboratory. At water temperatures of 27° to 29° C., the nauplius emerges about 13 or 14 hours after the eggs are spawned (Hudinaga, 1942). Prior to its emergence, the nauplius moves its appendages convulsively at short intervals. After the furcal spines puncture the egg membrane, the nauplius emerges, posterior half first, by pushing against the membrane with the first antennae. Emergence from the egg requires 2 to 3 minutes.

FIGURE 2.—Photomicrograph of eggs in several stages of development.

FIRST NAUPLIUS

Individuals of the first nauplial stage (fig. 3) ranged from 0.35 to 0.40 mm. in body length. Their greatest body width was from 0.18 to 0.20 mm. Body length was measured from the anterior to the posterior end exclusive of the furcal spines. Greatest body width between the lateral margins was measured dorsally and occurred at a point between the first two pairs of appendages. Description of the first nauplius is based on 13 specimens raised from eggs.

The nauplius is yellow brown in color and opaque, the opaqueness being more pronounced in preserved specimens. Viewed dorsally the body is pear-shaped, the anterior part being the wider.

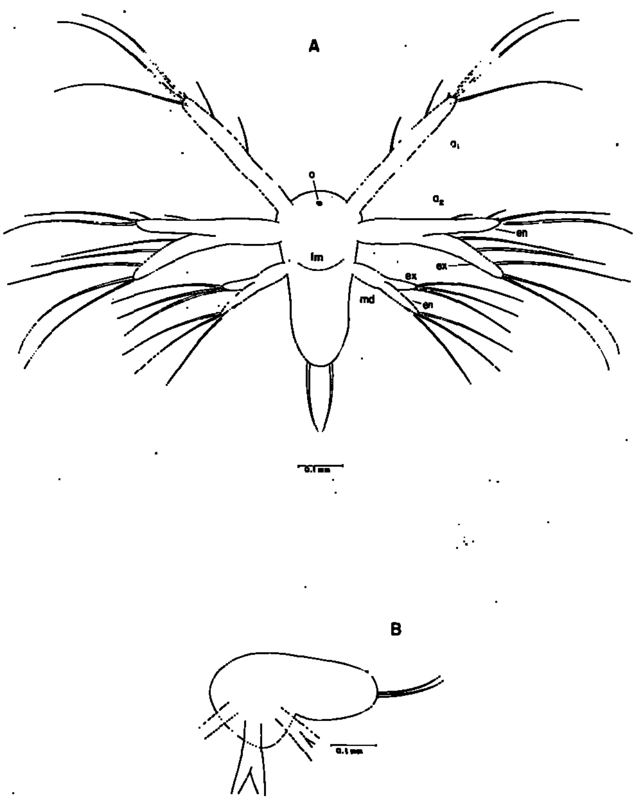

FIGURE 3.—First nauplius. (A) Ventral view. (B) Lateral view.

Newly hatched first nauplii resemble two spheres joined at the middle (fig. 4), but shortly thereafter they completely unfold and become typically pyriform (fig. 5).

Viewed laterally, the anterior part is elliptical, due to development of the labrum (fig. 3B). This structure is present at the point where the anterior and posterior halves join and where the posterior half is flexed ventrally. The body appears to be divided into anterior and posterior parts with a constriction between; nevertheless, it is not truly segmented.

An ocellus, or "nauplial eye," is present near the anterior end of the body. Posteriorly, there is a dorsally flexed pair of furcal spines which are approximately two-fifths as long as the body. A small dorsomedian triangle-shaped spine (fig. 3B) is present near the posterior end of the body.

Three pairs of appendages, natatory in function, are present: first antennae, second antennae, and mandibles. The antennae are considerably larger than the mandibles.

The first antenna is uniramous and finger-shaped and is slightly more than three-quarters the length of the body. It bears 2 short lateral setae, 2 long terminal setae, and a third long seta which appears to be terminal, but which actually arises from the dorsal surface of the appendage. The bud of a third terminal seta is present. "Short" setae measure less than 0.1 mm. in length, "moderate" setae between 0.1 and 0.2 mm., and "long" setae more than 0.2 mm.

The second antenna is biramous, the exopod slightly longer than the endopod and equal in length to the first antenna. The endopod bears 2 short lateral and 2 long terminal setae. The bud of a third terminal seta is present. The exopod bears 3 long lateral and 2 long terminal setae.

The mandible is biramous and approximately half the length of the first appendage. Each ramus bears 3 long setae. All setae on the exopod are terminal. Two of the setae on the endopod are terminal, the third seta arises from a constriction in the appendage approximately four-

FIGURE 4.—Photomicrograph of first nauplius immediately following hatching.

FIGURE 5.—Photomicrograph of first nauplius soon after hatching.

fifths of the distance from the body. Although setation of the first and the second appendage varies in the different nauplial stages, that of the mandibles remains constant.

During the nauplial stages, the larvae feed on yolk granules, which, because of their opaqueness, can easily be seen in the transparent body of the nauplius. The description of locomotion in the nauplius of *P. setiferus* (Pearson, 1939) and *P. japonicus* (Hudinaga, 1942) was found to hold true for *P. duorarum*. The nauplius swims upward by a rapid beating of its appendages, which lasts approximately 5 seconds; after that the nauplius sinks dorsal side down with its appendages extending upwards. This period of inactivity lasts several times longer than the period of activity, being from 15 to 30 seconds in duration.

SECOND NAUPLIUS

Specimens of the second nauplius (fig. 6) measured 0.40 to 0.45 mm. in length and 0.18 to 0.20 mm. in body width. The major differences between this stage and the preceding one are in the setation of the first and second antennae, the appearance of setules on the longer setae, and a slight change in the shape of the body. The description of the second nauplius is based on 27 specimens raised from eggs.

The single pair of furcal spines found in the first nauplius is still present, and no others have been added. The dorsomedian spine near the posterior end of the body is no longer present.

The first antenna bears 3 lateral setae, 2 of which are short and 1 is of moderate length; also 3 terminal setae, 1 of which is long, 1 moderate, and 1 short.

A short terminal seta has replaced the bud present in the preceding stage on the endopod of the second antenna. A short terminal seta is also added to the exopod of this appendage, making a total of 3 lateral and 3 terminal setae. The number of setae on the exopod of the second antenna increases by 1 in each successive nauplial stage and the setation of this appendage is therefore an excellent characteristic for differentiating between the various stages.

The endopod and exopod of the mandible continue to bear 3 long setae each, in the same position as in the preceding stage.

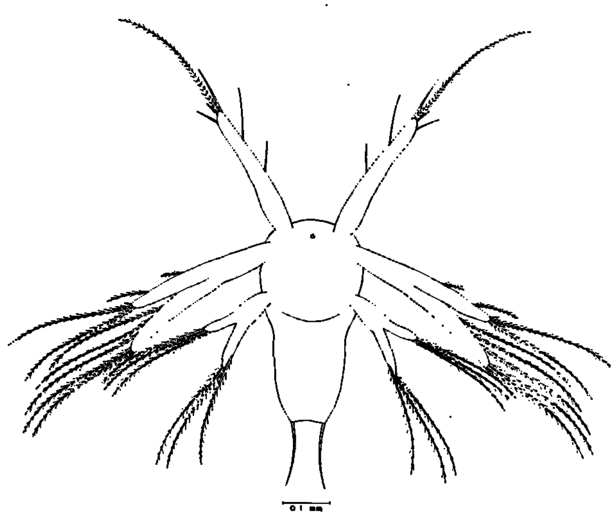

FIGURE 6.—Ventral view of second nauplius.

The posterior portion of the body of the second nauplius has become somewhat elongated. The caudal end is now truncate or concave rather than rounded.

The longer setae of the appendages have become plumose in the second nauplius with the addition of fine setules. The appendages remain unsegmented. The furcal spines do not acquire the distinct barbs reported by Hudinaga (1942) for *P. japonicus*, but their margins are no longer smooth.

THIRD NAUPLIUS

Specimens of the third nauplial stage (fig. 7) ranged in length from 0.45 to 0.49 mm. and from 0.17 to 0.20 mm. in greatest body width. Measurements were made on 24 specimens raised from eggs. The major differences between this and the preceding stage are the development of 2 distinct furcal processes, the addition of 2 spines on each of these, and differences in the setation and the first sign of segmentation of the appendages.

The caudal end of the body is now divided into 2 furcal processes with a distinct notch between. Each furca bears 3 spines, the middle one being approximately two-fifths the length of the body. The external spine measures about one-third the length of the median one and the internal spine about one-sixth. The median spine bears minute barbs but the other 2 spines are smooth. The furcal spines are flexed dorsally, as can be seen in lateral view.

The first antenna has lost its posterolateral seta and now bears 2 lateral and 3 terminal setae. The basal portion of this appendage shows traces of the segmentation that will appear in the next molt.

The endopod of the second antenna has the same complement of setae as in the preceding stage; however, the anteriormost of the terminal setae has grown to almost the length of the others.

The exopod of the second antenna has added another terminal seta, making a total of 3 lateral and 4 terminal setae.

The setation of the mandible remains the same.

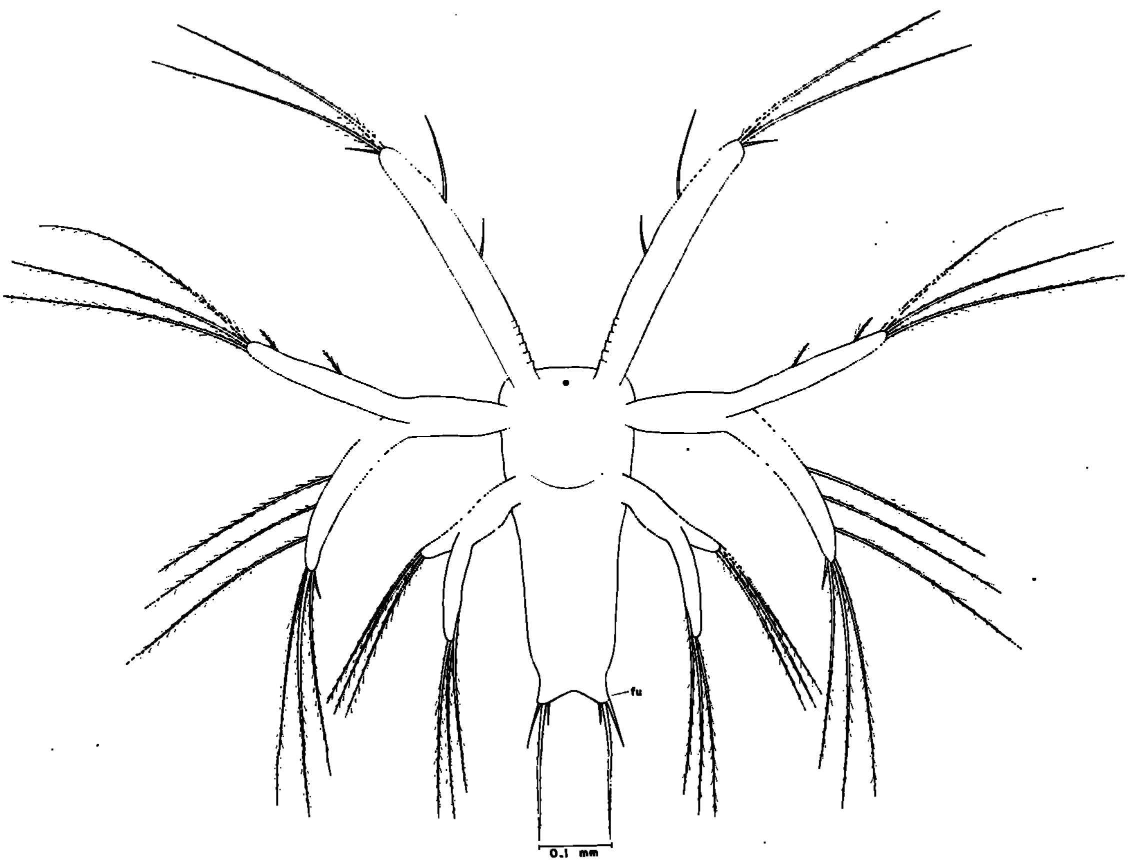

FIGURE 7.—Ventral view of third nauplius.

FOURTH NAUPLIUS

The fourth nauplii (fig. 8) examined measured from 0.48 to 0.55 mm. in body length and from 0.18 to 0.20 mm. in greatest body width. Six specimens that had been reared from eggs were studied. The major differences between this and the preceding stage are in the number of furcal spines, the appearance of the next four pairs of appendages, and segmentation and setation of the appendages.

