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Development and Metamorphosis of the Feeding Apparatus of the Stone Crab, *Menippe mercenaria* (Brachyura, Xanthidae)

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ABSTRACT Analysis of the feeding apparatus of the stone crab, *Menippe mercenaria* (Brachyura, Xanthidae), has demonstrated that substantial internal and external morphological alterations occur at metamorphosis and suggests that the mastication of food shifts from the mandibles to the gastric mill at that time. These changes correspond to the changes in environment and diet that take place at metamorphosis, when the previously planktotrophic larvae begin benthic life.

A detailed account of the structure and development of the mandibles is presented. The mandibles of all zoeal stages are similar: The incisor process has a series of teeth and denticles and the prominent molar process appears to be well adapted for grinding food. Megalopal mandibles are transitional but have the form that is typical of all subsequent stages: The expanded incisor process is rounded and toothless and the molar process is less prominent and has lost its grinding denticles. The cardiac stomach of the zoeal stages has no gastric mill; the medial and lateral teeth of the mill first appear in the megalopa.

A very simple procedure is described for preparing larval mandibles for scanning electron microscopy using the molted exoskeletons from larval rearing experiments.

Development, settlement, and metamorphosis of the larvae of many marine invertebrate groups have received considerable attention in recent years (Chia and Rice, '78). The crustaceans are no exception. Most of the work on the larval development of decapod crustaceans, however, has been concerned with the description of external features both to facilitate identification of larvae collected from the plankton and to answer taxonomic questions (Rice, '80). Functional considerations of external features are usually lacking, and the development of internal features of decapod larvae has been almost completely ignored. Studies that consider the development of the digestive system of larval decapods appear to be limited to the work of Thompson ('03), who included the gut in his description of metamorphosis in a hermit crab; Williams ('07), who described the ossicles of the foregut of the lobster, *Homarus americanus*; LeRoux ('71a,b), who studied the larval and juvenile foregut in the shrimp, *Palaemonetes varians*; Regnault ('72), who examined the larval development of the stomach of the shrimp, *Crangon septemspinosa*; and Factor ('81a), who described the development and metamorphosis of the digestive system of *Homarus americanus*.

The paucity of functional studies on larval appendages and internal development is in contrast to the considerable literature concerning the functional morphology of appendages and organ systems in adult decapods. Such studies include several in which the authors examined both the mouthparts and the gut and related their structure to feeding or diet. For example, Patwardhan ('35b) compared the gastric mill and mandibles of a variety of decapods; Caine ('75) studied feeding in the commensal crab, *Pinnotheres maculatus;* Barker and Gibson ('77, '78) examined the feeding mechanism and structure of the gut in the lobster, *Homarus gammarus,* and the portunid crab, *Scylla serrata;* Coombs and Allen ('78) described the feeding structures of the shrimp, *Hippolyte varians;* and Kunze and Anderson ('79) compared the mouthparts and gastric mill in several species of hermit crabs.

The life history of the stone crab, *Menippe mercenaria,* typically includes five zoeal stages, a megalopa, and a series of juvenile

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stages leading to the adult. The larval development of external structures in this species has been reported by Hyman ('25) and Porter ('60). The present study examines the principal masticatory structures of the feeding apparatus—the mandibles and the gastric mill—and follows their development from the first larval stage, through metamorphosis, to the adult. Metamorphosis from the last zoeal stage to the megalopa is accompanied by a variety of external changes, including the loss of the carapace spines, a change in the general shape and proportions of the cephalothorax, and the transfer of the swimming function from the thoracic maxillipeds to the newly developed abdominal pleopods. Metamorphosis also marks the transition of the planktotrophic larvae to the benthic environment. This change in habitat and diet is accompanied by substantial internal and external morphological alterations in the masticatory apparatus. The nature of these structural changes and their functional significance for the developing stone crab are the subject of this investigation.

MATERIALS AND METHODS

The adult stone crabs used in this study were trapped in the Indian River coastal lagoon near the Smithsonian Institution's laboratory in Ft. Pierce, Florida. Juvenile stone crabs were collected from the oyster bars in the Indian River and from the sabellariid worm reefs along the adjacent coast.

All larvae were hatched from a single ovigerous female, which was subsequently deposited in the Indian River Coastal Zone Museum (IRCZM 89:4703). Larvae were raised at 20–21 °C in compartmented plastic trays in seawater of 35–36‰ salinity by techniques previously described by Gore ('73). At least three specimens in each stage were examined.

Larval stone crabs were fixed for light microscopy in 3% glutaraldehyde in 0.1 M sodium cacodylate buffer at pH 7.0, postfixed in 1% OsO_4 in buffer, and embedded in a mixture of Epon 812-Araldite 506, according to a procedure used for transmission electron microscopy (Factor, '81b). Plastic sections 1 μm thick were stained with toluidine blue–azure II and observed with a compound microscope. Juvenile stone crabs were fixed in seawater Bouin's fluid (Humason, '62) and embedded in Paraplast (60–61 °C melting point). Serial paraffin sections 10 μm thick were stained with hematoxylin and eosin or Mallory's triple stain (Humason, '62).

Zoeal and megalopal mandibles were prepared for scanning electron microscopy from the molted exoskeletons (exuviae) collected during larval rearing using the following simple procedure.

Exuviae were preserved and stored in 70% ethanol. Deposition of debris on the specimen was minimized by removing all seawater before adding alcohol, thereby preventing precipitation of salts. Cleaning exoskeletons by sonication, even for a few seconds, caused them to break apart and was not feasible.

Specimens were mounted on a round glass coverslip with a diameter equal to or less than that of the stub for the microscope being used. The exoskeleton was transferred to the coverslip in a drop of alcohol, fine needles or forceps were used to tease the mandibles apart from the rest of the exoskeleton, and the preparation was simply allowed to air-dry. Special drying procedures, such as critical-point-drying or freeze-drying, were not necessary; the thick cuticle of the mandible prevented its collapse. (Some problem was encountered with thin-walled first-stage mandibles, however, which did tend to collapse. This was avoided by critical-point drying entire first-stage larvae and dissecting them to reveal details of the mandibles.) The coverslip was mounted on a stub with a conductive colloidal graphite adhesive (Electrodag 191, Acheson Colloids Co.). The coverslip was lowered carefully to minimize trapped air bubbles, which can cause it to pop off the stub in the vacuum of the microscope. Three or four small drops of the colloid were added around the periphery of the coverslip to increase the conductance of electrons to the stub. After the adhesive was thoroughly dried, specimens were sputter-coated with about 400 Å of gold/palladium in a Technics Hummer Coater and observed in a Novascan scanning electron microscope. Charging was reduced by insuring that the mandible had good contact with the coverslip, by increasing the thickness of the coating (double- or triple-coating), or by operating the microscope at a low accelerating voltage (5 kV or lower). Coverslips with specimens were removed from the stubs and stored in small petri dishes or micropaleontological slides. If further examination was necessary, they were remounted and recoated.

Because air-drying will cause distortion of most structures, this technique is not suitable for preparing entire larvae or for examining appendages other than mandibles. Entire larvae and dissected material were fixed in 70% ethanol, dehydrated in an ethanol series, treated with acetone, and critical-point-dried with CO_2 to replace the acetone. Juvenile and adult mandibles were dissected from entire specimens, sonicated to remove debris, and air-dried.

OBSERVATIONS

The feeding apparatus of the adult stone crab consists of the external mouthparts and the internal gastric mill. The mouthparts are paired appendages that are specially modified to handle food. The three anterior pairs of mouthparts (mandibles, maxillules, and maxillae) are cephalic in origin, and the three posterior pairs (first, second, and third maxillipeds) are thoracic appendages.

The zoeal maxillipeds are primarily locomotory appendages with exopodites well equipped for this purpose with natatory setae. During the zoeal stages the mandibles appear to be the primary masticatory structures, whereas the maxillules and maxillae function more as manipulative mouthparts. At metamorphosis to the megalopa, the function of locomotion is transferred from the maxillipeds to the newly developed abdominal pleopods and to a lesser extent to the thoracic pereiopods. The postmetamorphic maxillipeds may guide food into the mouth and, together with the mandibles and other mouthparts, prepare food for ingestion. They are not, however, important masticatory structures.

The digestive system of the stone crab is divided into foregut, midgut, and hindgut. The foregut, comprising the esophagus and the cardiac and pyloric stomachs, is lined with a layer of cuticle. In the cardiac stomach of the adult, this internal cuticle is organized into a series of plates or ossicles, some of which are elaborated and calcified to form the elements of the internal masticatory mechanism called the gastric mill. (Maynard and Dando, '74, and Meiss and Norman, '77a,b, provide detailed descriptions of the gastric mill in two brachyuran crabs.) Although the gastric mill is complex and consists of many ossicles, muscles, and nerves, there are three primary masticatory structures – the medial tooth, formed by the urocardiac and prepyloric ossicles, and the two lateral teeth, formed by the zygocardiac ossicles.

In the sections that follow, an account is provided of the structure of zoeal mandibles and the developmental changes by which they are transformed into the mandibles of the adult, as well as the corresponding changes in the major features of the gastric mill.

Position and structure of zoeal mandibles

The mandibles are the most massive and obvious of the feeding appendages in zoeal stone crabs (Figs. 1,2). Removal of the more posterior appendages makes it possible to view the mandibles from a posterior aspect and to appreciate their relationship to the cephalothorax of the larva (Fig. 3).

The line drawings in Figure 4 illustrate three views of a generalized zoeal mandible. The medial portion of the mandible which comes into contact with food is called the *gnathal lobe* (GL) and consists of a ventral *incisor process* (IP) and a dorsal *molar process* (MP). The incisor process bears a series of teeth along its ventral edge; there are three major *ventral teeth* (VT), one at each corner and one in the middle, with lesser *ventral denticles* (VD) interspersed between adjacent teeth. There is also a row of *posterior teeth* (PT) along the posterior edge of the incisor process. The medial surface of the incisor is concave and, when considered together with the molar process, gives the gnathal lobe a spoon-shaped appearance. The molar process protrudes from the dorsomedial portion of the mandible at the base of the incisor process; the truncate distal surface bears several *molar denticles* (MD) and the posterior side has a single large *molar tooth* (MT) directed distally. The *lateral lobe* (LL) of the mandible is a rounded, broadly sloping structure that provides support for the gnathal lobe and is the site of muscle attachment and the points of articulation between the mandible and the cephalothorax.

Abbreviations

A, anterior
ALT, accessory lateral tooth of gastric mill
D, dorsal
DCS, dorsal wall of cardiac stomach
GF, gland filter of pyloric stomach
GL, gnathal lobe of mandible
IP, incisor process of mandible
L, lateral
LL, lateral lobe of mandible
LT, lateral tooth of gastric mill
M, medial
MAP, mandibular palp
MD, molar denticles
MET, medial tooth of gastric mill
MP, molar process of mandible
MT, molar tooth
P, posterior
PT, posterior teeth of incisor process
V, ventral
VD, ventral denticles of incisor process
VT, ventral teeth of incisor process

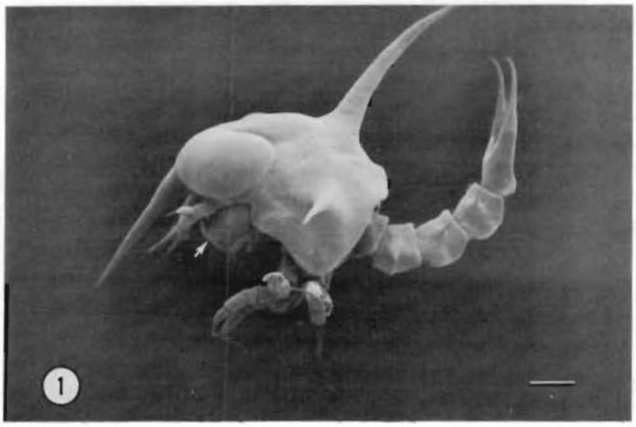


Fig. 1. First zoeal stage of the stone crab. Lateral view illustrating position of the prominent mandible (arrow). Scale bar, 100 μm.

Fig. 2. Ventral view of the first zoeal stage, indicating position of the mandibles (asterisks) in relation to other appendages. Anterior is to the top. Scale bar, 100 μm.

Fig. 3. Posterior view of a pair of fith-stage mandibles, illustrating posterior teeth and complementary molar processes with interdigitating molar teeth (arrows). Ventral is to the top. Scale bar, 50 μm.