There are now 5 spines on each furcal process, with the addition of 2 weak spines external to the 3 already present in the preceding stage. The longest spine bears minute barbs, while the other 4 are smooth.

This stage is the first in which there is a definite segmentation of the appendages. This segmentation is often indistinct and the best criterion for its determination is the presence of indentations along the margins of the appendages.

The frontal organs reported to be present in late naupliial stages in several other species of penaeids were never seen in this stage in *P. duorarum*, although several specimens were examined under 500 power specifically for this character.

FIFTH NAUPLIUS

Individuals of the fifth nauplial stage (figs. 9 and 10) measured from 0.53 to 0.61 mm. in body length and from 0.17 to 0.20 mm. in greatest body width, based on 28 specimens raised from eggs. The most noticeable differences between this and the preceding stage are the development of the masticatory portion of the mandible, the transparency of the endopod of that appendage, the increased number of furcal spines, the outline of a future carapace, and the setation of the appendages.

The furcal processes now bear 7 spines each, with the addition of 2 spines, 1 weak and 1 moderate, internal to the 5 found on each furca in the preceding stage. The 3 median spines bear minute barbs.

Frontal organs were observed on the anterior margin of several fifth nauplii taken from the

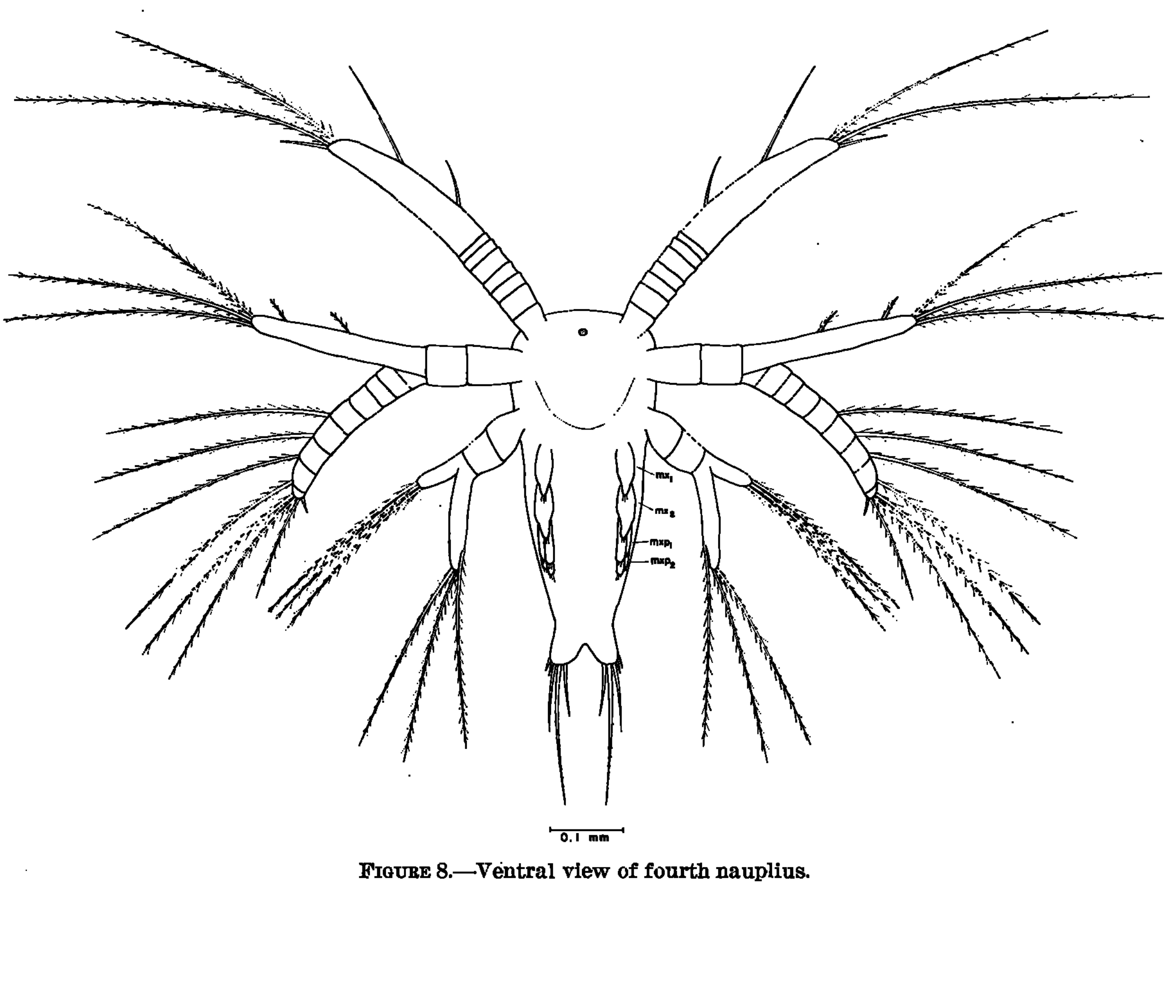

FIGURE 8.—Ventral view of fourth nauplius.

plankton. The original examination of material obtained from rearing experiments did not disclose these structures, but a photomicrograph (fig. 9) shows them clearly. With this proof of their existence and their subsequent discovery on the planktonic specimens, the presence of frontal organs was established.

The first antenna now bears 3 setae on the anterolateral and 2 on the posterolateral surfaces, as well as 3 terminal setae. This is a total of 8 setae as compared with the 5 found on this appendage in the preceding stage. The segmentation remains the same as in the fourth nauplius.

The endopod of the second antenna is unsegmented and bears 3 lateral and 4 terminal setae. Two of the lateral setae originate from the same point close to the distal end of the endopod. The exopod of the appendage now bears 9 setae, with the addition of a short lateral seta which is the most proximal to the body.

FIGURE 9.—Photomicrograph of fifth nauplius. (Note frontal organs.)

The basal portion of the protopod of the mandible has become swollen and knoblike and bears a ring of toothlike structures. The endopod has become transparent in some specimens due to loss of its musculature. The setation is the same as in previous stages.

The maxillae and maxillipeds are further developed, and cover the major portion of the ventral surface of the body posterior to the labrum. They remain nonfunctional. The developing maxillae and maxillipeds are biramous. The exopods of the maxillae take the form of swollen knobs protruding from the distal portions of the protopods and have been termed scaphognathites. The exopods of the maxillipeds are palplike in form.

In dorsal view the body appears to be in two segments. This is due to the outline of the posterior edge of the developing carapace, which can be seen under the cuticle at about the midpoint of the body.

FIRST PROTOZOEA

Forty-two first protozoea (figs. 11 and 12) of *P. duorarum* raised from eggs measured from 0.86 to 1.02 mm. in body length, from 0.35 to 0.44 mm. in body width at the widest part of the carapace, and from 0.40 to 0.49 mm. in carapace length. Seven first protozoea taken from the plankton measured from 0.98 to 1.14 mm. in body length.

The first protozoea represents the most radical change in the form of the larva up to this point. The body is clearly divided into two parts. The anterior part is covered by the carapace, which is just under one-half the body length. The carapace is rounded anteriorly with a notch at the midline. The posterior edge of the carapace is nearly straight and covers the basal portion of the second maxillipeds. The narrower posterior part is divided into a thorax of six segments and an unsegmented abdomen. The junction of thorax and abdomen is marked by a slight swelling in the latter.

Another feature differentiating this stage from the preceding one is the development of compound eyes. These can be seen under the carapace, but do not become stalked until the next stage. A 2-lobed labium just posterior and dorsal to the labrum and a digestive tract are other structures

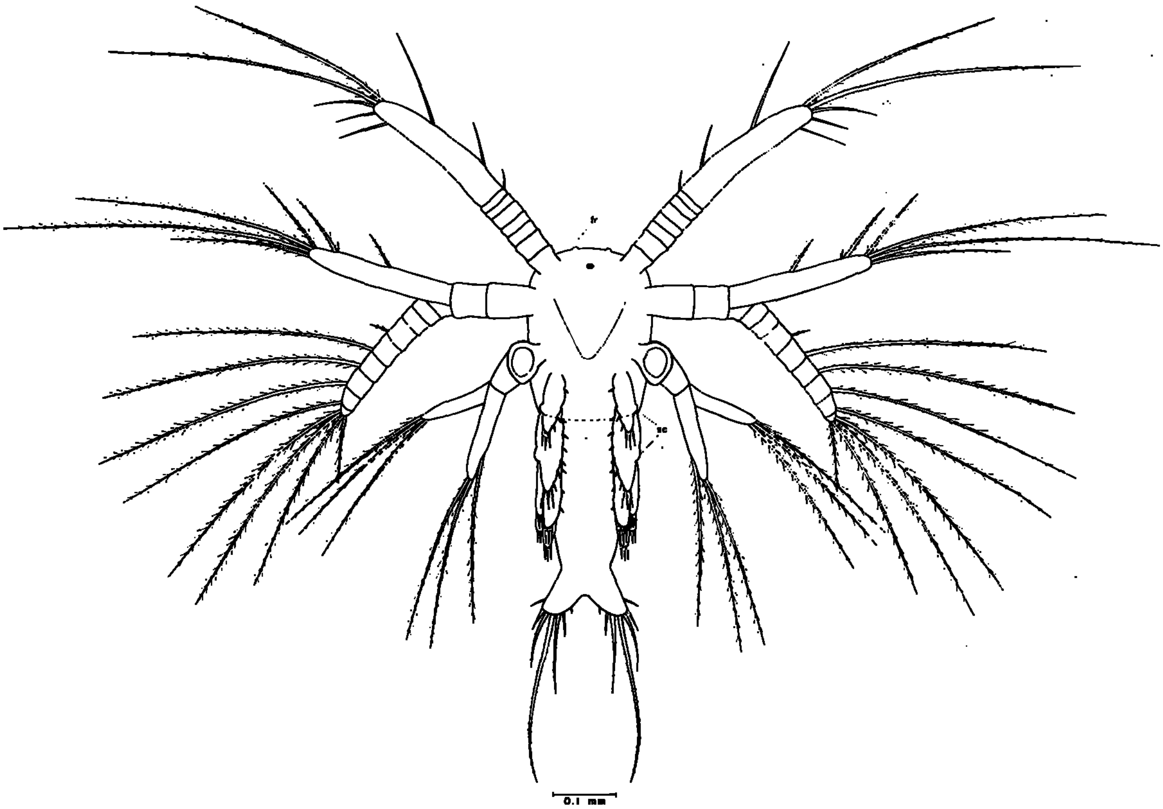

FIGURE 10.—Ventral view of fifth nauplius.

distinguishable in this stage. In addition, the mandible has lost its endopod and all but a small portion of its exopod. Its masticatory surface has, however, developed considerably. During this stage the larvae cease living on yolk and begin to seek nourishment in the water.

The ocellus persists in the midline between the developing compound eyes. Just posterior to the ocellus the two large lobes of the liver, which is dorsal to the mouth, can be seen in ventral aspect. The labrum is conspicuous as a roughly oval structure located ventrally in about the middle of the area covered by the carapace. Its posterior or free edge has a slight notch at the midline which is provided with short bristles, and the anterior edge is marked by a well-developed spine. The two lobes of the labium extend from under the labrum and have bristles along their median borders. The greater portion of the mandible consists of an irregularly shaped median masticatory lobe, which bears 6 to 8 small teeth and 3 or 4 larger ones, and a lateral rounded lobe, which bears a trace of the exopod.

The caudal furcae each bear 7 spines, as in the preceding stage. The spines have setules, except for the most external spine which is smooth. This external spine originates from the dorsal surface rather than from the lateral, terminal, or median surfaces of the furca, as do the other spines.

The first antenna is divided into three major parts. The basal portion bears 2 setae along its anterior margin. The middle portion bears 1 long seta on its anterior margin. The distal portion bears 1 dorsal and 3 terminal setae and, in addition, 1 short seta on its posterolateral margin. This is a total of 8 setae on the first antenna.

The protopod of the second antenna is 3-segmented and bears no setae. The endopod has 2 segments, the basal segment bearing 2 setae. Two additional setae are present at the junction of the 2 segments of the endopod. The distal segment bears 5 setae, making a total of 9 setae for this ramus. The exopod of the second antenna is divided into about 10 segments and bears 7 setae on its anterolateral and 2 on its posterolateral margins, as well as 4 terminal setae.