Zoeal development

The mandibles of the first zoeal stage (Fig. 5) have all of the elements of the generalized zoeal mandible described above. There are three ventral teeth on the incisor process and usually two ventral denticles between adjacent teeth, although the number of denticles may vary from one individual to the next. The incisor process generally has two or three posterior teeth on the right mandible but the left mandible may have only a single tooth or none in this position. The molar process is as wide as the incisor process and has several molar denticles on its distal surface. The position of the single molar tooth differs on right and left mandibles; it protrudes from the posteroventral corner of the molar process on the left mandible, but is somewhat offset on the right mandible and is located away from the truncate end of the molar process.

Several changes occur in the mandibles as the stone crab passes through the zoeal stages (Figs. 6–10). In addition to a general increase in size, there is also an increase in the number of posterior teeth and ventral denticles (Table 1). Although there is some variation among individuals, the right mandible of the third stage generally has two or three posterior teeth (Fig. 6), whereas the left mandible has two, and by the fifth stage there may be four or five poste-

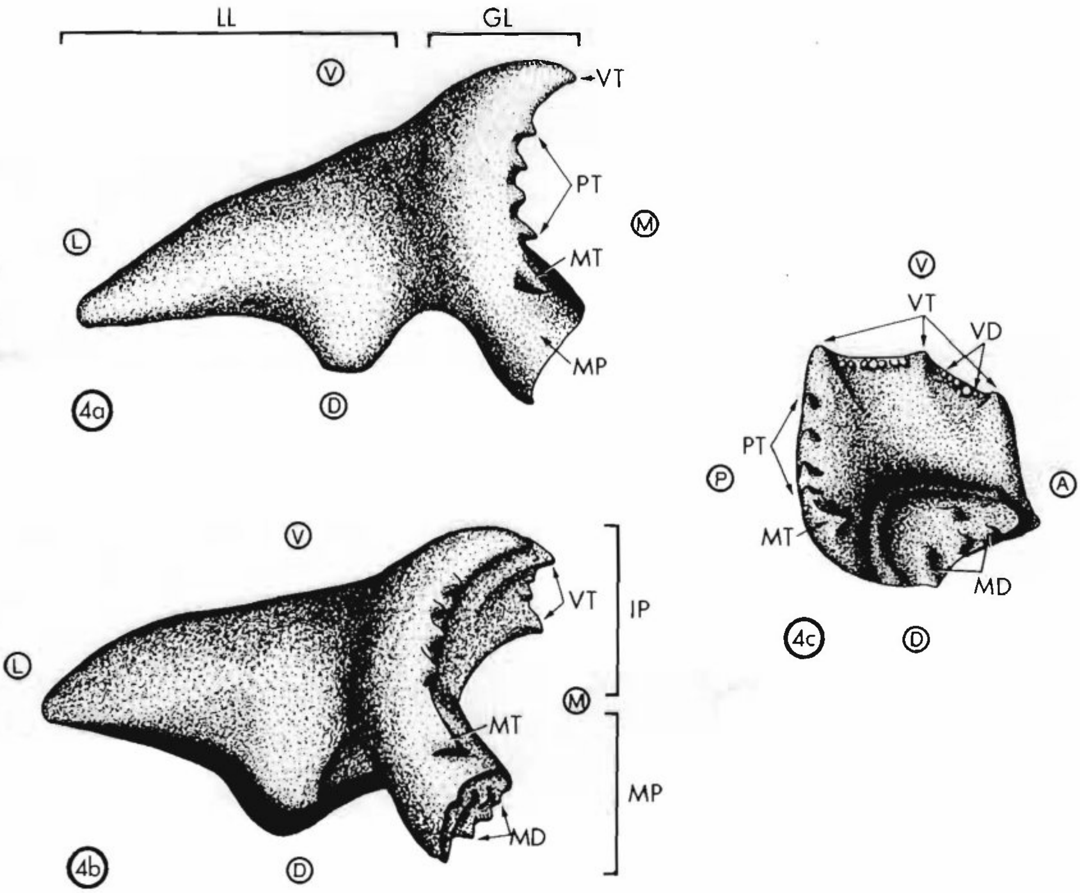
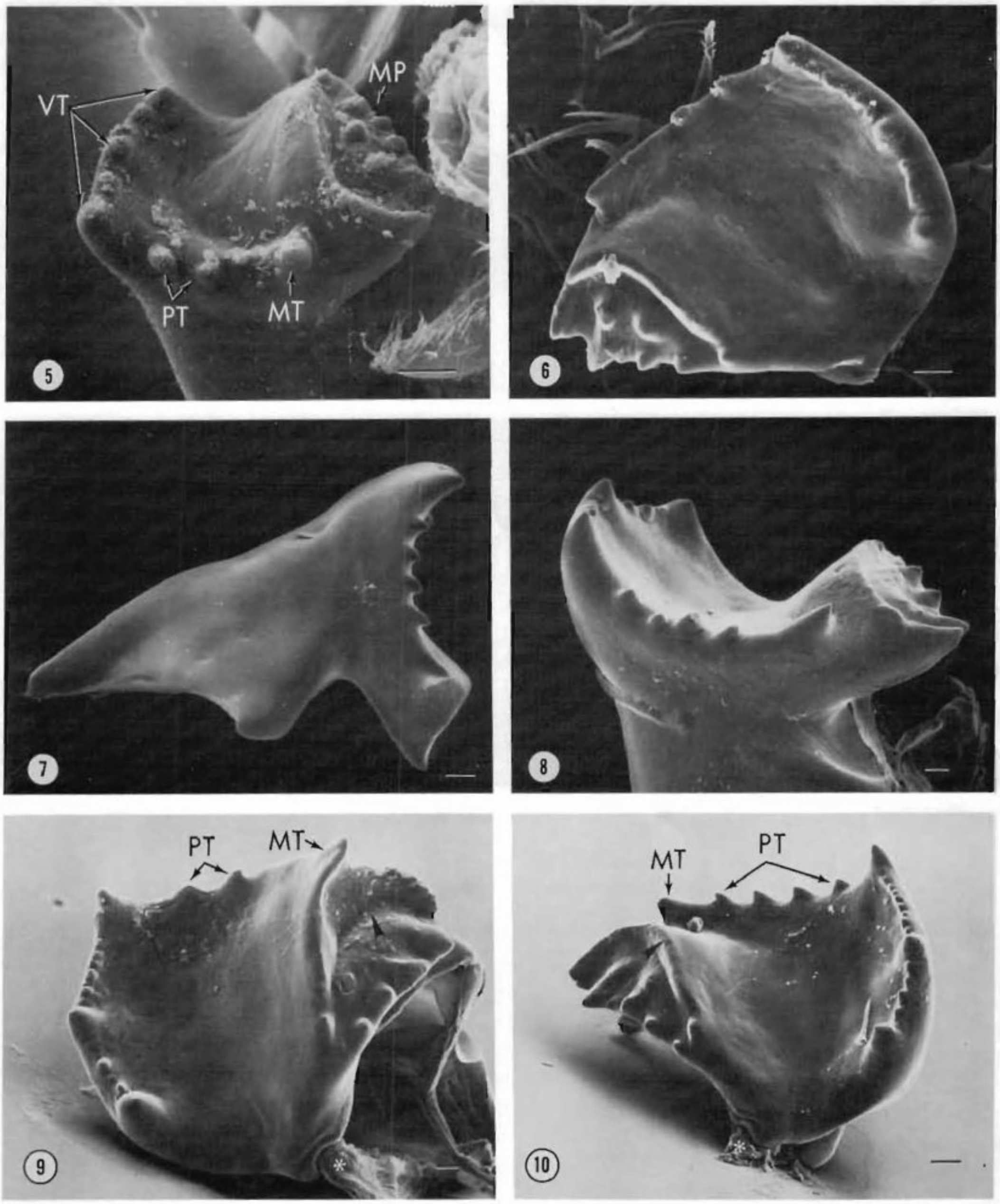


Fig. 4. Line drawings of a generalized zoeal mandible, illustrating important structural features. Posterior (4a) and posteromedial (4b) views of the entire mandible and a medial view of the gnathal lobe (4c) are shown.

rior teeth on the right mandible and two or three on the left (Figs. 9–10). The number of denticles usually increases to six on the posterior half of the ventral edge and three on the anterior half in the third stage, and finally to six and four by the fifth stage. There were three ventral teeth on the incisor process in all zoeal mandibles examined. Comparison of the first-stage mandible in Figure 5 with the fifth-stage mandible in Figure 8 demonstrates that the incisor process is gradually extended during the zoeal stages, creating an increasingly concave medial surface. The form of the entire zoeal mandible, including both lateral and gnathal lobes, is illustrated in Figure 7. The mandibular palp first appears as a rudimentary palp bud in the fifth stage, located on the anterior side of the mandible (Figs. 9,10).

Asymmetry of zoeal mandibles

The right mandible differs significantly from the left mandible in all zoeal stages. The larger number of posterior teeth on the right incisor process has already been noted. The more interesting differences, however, occur on the molar process. Examination of right and left molar processes shows that the truncate distal surfaces are complementary. The curved ridge that forms the posteroventral edge of the right molar fits into a depression on the left molar, and the molar denticles interdigitate (Figs. 9,10). The asymmetrical placement of the single molar tooth on each mandible also allows interdigitation of the molar process (Fig. 3). During feeding, the mandibles pivot on two points of articulation, causing a rocking motion that brings the molar processes



Figs. 5–10. Scanning electron micrographs of zoeal mandibles of the stone crab. Scale bars, 20 μm.

Fig. 5. First-stage zoea. Gnathal lobe of right mandible with prominent molar process.

Fig. 6. Third-stage zoea. Medial view of right gnathal lobe.

Fig. 7. Fourth-stage zoea. Posterior view of entire right mandible, illustrating gnathal and lateral lobes as well as molar and incisor processes.

Fig. 8. Fifth-stage zoea. Gnathal lobe of right mandible with concave medial surface and grinding molar process.

Figs. 9,10. Fifth-stage zoea. Anterior views of left (Fig. 9) and right (Fig. 10) gnathal lobes illustrating asymmetry of the mandibles. Complementary surfaces of the molar processes are visible: ridge on right molar process (arrowhead in Fig. 10) fits into depression in left molar process (arrowhead in Fig. 9); molar teeth and molar denticles interdigitate. Asterisk notes position of mandibular palp bud.

TABLE 1. Teeth and denticles of zoeal mandibles in Menippe mercenaria

Stage	Posterior teeth		Ventral teeth (right & left)	Ventral denticles (right & left)	
	Right	Left		Anterior	Posterior
First zoea	2–3	0–1	3	2	2
Third zoea	2–3	2	3	3	6
Fifth zoea	4–5	2–3	3	4	6

together; their complementary surfaces appear well adapted for grinding food.

Megalopal mandibles

The most drastic change during the development of the mandibles occurs at the molt from the last zoeal stage to the megalopa (Figs. 11,12). At this time the gnathal lobe becomes a relatively flattened structure that lies against the ventral surface of the cephalothorax and covers the mouth. The two surfaces of the gnathal lobe can be described as inner (or dorsal, toward the mouth) and outer (or ventral, away from the mouth). The inner surface of the gnathal lobe is concave. The incisor process is expanded to form most of the gnathal lobe; the incisor process of the left mandible has a rounded edge that no longer bears teeth or denticles (Fig. 11), and the right incisor process is similar but bears a single tooth-like projection (Fig. 12). The molar process is less prominent and is a fraction of the width of the incisor process–it is now a simple mound with two teeth and is located at the posterior side of the inner surface. The posterior tooth of the molar process forms the corner of the left mandible, but the molar process of the right mandible is offset slightly from the corner. It is in the megalopal stage that the mandibular palp is first well developed (Fig. 11). It lies in the concavity on the inner surface of the gnathal lobe and serves to push food toward the mouth. The palp has three segments, and the distal segment is setose.

Juvenile and adult mandibles

The general form, proportions, and orientation of the juvenile mandibles (Figs. 13, 14) are similar to those of the megalopal mandibles. The trend of simplification of the molar process, begun in the megalopa, continues; the two teeth of the megalopal stage are lost and the process is now a relatively flat, shelf-like structure at the posterior side of the gnathal lobe. The single tooth-like projection on the edge of the right incisor process in the megalopal mandible is absent in the juvenile. When viewed end-on, the incisor process can be seen to have a sharp cutting edge (Fig. 15).

Except for their increased size, adult mandibles appear to be identical to those of the juvenile (Figs. 16, 17).

Asymmetry is greatly reduced in juvenile and adult mandibles. There is only a slight difference in shape between right and left mandibles and no obvious complementarity (compare Figs. 13 and 14). There is, however, some difference in the posterior corner of the mandibles near the molar process. The left mandible has a slight inward lip in this position, which is formed by the end of the molar process (Figs. 13,16) and appears to have developed from the posterior tooth of the megalopal molar process (Fig. 11). The right mandible has no such lip and the molar process is not located at the very corner of the mandible (Figs. 12,14,17).