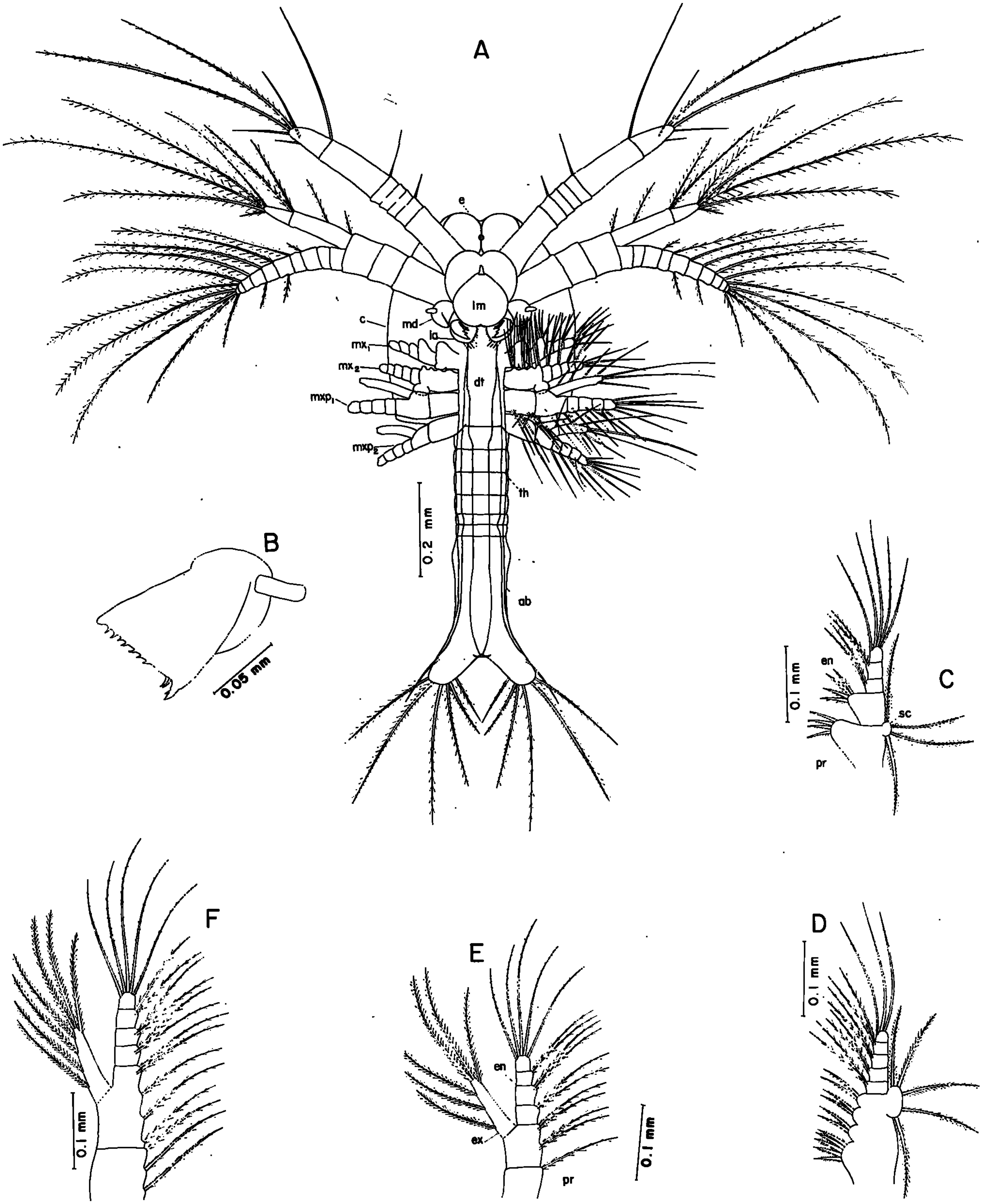

FIGURE 11.—First protozoea. (A) Ventral view. (B) Mandible. (C) First maxilla. (D) Second maxilla. (E) Second maxilliped. (F) First maxilliped.

The mandible has lost its endopod and all but a trace of its exopod, has a well-developed masticatory surface, and lies dorsal and posterior to the labrum.

The first and second maxillae and first and second maxillipeds are well developed and become functional in this stage.

The first maxilla consists of a protopod of 2 segments, an endopod of 3 segments, and a budlike exopod or scaphognathite. The inner margins of the segments of the protopod and the endopod are lobed and bear setae. The 2 segments of the protopod bear about 4 setae each. The basal and median segments of the endopod bear 2 setae each, and the terminal segment bears 5. The exopod, or scaphognathite, bears 4 setae. The 5 terminal setae of the endopod are present throughout the protozoeal and first two mysis stages. The 4 setae of the scaphognathite are present in the protozoeal and first mysis stages; the scaphognathite is not present beyond the first mysis.

The second maxilla is somewhat larger than the first. It has a protopod of 4 lobed segments. The basal segment bears about 5 setae, and the remaining 3 segments, 2 each. In the protozoeal and mysis stages the setae on the protopod of the maxillae are shorter and stouter than the setae found elsewhere on the body. Each segment of the 5-segmented endopod bears 2 setae except the terminal segment, which has 3. This latter number is constant for the protozoea, but in succeeding stages the scaphognathite increases in size and possesses an increasing number of setae.

The first maxilliped is the largest of the newly functional appendages. It consists of a 2-segmented protopod, a 4-segmented endopod, and an unsegmented exopod. Both of the latter are palplike. The segments of the protopod bear approximately 3 to 4 setae each; those of the endopod have 2 or 3 each except for the terminal segment, which bears 5 setae. The unsegmented exopod bears 7 setae.

The second maxilliped is almost identical to the first, except that it is smaller and bears fewer setae. The protopod has 2 segments and bears approximately 5 to 7 setae. The endopod is 4-segmented; the terminal segment bears 5 setae and the other 3 segments bear 2 setae each. The exopod is unsegmented and bears 6 setae.

The digestive tract runs from the mouth to the posterior end of the body. It is widest at its anterior and posterior portions. A pair of muscle bands is present along the margins of the body in the region of the thorax and abdomen.

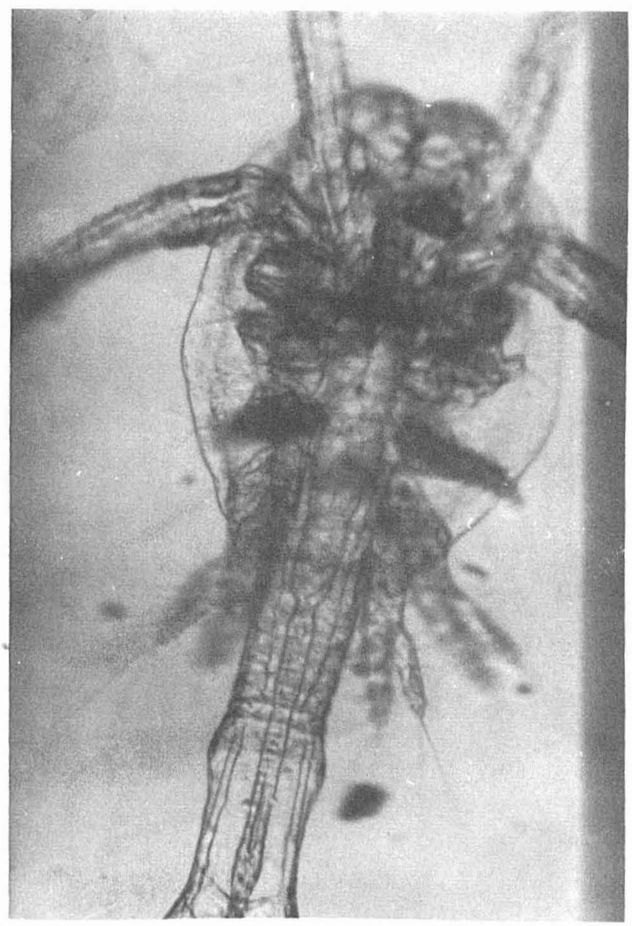

FIGURE 12.—Photomicrograph of first protozoea.

SECOND PROTOZOEA

The second protozoeal stage and succeeding larval stages were described from a series of specimens linked with the first protozoea and with each other by their simultaneous occurrence in plankton tows. Individuals of the second protozoeal stage (fig. 13) measured from 1.5 to 1.9 mm. in body length, based on the examination of 15 specimens taken from the plankton.

The main differences between this stage and the preceding one are the acquisition of a rostrum and supraorbital spines, the appearance of stalked compound eyes which are free from the carapace, and the segmentation of the abdomen.

583837 O—61——3

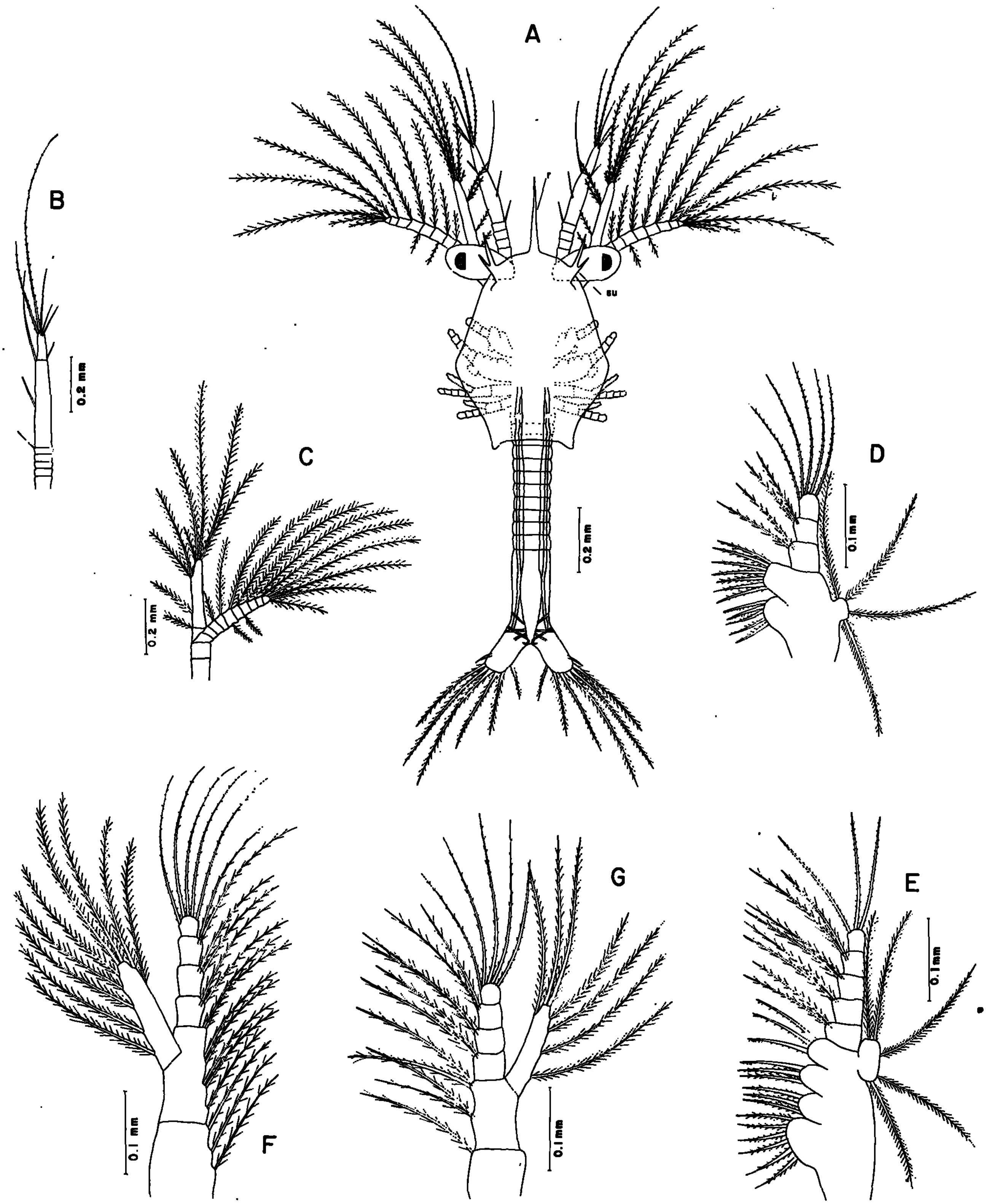

FIGURE 13.—Second protozoea. (A) Dorsal view. (B) First antenna. (C) Second antenna. (D) First maxilla. (E) Second maxilla. (F) First maxilliped. (G) Second maxilliped.