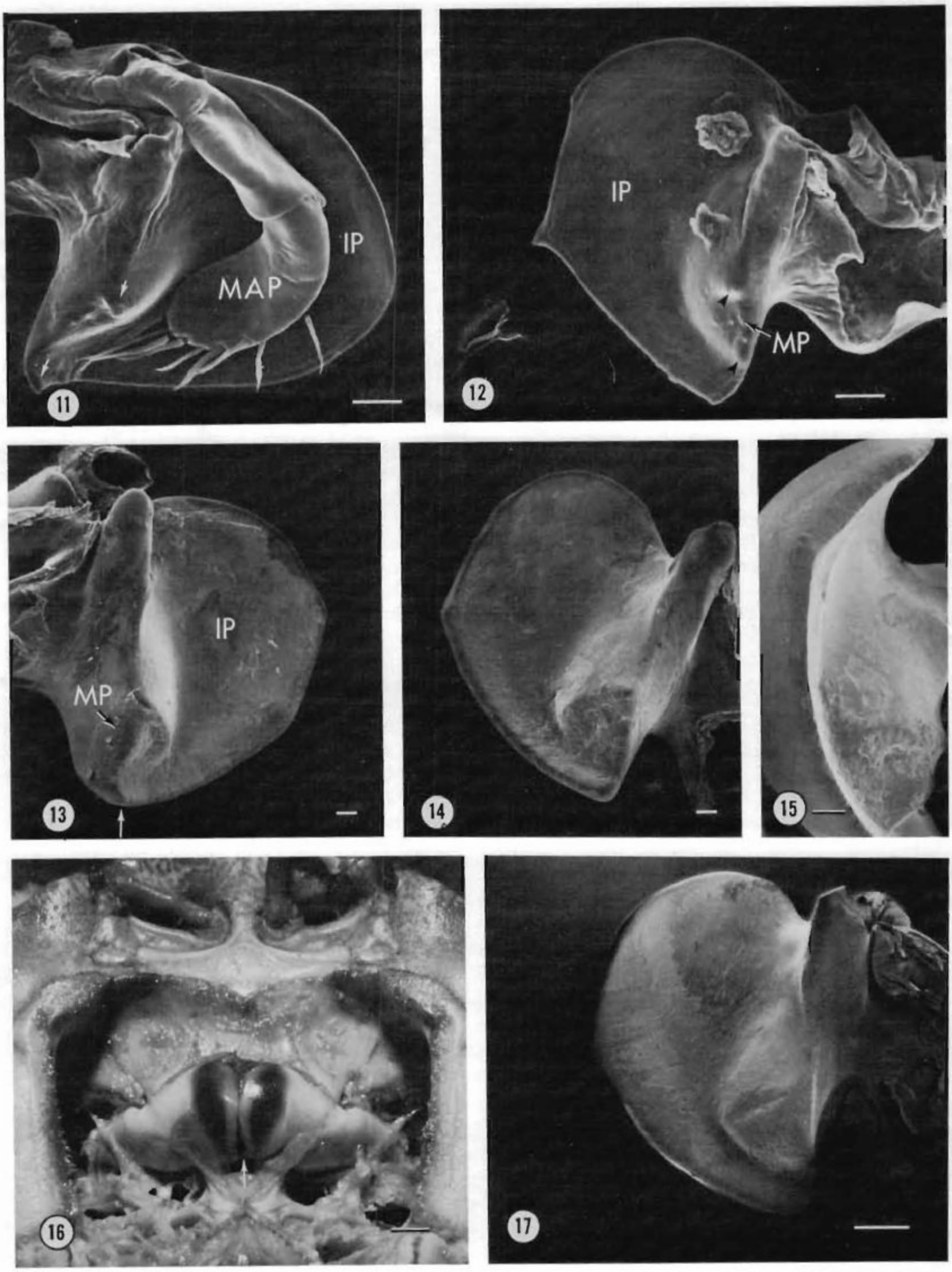
When the megalopal, juvenile, or adult mandibles pivot during feeding, the rocking motion brings together the sharp edges of the expanded incisor processes. In addition, it appears that the lip at the posterior corner of the left mandible overlaps the cutting edge of the right mandible and serves to grasp food. The structures and action of the postmetamorphic mandibles seem effective in cutting and grasping food, but not grinding.

Development of the gastric mill

The cardiac stomach of the first zoeal stage is a simple sac (Fig. 18a). Developmental trends throughout the zoeal stages include an increase in the size of the sac and the formation of several ridges and channels. As late as the fifth zoeal stage (Fig. 18b), the cardiac stomach remains essentially similar to that of the first stage–there are no obvious elaborations of the wall of the cardiac stomach during zoeal development.

As with the mandibles, the most drastic change in the cardiac stomach occurs at the molt from the last zoeal stage to the megalopal stage. Elements of the gastric mill, particularly the medial and lateral teeth, are first present in the megalopa (Fig. 18c).

The juvenile stone crab has a well-developed gastric mill that closely resembles that of the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adult (Figs. 18d, 19–23). The grinding surfaces of the medial and lateral teeth are heavily cuticularized (darkened areas, Fig. 18d) and presumably calcified. The medial tooth protrudes from the dorsal wall of the cardiac stomach, and lateral teeth and accessory lateral teeth extend toward the midline from the lateral walls (Figs. 19,20). During mastication, the medial tooth is moved ventrally and anteriorly at the same time the lateral teeth are brought toward the midline of the stomach. This action moves the sides of the medial tooth across the knobs and comb-like projections on the lateral teeth (Figs. 21–23). In this way food trapped among the medial and lateral teeth is ground into small particles in the gastric mill. The particles are then sorted on the basis of size, in both the cardiac stomach and the pyloric filter, and the smallest particles pass into the midgut gland for final digestion and absorption.

The medial and lateral teeth of the adult gastric mill (Figs. 24,25), as well as the general shape of the cardiac stomach, are similar to those of the juvenile stone crab.

DISCUSSION

A detailed account of the structure and development of the mandibles of the stone crab has been presented and the various parts of the mandible have been assigned names. The developmental trend in the structure of the zoeal mandibles is one of an increase in size, an increase in the number of teeth and denticles on the incisor process, and slight changes in shape and proportion, including increased concavity of the medial surface. Despite these changes, the mandibles of all five zoeal stages follow the same basic structural plan. The ventral and posterior edges of the incisor process bear teeth and the molar process is prominent, about as wide as the incisor process, and has complementary surfaces that are well adapted for grinding. Although the megalopal mandibles are transitional, they have already attained the form and orientation that is typical of all subsequent stages. The expanded incisor process is rounded and toothless, and the molar process has lost its prominence as well as its grinding denticles. The postmetamorphic mandibles appear to be better adapted for cutting and grasping than for grinding.

Developmental changes in the cardiac stomach correspond to those in the mandibles. The cardiac stomach of the zoeal stages has no gastric mill and is not capable of grinding food. The medial and lateral teeth of the mill are first recognizable in the megalopa.

This analysis of the feeding apparatus of the stone crab indicates that substantial morphological alterations occur at metamorphosis and suggests that the mastication of food shifts from the mandibles to the gastric mill at that time. These changes correspond to the changes in environment and diet that take place at metamorphosis, when the previously planktotrophic larvae begin benthic life.

Patwardhan ('35b), in the final paper of his comparative series on the gastric mill in adult decapods, also briefly described the structure of the mandibles. He concluded (p. 171), "The efficiency of the gastric mill is correlated with the efficiency of the external masticatory apparatus, chiefly the mandibles, the mandibles being simple in the forms in which the gastric mill is complex and *vice versa.*" Patwardhan generalized that in the reptantious Brachyura, Anomura, and Macrura, which have complex gastric mills (i.e., efficient internal mastication), the mandibles are relatively simple and have greatly reduced molar processes without any masticatory function (i.e., inefficient external mastication). Conversely, in the natantious Caridea, Penaeidea, and Stenopodidea, in which the gastric mill is absent or greatly reduced, the mandibles are relatively complex with well-developed molar processes.

Figs. 11–17. Postlarval mandibles of the stone crab. In all views, anterior is to the top.

Fig. 11. Megalopa. Gnathal lobe of left mandible with well-developed mandibular palp, expanded incisor process, and molar process with two teeth (arrows). Inner (dorsal) view. Scale bar, 50 μm.

Fig. 12. Megalopa. Gnathal lobe of right mandible. Inner view. Incisor process has a single tooth-like projection and molar process has two teeth (arrowheads). Mandibular palp has been removed. Scale bar, 50 μm.

Fig. 13. Juvenile. Gnathal lobe of left mandible (From a stone crab of 15-mm carapace width). Inner view. White arrow indicates inward lip of posterior molar process (also visible in Fig. 16). Mandibular palp has been removed. Scale bar, 100 μm.

Fig. 14. Juvenile. Gnathal lobe of right mandible (from a stone crab of 15-mm carapace width. Inner view. Scale bar, 100 μm.

Fig. 15. Juvenile. Medial view of the sharp cutting edge of the incisor process. Scale bar, 100 μm.

Fig. 16. Adult. Left and right mandibles, in situ (from a stone crab of 70-mm carapace width). Outer (ventral) view. Arrow indicates inward lip at posterior corner of left gnathal lobe. Scale bar, 2.0 mm.

Fig. 17. Adult. Gnathal lobe of right mandible. Inner view. Mandibular palp has been removed. Scale bar, 1.0 mm.

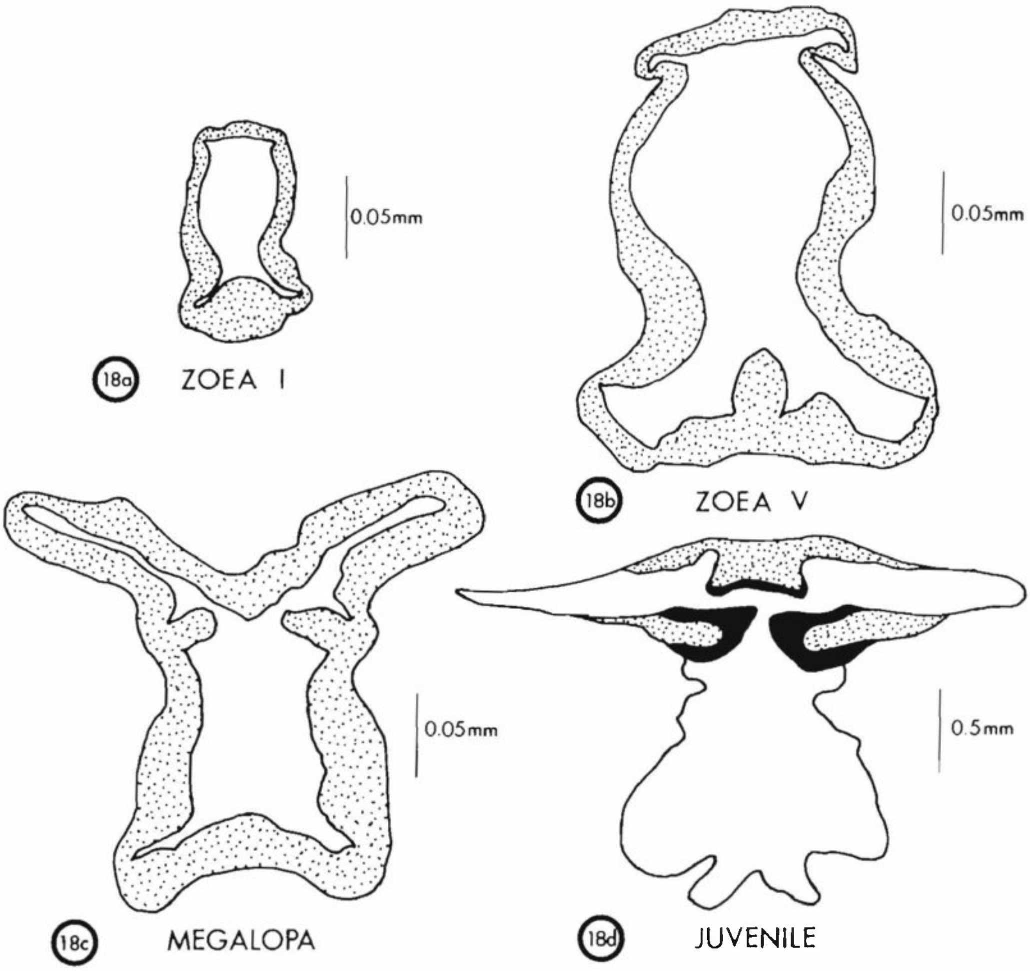


Fig. 18. Line drawings representing cross sections through the cardiac stomach of first-stage zoeal (18a), fifth-stage zoeal (18b), megalopal (18c), and juvenile (15-mm carapace width) (18d) stone crabs.