A ventrally curved rostrum is present on the carapace. It measures from one-fourth to one-third the total length of the carapace. The carapace also bears a pair of bifurcated supraorbital spines. It attains its maximum width at about the level of the point of attachment of the second maxillae and then gradually narrows to about half that width. The posterior margin covers the anterior part of the third thoracic somite. The lateral portions of the carapace extend back slightly farther than the dorsal surface.

Gill plates are present for the first time.

There is no great change in the structure of the appendages from those of the first protozoea. A single seta is added to the first antenna. Buds of the thoracic appendages, the third maxillipeds, and the five pairs of pereiopods appear in this stage but are very rudimentary.

The 6 thoracic and 6 abdominal segments are apparent and appear very similar except for the sixth abdominal segment, which is more elongate than the rest. There is no line of demarcation between this segment and the telson.

Each furcal process continues to bear 7 spines.

THIRD PROTOZOEA

Individuals of the third protozoeal stage (fig. 14) measured from 2.2 to 2.7 mm. in body length, based on the examination of 18 specimens taken from the plankton.

The major differences between this and the preceding stage are the appearance of a pair of biramous uropods and of spines on the abdominal somites. All of the somites are fully developed at this stage.

The carapace now covers the first five thoracic somites. The small exterior spines on the supraorbital spines disappear and the latter are thus no longer bifurcated.

The 5 segments of the basal portion of the first antenna are united in this stage. The second antennae, first and second maxillae, and first and second maxillipeds are essentially the same as in the preceding stage. The third maxillipeds and 5 pairs of pereiopods have developed further, but still remain rudimentary and functionless. They all are biramous.

The abdominal somites are now considerably longer than those of the thorax. The sixth abdominal somite is about equal in length to the preceding four combined. The sixth abdominal somite is separated from the telson and differentiation of the body somites is complete. Each of the first 5 abdominal somites bears a dorsomedian spine on its posterior border. In addition, the fifth somite bears a pair of posterolateral spines and the sixth somite bears a pair of posterolateral and a pair of posteroventral spines. All of the spines on the abdominal somites are directed posteriorly.

The biramous uropods are not fully developed. The exopod is somewhat longer than the endopod. The exopod bears 6 short terminal setae and the endopod 2.

There are now 8 spines on each furcal process, with 1 having been added internally to the 7 already existing.

FIRST MYSIS

The second profound metamorphosis occurs at the end of the third protozoeal stage and the larva enters the first mysis stage (fig. 15). Specimens in this stage measured from 2.9 to 3.4 mm., based on the examination of 23 specimens taken from the plankton. The larva now assumes a more familiar shrimplike appearance. The major changes are the development of the thoracic appendages and the nature of the first and second antennae. The carapace, uropods, and telson have also undergone extensive development.

The carapace fits the body more closely than in the protozoeal stages. The smooth rostrum does not curve ventrally in as pronounced a manner as in the preceding stage but projects almost straight forward. There is, however, a good deal of variation in its form. Supraorbital spines are still present, though smaller than in the protozoeal stages. A spine is present at the anteroventral corner of the carapace. A hepatic spine, somewhat removed from the anterior margin of the carapace, is also present. Cephalic and thoracic somites are fused in this stage. The carapace does not quite cover the thorax.

The first and second antennae have changed in form as well as in function: they are no longer natatory, but tactile. The first antenna is divided into 3 segments, the basal segment being equal in length to the other 2 segments. The distal segment bears 2 branches, the external being twice the length of the inner branch. The external branch bears 6 smooth setae and the inner branch 2.

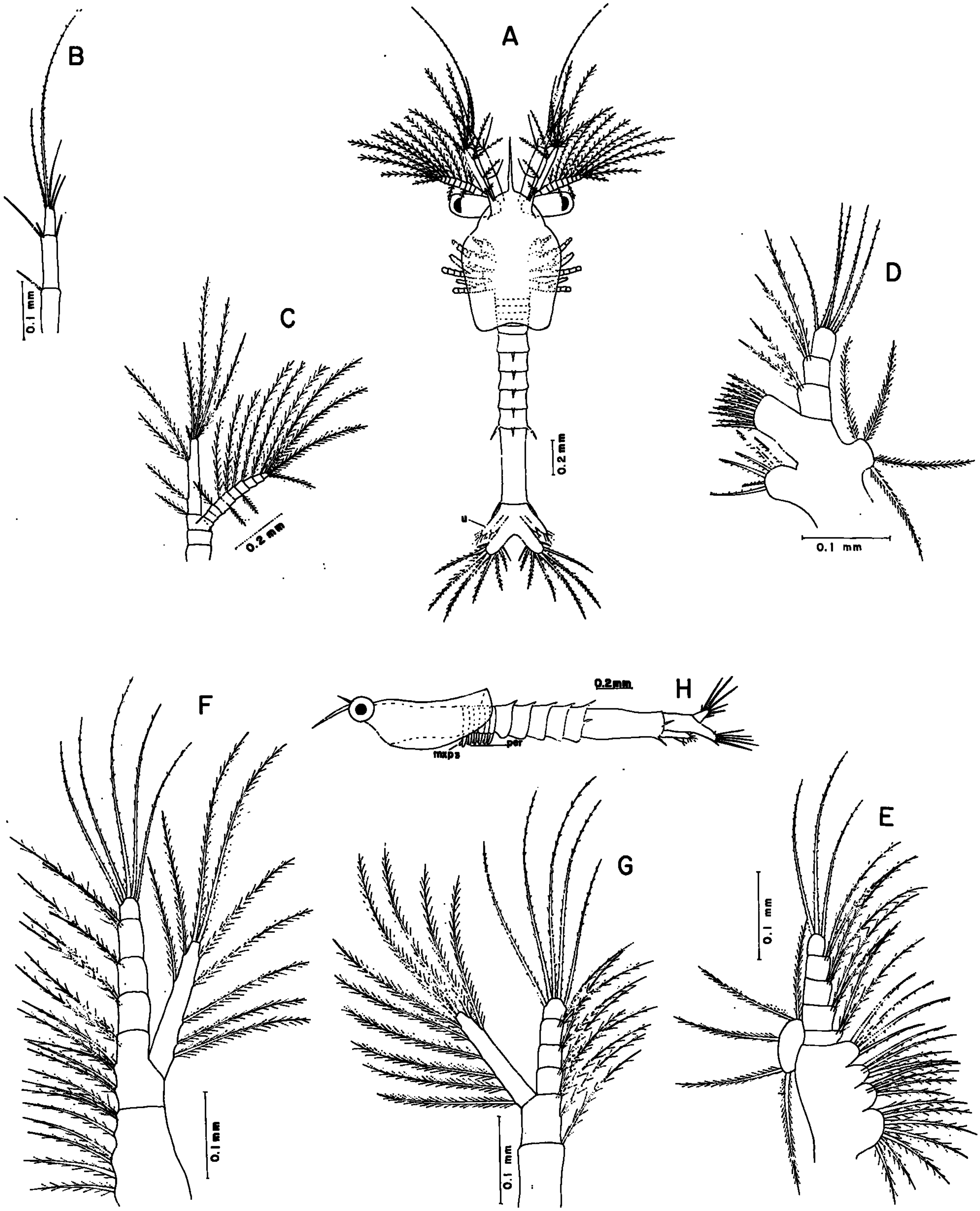

FIGURE 14.—Third protozoea. (A) Dorsal view. (B) First antenna. (C) Second antenna. (D) First maxilla. (E) Second maxilla. (F) First maxilliped. (G) Second maxilliped. (H) Lateral view.

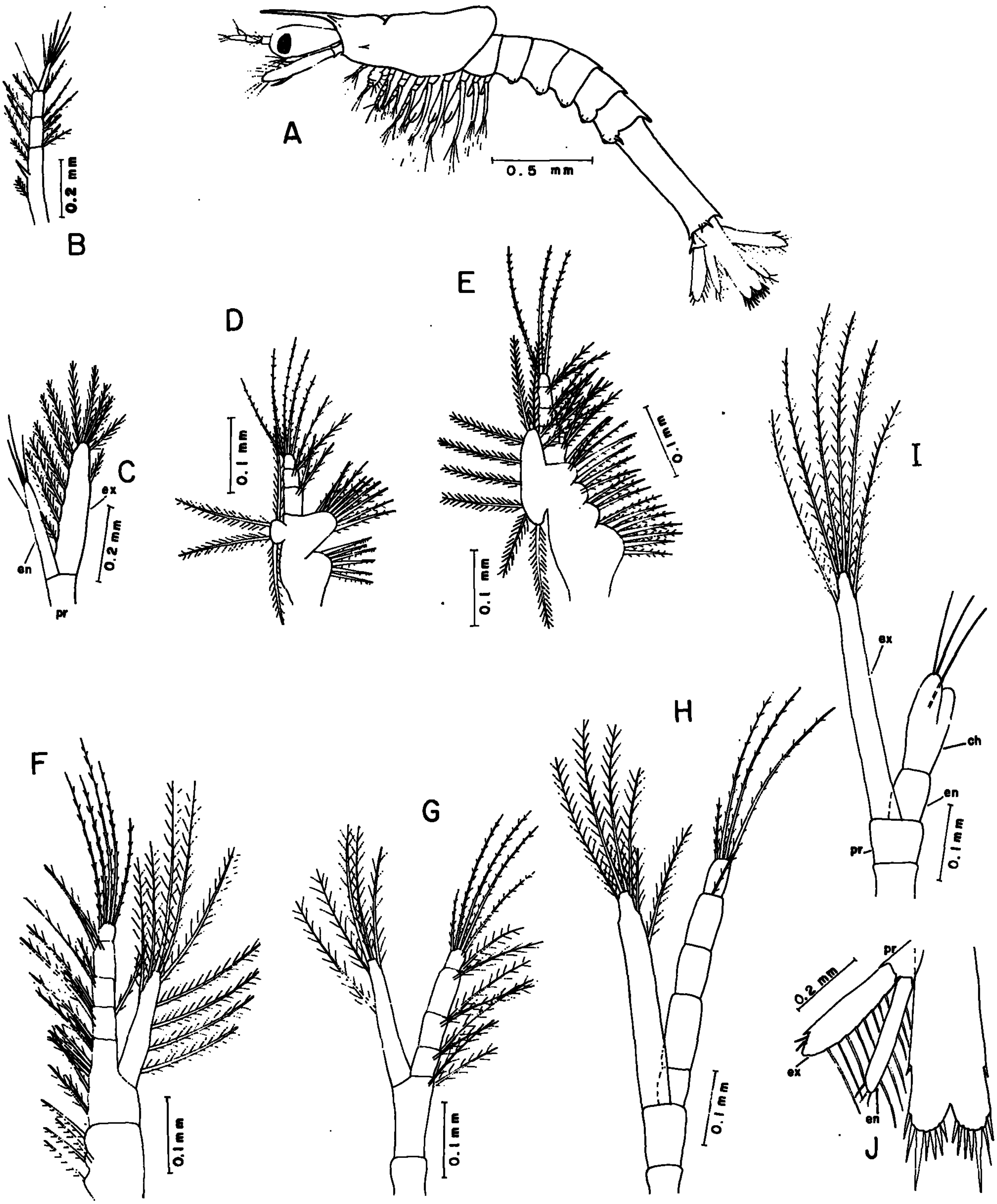

FIGURE 15.—First mysis. (A) Lateral view. (B) First antenna. (C) Second antenna. (D) First maxilla. (E) Second maxilla. (F) First maxilliped. (G) Second maxilliped. (H) Third maxilliped. (I) First pereiopod. (J) Telson and uropod.

There is a series of plumose setae along the margins of the appendage. All of the setae are considerably shorter than in the preceding stage. A large spine is present about midway along the inner margin of the basal segment.

The segments of the exopod of the second antenna have fused to form a flattened scalelike structure. A series of 11 setae is present along the inner and terminal margins, with a twelfth present on the outer margin. The endopod has developed into an unsegmented rodlike structure about two-thirds the length of the exopod. It bears approximately 4 smooth setae, 3 of which are terminal. The protopod consists of 2 segments.

The first and second maxillae are essentially the same as in the preceding stage with the exception that the scaphognathite of the second maxilla has become enlarged and now bears 10 setae. The first and second maxillipeds likewise show no appreciable change.