Because so few studies of internal development have been carried out, only limited comparisons are possible between the trends in adult decapods noted by Patwardhan and the situation found in the larval stages. A comparison of the condition of the mandibles and gastric mill in those decapods for which information about both larvae and adults is available is summarized in Table 2 and presented below.

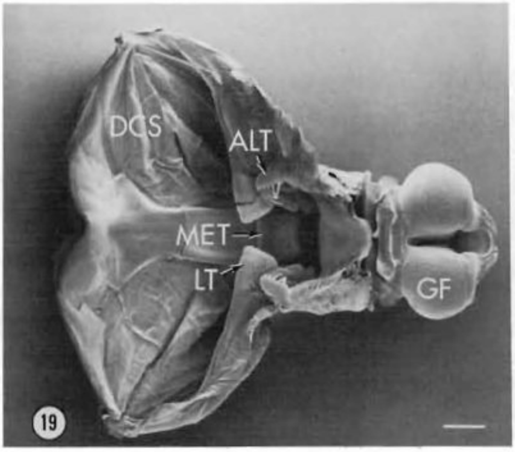
The condition of the mandibles and gastric mill in the adult stone crab is typical of Patwardhan's generalization about the Reptantia (simple mandibles, complex stomach). The situation is reversed, however, in the zoeal stages

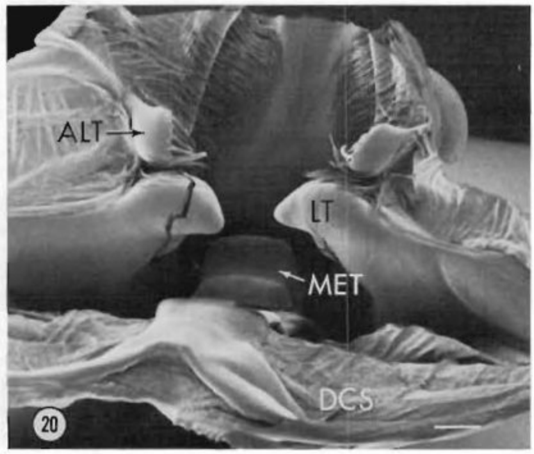
Figs. 19–25. Scanning electron micrographs illustrating structures of the juvenile and adult gastric mill.

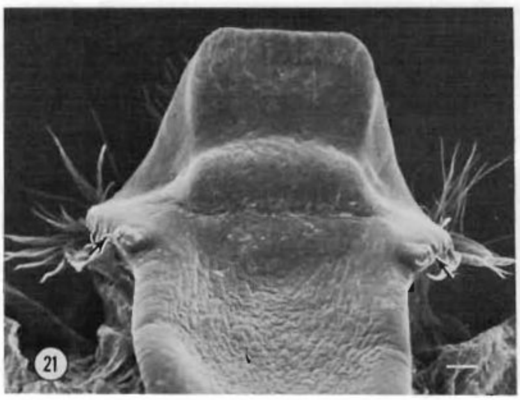
Fig. 19. Juvenile. Ventral view of a dissected foregut (from a stone crab of 15-mm carapace width) illustrating position and orientation of elements of the gastric mill. Esophagus and ventral wall of cardiac stomach have been removed. Anterior is to the left. Scale bar, 0.5 mm.

Fig. 20. Juvenile. Anterior view of gastric mill showing relationship of medial, lateral, and accessory lateral teeth. Ventral is to the top. (Crack in left lateral tooth is an artifact of preparation.) Scale bar, 0.25 mm.

Fig. 21. Juvenile. Medial tooth of gastric mill. Arrows indicate denticles on each side of medial tooth. Ventral is to the top. Scale bar, 100 μm.







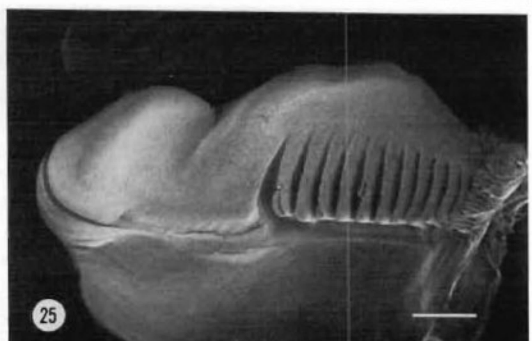


Fig. 22. Juvenile. Details of denticles on sides of medial tooth (indicated by arrows in Fig. 21). Scale bar, 50 μm.

Fig. 23. Juvenile. Lateral tooth (left) of gastric mill, illustrating knobs and row of comb-like projections. Dorsal view with anterior to the left. Scale bar, 100 μm.

Fig. 24. Adult. Medial tooth of gastric mill. Scale bar, 0.5 mm.

Fig. 25. Adult. Lateral tooth (left) of gastric mill. Anterior is to the left. Scale bar, 1.0 mm.

TABLE 2. Comparison of masticatory apparatus in larval and postlarval decapods[1]

	Larval		Postlarval	
	Mandibles	Stomach	Mandibles	Stomach
Stone crab, *Menippe mercenaria*, (Brachyura; Xanthidae) Present study	complex	simple	simple	complex
Shrimp, *Palaemonetes varians*, (Natantia: Palaemonidae) Patwardhan ('35a), LeRoux ('71a,b), Fincham ('79)	complex	simple	complex	simple
Shrimp, *Crangon septemspinosa*, (Natantia: Crangonidae) Regnault ('72)	complex	simple	complex	simple
Hermit crab, *Pagurus annulipes*, (Anomura: Paguridae) Thompson ('03), Nyblade ('70)	complex	simple	simple	complex
Lobster, *Homarus americanus*, (Macrura: Nephropidae) Herrick ('11), Factor ('78, '81a)	simple	simple	simple	complex

[1]Complex: Grinding molar process in mandibles; grinding gastric mill in stomach. Simple: Cutting/grasping mandibles (no grinding molar process); no grinding gastric mill.

(complex mandibles, simple stomach), which display the condition reported for adult Natantia.