The third maxilliped is now longer than the first 2. It consists of a 2-segmented protopod, a 5-segmented endopod, and an unsegmented exopod. The endopod bears at least 5 setae, 4 of which are terminal. The exopod bears approximately 6 setae.

The 5 pairs of pereiopods have developed considerably, and are the chief natatory structures of the larva at this stage. In swimming they are assisted by the 3 pairs of maxillipeds. The first 3 pairs of pereiopods are chelate and show a slight increase in size from the anterior to the posterior part of the body. They are composed of a 2-segmented protopod, an endopod of 2 segments (the distal end of the endopod is the rudimentary chela), and an unsegmented exopod. The chela bears 2 or 3 short terminal setae and the endopod 6. The fourth and fifth pereiopods are composed of a 2-segmented protopod, a very short unsegmented endopod, and an unsegmented exopod which is 3 or 4 times the length of the endopod. The endopod bears about 6 terminal setae.

The first and second abdominal segments have lost their dorsal spines, and those of the third and fourth segments are much reduced. The dorsal spines on the fifth and sixth abdominal segments are still fairly prominent. In addition, the fifth segment bears a pair of posterolateral spines, and the sixth segment bears 2 pairs of posterolateral and 1 pair of posteroventral spines and a ventromedian spine on its posterior margin. Buds of the pleopods can be seen on the first 5 abdominal segments.

The uropod now has a protopod which bears 3 spines on its distal border. The exopod and endopod are about equal in length, however, the former is much the wider. The exopod bears about 8 setae on its inner margin, as well as 2 or 3 short setae between the subterminal spine on the outer margin and its distal edge. The endopod bears about 6 lateral and 3 terminal setae.

The telson bears 7 pairs of terminal spines and a pair of small lateral spines. The median notch in the distal margin of the telson is quite well developed, the height of the tip of the notch falling between the lateral and terminal spines. The depth of the notch and the level of its tip in relation to the spines on the telson are important characters in differentiating the three mysis stages.

SECOND MYSIS

Specimens of the second mysis stage (fig. 16) measured from 3.3 to 3.9 mm., based on examination of 8 specimens found in the plankton. The distinguishing characteristic of this stage is the development of rudimentary pleopods.

The carapace now extends back, completely covering the thorax. The appearance of the rostrum and the spination of the carapace are the same as in the preceding stage.

The branches from the distal segment of the first antenna are now almost equal in length. Numerous setae are present at the junction of the segments of the appendage. A bulge, which is the developing statocyst, appears in the basal segment.

A subterminal spine appears on the outer margin of the exopod of the second antenna. The latter bears 8 setae along its inner margin, 4 terminal setae, and 3 setae between the distal tip and the subterminal spine. The endopod remains unsegmented and rodlike, and in this stage is approximately half the length of the exopod. The distal segment of the protopod bears a median spine.

The scaphognathite of the first maxilla has disappeared, while that of the second maxilla has increased in size and now bears 14 setae.

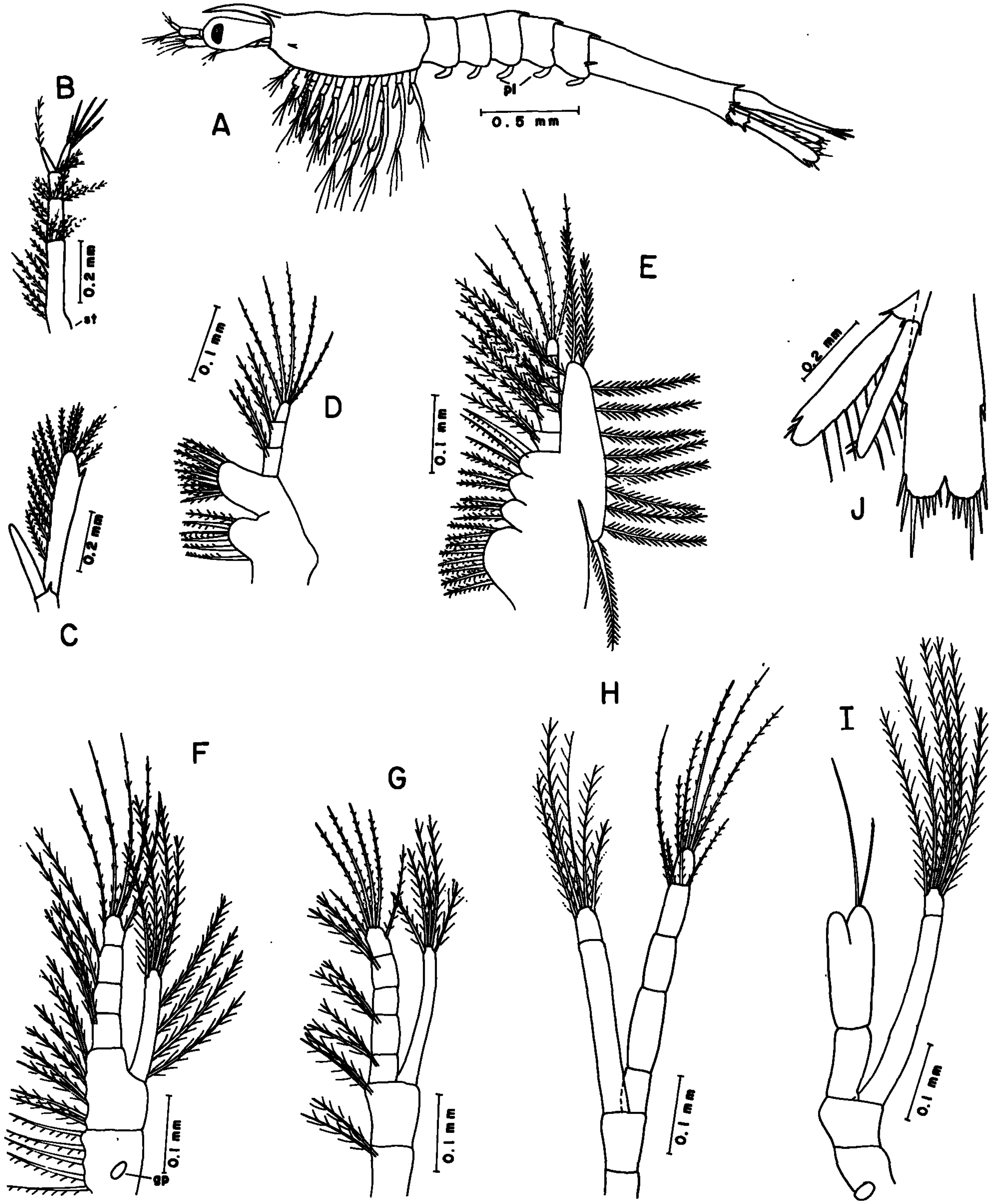

FIGURE 16.—Second mysis. (A) Lateral view. (B) First antenna. (C) Second antenna. (D) First maxilla. (E) Second maxilla. (F) First maxilliped. (G) Second maxilliped. (H) Third maxilliped. (I) First pereiopod. (J) Telson and uropod.

The maxillipeds are much the same as in the preceding stage, except that the exopod of the third maxilliped now has 2 segments.

The pereiopods have grown considerably but their structure remains essentially the same. Of the 3 pairs of chelate pereiopods, the third pair is the longest and the first pair the shortest.

Rudimentary pleopods appear on the abdominal segments in this stage. They are uniramous.

The spination of the abdomen and the appearance of the uropods is the same as in the preceding stage.

The notch at the distal end of the telson is shallower than before. The tip of the notch now reaches only the level of the most external pair of the 7 pairs of terminal spines. The most external 2 pairs of terminal spines are farther apart than in the first mysis.

THIRD MYSIS

Individuals of the third mysis stage (fig. 17) measured from 3.7 to 4.4 mm., based on the examination of 6 specimens taken from the plankton.

The distinguishing characteristics of the third mysis stage are the appearance of a dorsal spine on the rostrum and of well-developed pleopods.

The first and second antennae are much the same as in the second mysis. However, the external branch from the distal segment of the first antenna is now divided into 2 segments. The same is true of the endopod of the second antenna.

The first and second maxillae are essentially the same as in the preceding stage except that the scaphognathite of the latter has continued to increase in size and bears 16 setae.

The endopod of the second maxilliped has 5 segments instead of 4 and the exopod is 3-segmented.

The first 3 pairs of pereiopods are made up of a protopod of 2 segments, an endopod of 4 segments, and an exopod of 2 segments. The endopods of the fourth and fifth pereiopods have 3 or 4 segments, the protopod and exopod 2 each.

The pleopods are well developed although still functionless at this stage. They are divided into 2 segments.

The telson has become somewhat more elongate with the result that the external pair of terminal spines of the second mysis is now in a lateral position. The distal notch has become narrower and shallower, and the height of the tip of the notch is now at the level of the most external of the 6 pairs of terminal spines.

FIRST POSTLARVA

Thirteen specimens of the first postlarval stage measured from 3.8 to 4.8 mm. in body length. All specimens of postlarvae were taken from the plankton.

No great metamorphosis takes place at the molt which gives rise to the first postlarval stage (fig. 18). The pereiopods lose their exopods and the exopods of the maxillipeds are lost or modified. The pleopods take over the swimming function.

The rostrum continues to bear 1 spine near its base and is about equal in length to the eye when the latter is extended forward. The spine at the anteroventral corner of the carapace has disappeared. In most of the specimens examined, the supraorbital spines were absent and a supraorbital crest was developed. In a few cases, however, a small spine remained.

The inner and outer branches from the distal segment of the first antenna now have 2 and 3 segments, respectively. The statocyst at the base of the first antenna is fully developed.

The endopod of the first maxilla is much reduced, unsegmented, and without setae. There is no line of demarcation between it and the peduncle. The same can be said for the endopod of the second maxilla, except that it still has 3 segments. The scaphognathite, which now bears 18 setae, is the dominant structure of the appendage.

Striking changes have taken place in the appearance of the first maxilliped. The endopod is unsegmented, and the exopod has lost its setae. The peduncle has become greatly widened and bears numerous setae along its inner margin.

The second maxilliped has lost its exopod. The endopod consists of 5 segments of which the distal 3 curve inward. The peduncle consists of 2 segments.

The third maxilliped has undergone little change, with the exception of the loss of the exopod. The endopod still has 5 segments and the peduncle 2.

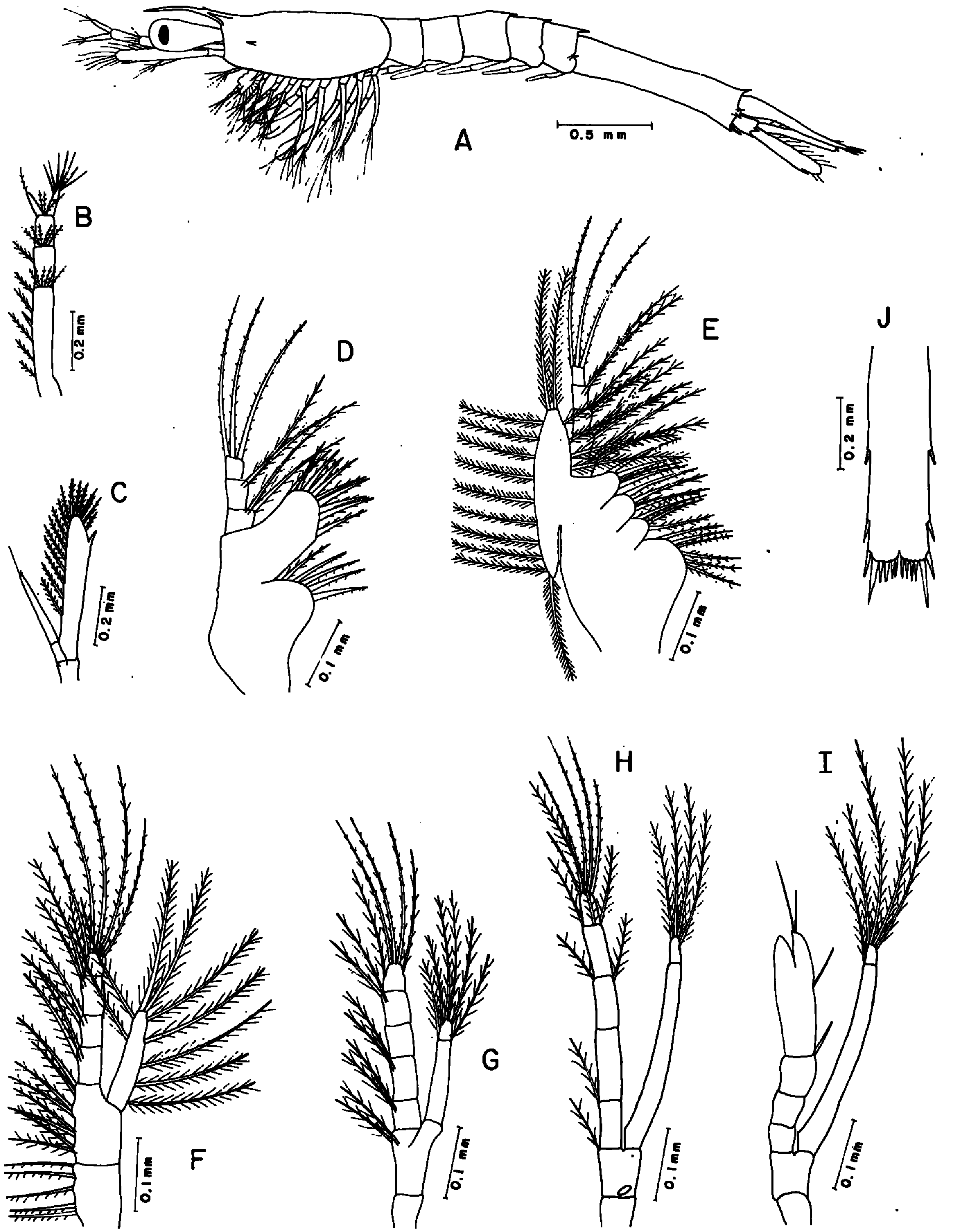

FIGURE 17.—Third mysis. (A) Lateral view. (B) First antenna. (C) Second antenna. (D) First maxilla. (E) Second maxilla. (F) First maxilliped. (G) Second maxilliped. (H) Third maxilliped. (I) First pereiopod. (J) Telson.

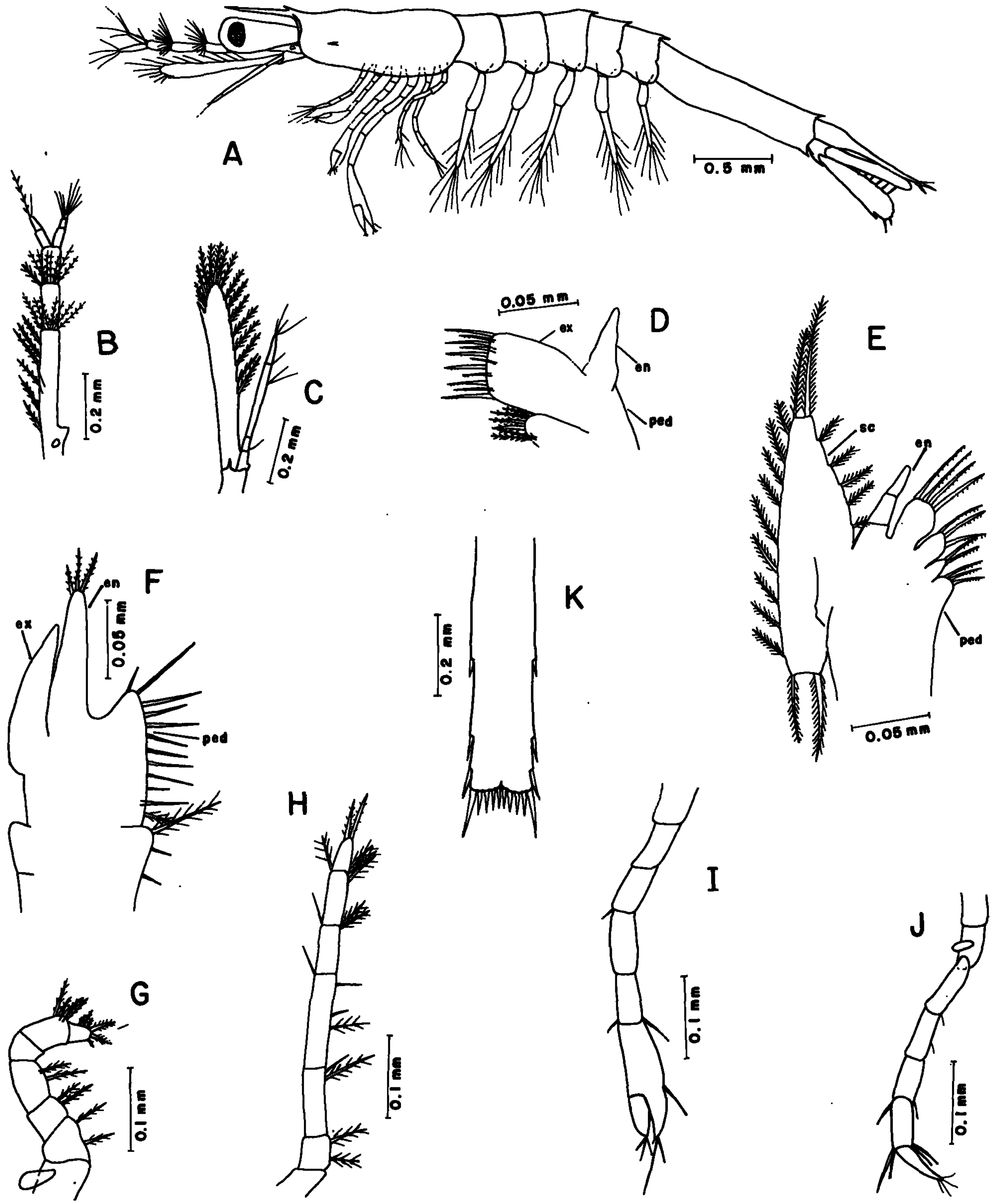

FIGURE 18.—First postlarva. (A) Lateral view. (B) First antenna. (C) Second antenna. (D) First maxilla. (E) Second maxilla. (F) First maxilliped. (G) Second maxilliped. (H) Third maxilliped. (I) First pereiopod. (J) Fourth pereiopod. (K) Telson.

The first 3 pairs of pereiopods consist of a peduncle of 2 segments and an endopod of 5. The chela is formed by the fourth and fifth segments of the endopod. The fourth and fifth pereiopods have the same number of segments as the first three but do not bear chelae. Instead, the fifth segment of the endopod is slightly curved and pointed.

The pleopods have 3 segments, the most distal of which bears about 10 setae. The first three pleopods are better developed than the fourth and fifth.

The dorsal abdominal spines are variable in this stage. Almost all specimens examined had a dorsal spine on the fifth segment. Some had small spines on the third and fourth segments, but others did not. The dorsal spine on the third abdominal segment was the one most often missing. The lateral spines on the fifth abdominal segment were absent on almost all first postlarvae examined, but were present, although reduced, on at least 1 specimen. The 2 pairs of lateral spines on the sixth abdominal segment have disappeared.

The telson is further elongated and now bears 3 pairs of lateral and 5 pairs of terminal spines. The notch is further reduced, its tip falling between the most posterior pair of lateral spines and the terminal spines.

SECOND POSTLARVA

Individuals of the second postlarval stage (fig. 19) measured from 4.7 to 6.6 mm., based on 22 specimens taken from the plankton.

The chief difference between this stage and the first postlarval stage is the presence of a second dorsal spine on the rostrum. In addition, the rostrum is shortened and does not reach the end of the eye when the latter is extended forward.

The inner of the 2 branches from the distal end of the first antenna is now somewhat longer than the external branch and has 3 segments. The flagellum of the second antenna is larger and is composed of 5 segments.

The maxillae are more developed. The scaphognathite of the second maxilla is larger and bears approximately 30 setae.

The endopod of the first maxilliped is much smaller than the exopod, and the mastigobranchial plate has developed greatly. The second maxilliped is curved to a greater degree than in the first postlarva, while the third maxilliped is essentially the same. The same is true of the pereiopods and pleopods.

There are no spines on the third through fifth abdominal segments.

The telson does not differ markedly from the preceding stage. The notch, however, is somewhat less evident.

ADVANCED POSTLARVAE

A series of specimens of postlarvae (fig. 20) from the 3-dorsal rostral-spine stage through the 10-dorsal and 2-ventral rostral-spine stage, measuring from 5.7 to 18.6 mm., was examined (see table 2). From the work of Hudinaga (1942) on *P. japonicus*, it appears probable that several molts occur, with the postlarvae retaining the same number of rostral spines. Hudinaga's observations were made on living material. Although the present study dealt exclusively with preserved material, it was noted that the anteriormost rostral spine of a group of postlarvae having the same number of rostral spines often varied in size. Since this spine is always the one most recently developed, this may be added proof for the supposition that the same number of rostral spines are retained through several molts.

The first ventral spine on the rostrum appears in the stage that has 7 dorsal rostral spines (at approximately 10 to 11 mm.), although the stage or stages preceding it have 7 dorsal and no ventral rostral spines. Likewise, the second ventral spine appears when 8 dorsal spines are present (at approximately 12.5 to 13.5 mm.), although there are specimens with 8+1 rostral spines.

The biramous condition of the pleopods is first clearly evident in the 8+1 stage, but development may have begun in the preceding stage.

TABLE 2.—*Measurements of 48 advanced-stage postlarvae examined*

Number of rostral spines (dorsal+ventral)	Number of specimens examined	Body length, (mm.)
3+0	16	5.7- 7.0
4+0	2	7.2- 7.3
5+0	5	8.1- 9.4
6+0	3	10.2-10.4
7+0	2	9.3- 9.6
7+1	4	10.4-11.3
8+1	4	10.0-11.7
8+2	3	12.5-13.6
9+2	6	[1] 13.7+
10+2	3	[1] 15.5+

[1] Adult *P. duorarum* have 9 or 10 rostral spines.

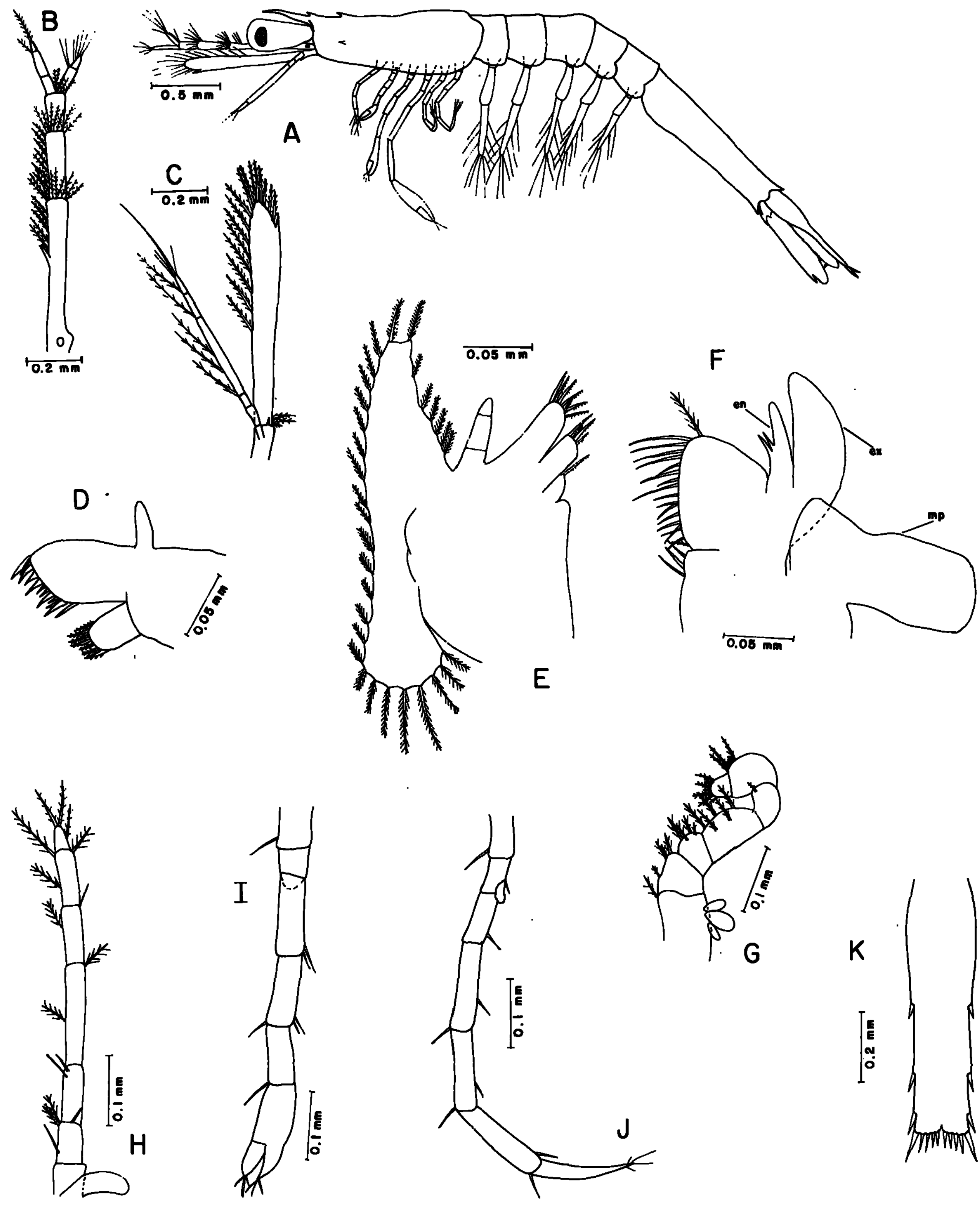

FIGURE 19.—Second postlarva. (A) Lateral view. (B) First antenna. (C) Second antenna. (D) First maxilla. (E) Second maxilla. (F) First maxilliped. (G) Second maxilliped. (H) Third maxilliped. (I) First pereiopod. (J) Fourth pereiopod. (K) Telson.