LeRoux ('71a,b) showed that the caridean shrimp *Palaemonetes varians* has a simple stomach that lacks a gastric mill in the larval and juvenile stages, and Patwardhan ('35a) demonstrated the absence of the mill in the adult. Information on the mandibles comes from Fincham ('79), who described the larval development of this species. From his drawings, the zoeal mandibles appear to have well-developed molar and incisor processes. Unlike megalopal and juvenile stone crabs, however, the first postlarval stage of *Palaemonetes varians* clearly retains the well-developed molar process. The adult mandible is similar to that of the postlarva (Patwardhan, '35a). This shrimp, then, has complex mandibles and simple stomach in both larval and postlarval stages. The dramatic changes in the feeding apparatus that characterize metamorphosis in the stone crab do not occur in *P. varians*.

Regnault ('72) studied the development of the stomach and mandibles in another caridean shrimp, *Crangon septemspinosa*. In this species the foregut develops gradually through larval life and reaches its most complex form in the last larval stage, when it is lined by plates and setae and has a well-developed region between the cardiac and pyloric portions. It does not appear, however, to have the medial and lateral teeth characteristic of the gastric mill. The adult, as is typical of other carideans, also lacks the gastric mill. Larval mandibles in this species have both an incisor process bearing setae that may serve as filters and a grinding molar process. The adult mandible loses the incisor process but retains a grinding molar process. *Crangon septemspinosa*, then, appears to have complex mandibles and simple stomach in both larval and postlarval stages, although the larval stomach is somewhat more complex than that of *Palaemonetes varians*.

Thompson ('03) discussed the digestive system, including the gastric mill, in his description of the metamorphosis of the anomuran hermit crab *Eupagurus longicarpus* (actually *Pagurus annulipes*; Roberts '70). He asserts that there is no dorsal tooth during the zoeal stages and that lateral teeth are "simple and project upward instead of horizontally." Thompson continued (p. 162), "The stomach of the glaucothoë [first postlarval stage, equivalent to the megalopa] ... may be regarded as transitional in type, its more elongate form, horizontal lateral teeth ..., and well developed lateral-valve ridges recalling the stomach of the adult. There are indications of a dorsal tooth...." The sixth stage, or first juvenile stage, has a stomach "of adult type, but with the parts less specialized."

From Thompson's description, the development of the gastric mill of this hermit crab is similar to that of the stone crab, except for the presence of lateral teeth during the zoeal stages. Examination of Thompson's plates does not fully clarify this point but suggests that he might have mistaken the ridges of the zoeal stomach for lateral teeth. In any event, it seems reasonable to assume that even if lateral teeth are present in the zoeae, the gastric mill is not functional before the medial tooth first appears in the glaucothoë.

The larval development of external features of *Pagurus annulipes* is described by Nyblade ('70). He clearly showed an abrupt change from the zoeal to the megalopal mandibles, although it is difficult to determine from his illustration whether the zoeal mandibles have a molar process. Roberts ('70) showed the mandibles of a closely related species to have well-developed molar processes in the zoeal stages and megalopal mandibles that are similar to those of the adult. Thompson ('03) also illustrated a similar transition from the zoeal to the megalopal mandibles. On the basis of information collected from several sources, we can tentatively conclude that this hermit crab has complex mandibles and simple stomach in the zoeal stages, but that the converse is true of the postmetamorphic stages (beginning with the megalopa or glaucothoë), just as in the stone crab.

A final comparison may be made with the American lobster, *Homarus americanus*. The lobster has three larval stages; since there is no megalopa, the fourth stage can be considered the first postlarval or first juvenile stage. The early larval stages of the lobster have no gastric mill, and the full complement of medial, lateral, and accessory lateral teeth are first present in the fourth stage (Factor, '81a). Development of the mandibles corresponds to the development of the gastric mill; the comparatively delicate teeth of the first-stage mandibles are transformed into the more massive, molar-like teeth of the fourth stage (Factor, '78). These teeth on the incisor process should not be confused, however, with a molar process. There is no evidence of a grinding molar process in either the larval or postlarval stages of the lobster. The adult mandibles (Herrick, '11) are essentially similar to those of the fourth stage. The larval lobster, then, is characterized by simple mandibles and simple stomach, and the manner in which food is masticated is not clear. Postlarval lobsters have the simple mandibles and complex stomach typical of the Reptantia, and metamorphosis brings about the feeding apparatus necessary to process the substantial food they encounter in the benthic environment.

Additional information on the internal development of decapods is needed before meaningful generalizations can be made. Despite the limited information available, the comparison presented here may be useful in providing a framework for future analysis.

Details of larval development of decapod crustaceans are contained in the substantial literature on this subject, which comprises several hundreds of papers. Recent studies have demonstrated that this wealth of information, perhaps uniquely available for the crustaceans among major invertebrate taxa, can be analyzed to provide insight into matters of taxonomic and systematic importance. The structure of appendages, including the mouthparts, has proven to be of considerable importance in such analyses (Rice, '80; Van Dover et al., in press). In addition, phylogenetic implications have been reported for mandibular structure in adult crayfishes (Bouchard, '77) and adults in several species of the genus *Daphnia* (Edwards, '80).

Most papers on larval development include descriptions of the mandibles, as well as other appendages. The accompanying illustrations are often (but by no means always) simple line drawings, which are adequate for illustrating most of the appendages, but which give little or no indication of the complex, three-dimensional structure of the mandibles. Reasons for this include the difficulty of extracting information on three-dimensional structure from mouthparts mounted on microscope slides and viewed with a compound microscope, and the difficulty of preparing line drawings with a realistic sense of depth. Sometimes only a single mandible is illustrated, despite their tendency to be asymmetrical. Although scanning electron microscopy is perfectly suited to the task of accurately illustrating the mandibles, almost none of the papers on larval development include scanning electron micrographs (a notable exception is Greenwood and Fielder, '79).

Studies of larval development generally involve rearing specimens in the laboratory; molted exoskeletons are routinely collected and fixed in alcohol and provide the history of each animal, stage by stage. It is hoped that the availability of the very simple preparative procedure described in this paper will encourage investigators to pay additional attention to mandibular structure in future studies of larval development in decapods. This would make available detailed, accurate descriptions and illustrations of these important mouthparts for a wide variety of decapod larvae and would enable future comparisons of larval development, whether for taxonomic or functional purposes, to include the mandibles.

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