Development of the carapace is marked by an increase in size of the hepatic spines. An anterolateral spine just ventral to the eye appears in the 7+0-rostral-spine stage and increases in size at each molt thereafter.

The relative lengths of the rostrum and eye differ through the postlarval stages. In the first postlarval stage, the rostrum extends to the edge of the eye or exceeds it in length when the eye is extended forward. The rostrum becomes shortened in the second postlarval stage to about two-thirds the length of the eye, and does not again equal it in length until approximately the 8+2-rostral-spine stage is reached. Thereafter, the rostrum is somewhat longer than the extended eye.

DISCUSSION

The number of stages in each of the phases through which the larvae pass has been found to vary with the species. Hudinaga (1942) reared

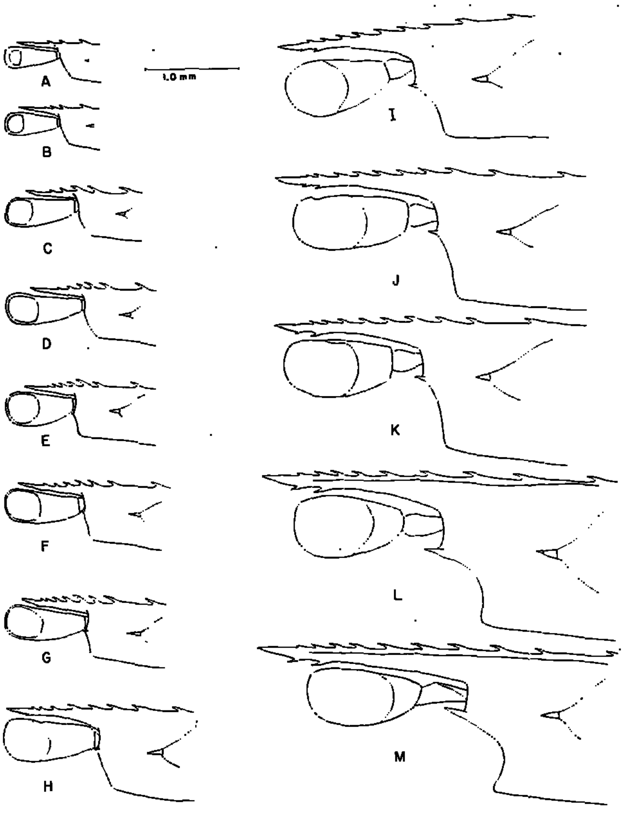

FIGURE 20.—Carapace and rostrum in advanced postlarvae. (A) 6.9 mm. (B) 7.2 mm. (C) 9.0 mm. (D) 10.2 mm. (E) 9.3 mm. (F) 10.4 mm. (G) 11.1 mm. (H) 12.6 mm. (I) 13.5 mm. (J) 15.5 mm. (K) 15.5 mm. (L) 17.8 mm. (M) 18.6 mm.

the larvae of *P. japonicus* through 6 nauplial stages, while Heldt (1938) found 8 in *P. trisulcatus*. Pearson (1939) found 5 nauplial stages in *P. setiferus*, while Heegaard (1953), working only with planktonic material, found 3 stages for the same species. All of these authors found that the species with which they were working passed through 3 protozoeal stages, while 3 mysis stages were observed in *P. japonicus*, 4 in *P. trisulcatus*, and 2 in *P. setiferus*. Broad (1957) noted a variation in the number of larval stages in *Palaemonetes*, depending on the quantity of food available.

COMPARISON WITH *P. SETIFERUS*

The number of nauplial stages found in this study for *P. duorarum* was five, the same as was found by Pearson for *P. setiferus*, but there are slight differences between the corresponding stages of the two species. In the first nauplius, Pearson made no mention of the dorsomedian spine near the posterior end of the body that was noted in *P. duorarum*. Pearson found the second nauplius of *P. setiferus* possessed two pairs of furcal spines. Heegaard described as a first nauplius of the same species a stage which the editors of his paper concluded was a second nauplius because of the appearance of setules on its setae. This stage had a single pair of furcal spines, the condition found in the second nauplius of *P. duorarum*. Pearson found frontal organs on the fourth and fifth nauplial stages, while Heegaard found them on his "last" nauplial stage and first protozoea. Frontal organs were seen only on the fifth nauplius of *P. duorarum*; however, they may also be present on the fourth nauplius.

Of considerable interest is the number of mysis stages. Pearson describes two mysis stages and Heegaard does likewise. An editorial note in Heegaard's paper states, "Heegaard's 'Second Mysis' appears to represent a considerably less advanced stage than Pearson's and it seems probable that there are more than two mysis molts in *P. setiferus* (cf. Heldt, 1938, and Hudinaga, 1942, on other species of *Penaeus*)." This appears true for certain characters, e.g., the absence of a rostral spine, but other structures, such as the telson, appear to be well developed.

Three mysis stages were found in the development of *P. duorarum*. The presence of three stages was based upon the development of the pleopods and the telson as mentioned above. In addition, the third mysis could be distinguished by the presence of a rostral spine.

A comparison of the corresponding stages in the development of *P. setiferus* (based on Pearson's work) and of *P. duorarum* is presented in table 3. The mysis stages were not included since they may not be comparable in the two species.

TABLE 3.—*Corresponding stages in* Penaeus duorarum *and* P. setiferus

[Data on *P. setiferus* from Pearson, 1939]

Stage and structure	*P. duorarum*	*P. setiferus*
Nauplius I:		
Length	0.35–0.40 mm	0.30–0.34 mm.
Width	0.18–0.20 mm	0.16–0.20 mm.
Ocellus	Present	Present.
Labrum	Rounded, ventrally projecting; ends at level of mandible.	Same as in *P. duorarum*.
Antenna I	Uniramous and unsegmented; bears 2 lateral and 3 "terminal" setae (2 terminal and 1 dorsal). Bud of another terminal seta present.	Uniramous and unsegmented; bears 2 lateral and 3 terminal setae.
Antenna II	Biramous and unsegmented. Endopod bears 2 lateral and 2 terminal setae. Bud of another terminal seta present. Exopod bears 3 lateral and 2 terminal setae.	Biramous and unsegmented. Endopod bears 2 lateral and 2 terminal setae. Exopod bears 3 lateral and 2 terminal setae.
Mandible	Biramous and unsegmented. Endopod and exopod bear 3 terminal setae each.[1]	Same as in *P. duorarum*.
Caudal furcae and spines.	Furcae undeveloped. Caudal end bears 1 pair furcal spines. Dorsomedian spine present near posterior end of body.	Furcae and furcal spines the same as in *P. duorarum*. No mention of dorsomedian spine.
Setae	Smooth	Smooth.
Nauplius II:		
Length	0.40–0.45 mm	0.32–0.34 mm.
Width	0.18–0.20 mm	0.16–0.18 mm.
Ocellus	Present	Present.
Labrum	Same as Nauplius I	Same as in Nauplius I.
Antenna I	Unsegmented. Bears 2 setae on anterolateral and 1 on posterolateral surface, and 3 terminal setae.	Same as in *P. duorarum*.
Antenna II	Unsegmented. Endopod bears 2 lateral and 3 terminal setae. Exopod bears 3 lateral and 3 terminal setae.	Same as in *P. duorarum*.
Mandible	Same as Nauplius I	Same as in Nauplius I.
Maxillae and maxillipeds.	Not observed	Faint anlages of first and second maxillipeds appear posterior to mandibles.
Caudal furcae and spines.	Furcal processes undeveloped. Caudal end still bears 1 pair strong furcal spines.	Slight furcal processes, each bears 1 strong and 1 weak furcal spine.
Setae	Longer setae of appendages bear numerous setules.	Same as in *P. duorarum*.
Nauplius III:		
Length	0.45–0.49 mm	0.36–0.40 mm.
Width	0.17–0.20 mm	0.14–0.16 mm.
Ocellus	Present	Present.
Labrum	Same as in preceding stages.	Same as in preceding stages.
Antenna I	Shows signs of segmentation. Bears 2 lateral and 3 terminal setae.	Unsegmented. Setation same as in *P. duorarum*.

See footnote at end of table.

TABLE 3.—*Corresponding stages in* Penaeus duorarum *and* P. setiferus—Continued

Stage and structure	*P. duorarum*	*P. setiferus*
Nauplius III—Con.		
Antenna II	Unsegmented. Endopod bears 2 lateral and 3 terminal setae. Exopod bears 3 lateral and 4 terminal setae.	Same as in *P. duorarum*.
Mandible	Same as in preceding stages.	Same as in preceding stages.
Maxillae and maxillipeds.	Not observed	Still under cuticle in midline.
Caudal furcae and spines.	Well-developed. Each furca bears 3 spines.	Same as in *P. duorarum*.
Nauplius IV:		
Length	0.48–0.55 mm	0.38–0.44 mm.
Width	0.18–0.20 mm	0.16–0.18 mm.
Frontal organs	Absent?	Present.
Ocellus	Present	Present.
Labrum	Pointed posteriorly	Same as in *P. duorarum*.
Antenna I	Segmented. Bears 2 lateral and 3 terminal setae.	Same as in *P. duorarum*.
Antenna II	Endopod appears unsegmented and bears 2 lateral and 3 terminal setae. Exopod has about 9 segments and bears 4 lateral and 4 terminal setae.	Endopod may or may not be segmented and bears 2 lateral and 3 terminal setae. Exopod has about 8 segments and bears 4 lateral and 4 terminal setae.
Mandible	Swelling appears in base. Endopod and exopod unsegmented. Setation same as in previous stages.	Same as in *P. duroarum*, except that the endopod appears to be segmented.
Maxillae and maxillipeds.	First and second maxillae and first and second maxillipeds appear externally on ventral surface. Biramous; however, exopods of maxillae knoblike.	First and second maxillae and first and second maxillipeds appear externally on ventral surface. Biramous.
Caudal furcae and spines.	Bear 5 spines each	Same as in *P. duorarum*.
Nauplius V:		
Length	0.53–0.61 mm	0.46–0.56 mm.
Width	0.17–0.20 mm	0.16–0.20 mm.
Frontal organs	Present	Present.
Ocellus	Present	Present.
Labrum	Large and pointed posteriorly.	Same as in *P. duorarum*.
Carapace	Can be seen dorsally under cuticle.	Same as in *P. duorarum*.
Antenna I	Segmented; bears 3 setae on anterolateral and 2 setae on posterolateral surfaces; 3 terminal setae.	Same as in *P. duorarum*.
Antenna II	Endopod bears 3 lateral and 4 terminal setae. Exopod bears 5 lateral and 4 terminal setae.	Endopod bears 2 lateral and 4 terminal setae. Exopod bears 4 lateral and 5 terminal setae.
Mandible	Swelling at base of mandible pronounced; shows spherical masticatory surface. Endopod may or may not be transparent due to lack of musculature.	Swelling at base of mandible pronounced; shows spherical masticatory surface. Endopod transparent due to lack of musculature.
Maxillae	Larger and biramous. Exopods small and knoblike. Endopods bear both terminal and lateral setae. Second maxillae larger than first.	Larger and biramous. Possess short terminal setae. No other description given.
Maxillipeds	Larger and biramous. Exopods typically palplike and bear terminal setae. Endopods bear both terminal and lateral setae.	Larger and biramous. Possess short terminal setae.
Caudal furcae and spines.	Each bears 7 spines. Buds of barbs appear on longer spines.	Each bears 7 spines.
Protozoea I:		
Body length	0.86–1.02 mm. (reared larvae). 0.98–1.14 mm. (from plankton).	0.80–1.14 mm.
Carapace length.	0.40–0.49 mm	0.46 mm. in first protozoea with a body length of 0.86 mm.

TABLE 3.—*Corresponding stages in* Penaeus duorarum *and* P. setiferus—Continued

Stage and structure	*P. duorarum*	*P. setiferus*
Protozoea I—Con.		
Carapace width.	0.35-0.44 mm	0.36 mm. in first protozoea with a body length of 0.86 mm.
Compound eyes.	Developing under carapace.	Same as in *P. duorarum*.
Frontal organs	Absent	Absent.
Ocellus	Present between developing compound eyes.	Same as in *P. duorarum*.
Labrum	Roughly oval. Anterior edge has large spine; posterior margin slight notch and short bristles.	Anterior edge sharply pointed; posterior edge rounded and covers a section of mandibles.
Labium	2 lobed; extends from under labrum; bristles along median border of lobes.	No description given.
Antenna I	Divided into 3 major segments; with basal segment subdivided into 5 segments. Bears 8 setae.	Same as in *P. duorarum*.
Antenna II	Protopod, 3 segments and without setae. Endopod, 2 segments and 9 setae. Exopod, approximately 10 segments and 13 setae.	Protopod, 2 segments and without setae. Endopod, 2 segments and 8 setae. Exopod, 9 or 10 segments and 12 setae.
Mandible	Has lost endopod and all but trace of exopod. Well-developed masticatory surface.	Mandible modified into flattened plate with serrated edge on inner margin. Both endopod and exopod temporarily lost.
Maxilla I	Protopod has 2 segments; endopod 3. Inner margins of these segments lobed. Exopod (scaphognathite) is budlike. Protopod has about 8 setae, endopod approximately 9, and exopod 4.	Protopod has 2 segments; lobed on inner margins. Each lobe bears about 4 setae. Endopod has 3 segments and bears 8 setae. Several additional outer lateral setae also present on endopod. Exopod (scaphognathite) a small lobe bearing about 2 setae.
Maxilla II	Larger than first maxilla. Protopod has 4 lobed segments and about 10 setae. Endopod has 5 segments with approximately 11 setae. Exopod (scaphognathite) budlike and bears 5 setae.	Larger than first maxilla. Protopod has inner margin divided into 4 small lobes each bearing 2 setae. Endopod has 4 or 5 segments each with pair of setae. Exopod (scaphognathite) knoblike and bears 3 setae.
Maxilliped I	Largest of maxillae and maxillipeds. Protopod has 2 segments (not lobed), each segment bearing 3 to 5 setae. Endopod has 4 segments and about 11 setae. Exopod unsegmented and bears 7 setae. Both endopod and exopod palplike.	Elongate biramous structure. Protopod has 2 segments and 4 setae. Endopod has 9 segments, each segment except distal bearing pair of setae. Distal segment has 4 setae at the tip. Exopod has single segment and bears about 4 lateral and 4 terminal setae.
Maxilliped II	Smaller than first maxilliped. Protopod has 2 segments and about 5 to 7 setae. Endopod has 4 segments and 9 or 10 setae. Exopod unsegmented and bears 6 setae.	Considerably smaller than the first. Protopod has 2 segments and 4 setae. Endopod has 5 segments and 10 setae. Exopod has single segment and bears 7 setae.
Caudal furcae and spines.	Each furca bears 7 spines, the most external of which emanates from dorsal surface. Longer spines bear setules.	Bifurcation of tail stronger than in fifth nauplius. Median notch made by bifurcation is semiovate. 7 spines on each furca.
Digestive tract.	Wider in anterior and posterior portions than between.	Consists of oesophagus, stomach, and intestine and ends in anus which opens somewhat ventrally at the apex of the notch at the posterior end of the body.

[1] One of the 3 terminal setae of the exopod actually arises from a constriction in the ramus approximately four-fifths the distance from the body.

The descriptions of the second and third protozoea of *P. setiferus* are not detailed enough to allow a tabular comparison of the two species. The second protozoea measured from 1.5 to 1.9 mm. in *P. duorarum* compared with 1.3 to 1.7 mm. in *P. setiferus*. Measurements of the third protozoea were 2.2 to 2.7 mm. in the pink shrimp and 2.2 to 2.6 mm. in the white shrimp.

From Pearson's drawing (1939: fig. 9, p. 18) it can be seen that the second protozoea of *P. setiferus* lacks a seta at the junction of the distal two segments on the posterolateral margin of the first antenna. The corresponding stage of *P. duorarum* has a short seta at this location. Otherwise, little difference can be noted at this stage between the two species.

The first and second postlarval stages of *P. duorarum* and *P. setiferus* are also very similar on the basis of available descriptions. Pearson reports that the supraorbital spines of the first postlarva are still present, although reduced, while examination of that stage of *P. duorarum* reveals that the spines are almost always missing. Size ranges of these stages are similar.

COMPARISON WITH *P. AZTECUS*

Unfortunately, the larval stages of the brown shrimp, *P. aztecus*, have not been described. Pearson (1939) compared various-sized postlarvae that he originally called *P. braziliensis* (and, in a footnote, tentatively referred them to *P. aztecus*) with similar-sized specimens of *P. setiferus*. He found four principal characters separating the two species in these stages. These characters concern the spination of the rostrum and the relationships of the lengths of the rostrum and the third pereiopod to the length of the eye.

Williams (1959) reviewed the characters described by Pearson and presented a provisional key which could be used to distinguish the postlarvae of *P. setiferus*, *P. aztecus*, and *P. duorarum* under 12 mm. total length. In this key, a difference is noted between the antennal scales of the young postlarvae of the latter two species. In *P. aztecus*, the antennal scale is "nearly uniform in shape with the lateral spine extending beyond the broadly rounded tip," while in *P. duorarum*, "the tip was more or less acutely rounded with the apex near the mesial aspect of the tip. The lateral spine did not reach the tip." Examination of postlarvae of the two species under 12 mm. total length showed this to be an accurate description.

Williams (1953) compared postlarval and juveniles of *P. setiferus*, *P. aztecus*, and *P. duorarum*. He included drawings of the rostra of 17-, 27-, 37-, and 47-mm. shrimp of the three species; hence the series of rostral drawings of *P. duorarum* were terminated at approximately 18 mm. in this paper.

Lebour (1959) reported larvae of *P. duorarum* in collections made off the coast of tropical West Africa. She figured a 4+0-rostral-spine stage (fig. 1a, p. 141), having well-developed biramous pleopods—a condition not appearing in postlarval *P. duorarum* from Florida waters until the stage in which 8 or 9 dorsal spines are present on the rostrum.

SUMMARY

Four rearing experiments were conducted in which the larvae of *Penaeus duorarum*, the pink shrimp, were raised from eggs obtained from mature females. Young were reared through five nauplial stages and into the first protozoeal stage.

The egg, five nauplial, three protozoeal, three mysis, and two postlarval stages are described and illustrated. In addition, a series of thirteen drawings of the rostra of advanced postlarvae is included. The first six stages were described from specimens raised from eggs, while the remainder of the stages were described from specimens collected from the plankton.

The larval stages of *P. duorarum* are compared with those of *P. setiferus* as described by Pearson (1939). Differences between the postlarvae of *P. duorarum* and *P. aztecus*, as noted by Williams (1959), are discussed.

REFERENCES

ANDERSON, WILLIAM W., JOSEPH E. KING, and MILTON J. LINDNER.
1949. Early stages in the life history of the common shrimp, *Penaeus setiferus* (Linnaeus). Biological Bulletin, vol. 96, no. 2, p. 168–172.

BROAD, ALFRED CARTER.
1957. The relationship between diet and larval development of *Palaemonetes*. Biological Bulletin, vol. 112, no. 2, p. 162–170.

BURKENROAD, MARTIN D.
1939. Further observations on Penaeidae of the Northern Gulf of Mexico. Bulletin Bingham Oceanographic Collection, vol. 6 (art. 6), p. 1–62.

CHIN, EDWARD, and DONALD M. ALLEN.
1959. A list of references on the biology of shrimp (family Penaeidae). U.S. Fish and Wildlife Service, Special Scientific Report—Fisheries No. 276, 143 p.

COSTLOW, JOHN D., JR., and C. G. BOOKHOUT.
1959. The larval development of *Callinectes sapidus* Rathbun reared in the laboratory. Biological Bulletin, vol. 116, no. 3, p. 373–396.

DAKIN, WILLIAM J.
1938. The habits and life-history of a penaeid prawn (*Penaeus plebejus* Hesse). Zoological Society of London, Proceedings, series A, vol. 108, pt. 2, p. 163–183.

DAVIS, HARRY C., and ROBERT R. GUILLARD.
1958. Relative value of ten genera of micro-organisms as foods for oyster and clam larvae. U.S. Fish and Wildlife Service, Fishery Bulletin No. 136, vol. 58, p. 293–304.

GURNEY, ROBERT.
1927. Report on the larvae of the Crustacea Decapoda. Cambridge Expedition to the Suez Canal. Zoological Society of London, Transactions, vol. 22, no. 15, p. 231–286.
1942. Larvae of decapod Crustacea. Ray Society No. 129, 306 p.
1943. The larval development of two penaeid prawns from Bermuda of the genera *Sicyonia* and *Penaeopsis*. Zoological Society of London, Proceedings, series B, vol. 113, p. 1–16.

HEEGAARD, POUL E.
1953. Observations on spawning and larval history of the shrimp, *Penaeus setiferus* (L.). University of Texas, Publications of the Institute of Marine Science, vol. 3, no. 1, p. 73–105.

HELDT, JEANNE H.
1938. La reproduction chez les Crustacés Décapodes de la famille des Pénéides. Annales de l'Institute Oceanographique de Monaco, vol. 18 (fasc. 2), p. 31–206.

HUDINAGA, MOTOSAKU.
1942. Reproduction, development and rearing of *Penaeus japonicus* Bate. Japanese Journal of Zoology, vol. 10, no. 2, p. 305–393.

JOHNSON, MALCOLM C., and J. R. FIELDING.
1956. Propagation of the white shrimp, *Penaeus setiferus* (Linn.), in captivity. Tulane Studies in Zoology, vol. 4, no. 6, p. 173–190.

LEBOUR, MARIE V.
1959. The larval decapod Crustacea of tropical West Africa. "Atlantide" Report No. 5, p. 119–143, fig. 1a.

MENON, M. KRISHNA.
1952. The life history and bionomics of an Indian penaeid prawn *Metapenaeus dobsoni* Miers. Indo-Pacific Fisheries Council, Proceedings, Third Meeting, Section 2, p. 80–93.

MORRIS, MURIEL C., and ISOBEL BENNETT.
1952. The life history of a penaeid prawn (*Metapenaeus*) breeding in a coastal lake (Tuggerah, New South Wales). Proceedings, Linnaean Society of New South Wales, vol. 76, nos. 5–6, p. 164–182.

PEARSON, JOHN C.
1939. The early life histories of some American Penaeidae, chiefly the commercial shrimp, *Penaeus setiferus* (Linn.). U.S. Bureau of Fisheries, Bulletin 30, vol. 49, p. 1–73, figs. 2–18, 21–30.

WEYMOUTH, FRANK W., MILTON J. LINDNER, and WILLIAM W. ANDERSON.
1933. Preliminary report on the life history of the common shrimp. *Penaeus setiferus* (Linn.). U.S Bureau of Fisheries, Bulletin 14, vol. 48, p. 1–26.

WILLIAM, AUSTIN B.
1953. Identification of juvenile shrimp (Penaeidae) in North Carolina. Elisha Mitchell Scientific Society, Journal, vol. 69, no. 2, p. 156–160, figs. 1 and 2.
1955. A contribution to the life histories of commercial shrimps (Penaeidae) in North Carolina. Bulletin of Marine Science of the Gulf and Caribbean, vol. 5, no. 2, p. 116–146.
1959. Spotted and brown shrimp postlarvae (*Penaeus*) in North Carolina. Bulletin of Marine Science of the Gulf and Caribbean, vol. 9, no. 3, p. 281–290, figs. 1–3.

O