THE FUNCTIONAL MORPHOLOGY OF STOMATOPOD CRUSTACEA

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[Plates 1–3]

CONTENTS

A comparative study has been made of the mouthparts, mandibular mechanism, feeding mechanism and proventricular functional morphology of stomatopods.

The mandibles have well developed, cusped, molar processes that extend into the proventriculus. In *A. laevis*, the mandibles retain a near-vertical axis of swing and a promotor–remotor rolling action. The mandibular musculature is basically similar to those of *Chirocephalus*, *Anaspides*, *Paranaspides* and *Hemimysis* but is uniquely modified for mastication. Functionally important differences in the stomatopod mandibular arrangement include the replacement of the transverse mandibular tendon with an extensive endophragmal bridge and the enlargement of muscles 4, 5b and 6 (Manton's terminology). The persistence in stomatopods of well developed molar processes and a primitive musculature is related to the use of the molar processes as the major masticatory structures within the proventriculus. Prior to ingestion, food is held between the incisor processes of the mandibles and torn apart by the maxillipeds. These fragments are passed into the proventriculus by the rolling action of the mandibles in combination with anterior movements of the labrum. Mastication is achieved by the powerful promotor–remotor rolling actions of the mandibular molar processes operated by enlarged muscles 3, 5b and 6. Muscles 4, 5a and 5c are also large and provide strong transverse adduction of the incisor processes in the absence of a wide mandibular gape. Transverse movements of the incisor processes grip the food; they do not masticate it.

Comparisons of the diet and structure of the mouthparts of *A. laevis* with those of *Anchisquilla fasciata*, *Oratosquilla nepa*, *Harpiosquilla stephensoni*, *Odontodactylus cultrifer* and *Gonodactylus graphurus* indicate differences in trophic specialization both within and between the families Squillidae and Gonodactylidae.

Feeding in stomatopods is subdivided into three phases: prey-capture by the raptorial limbs; manipulation by the third, fourth and fifth maxillipeds; and ingestion. Morphological and functional differences are associated with the 'spearing' and 'smashing' mechanisms of prey-capture in squillids and gonodactylids respectively. Similarly, the degree of food manipulation and associated movements of the maxillipeds differ between the two families.

The palaeontological, ontogenetic and morphological evidence concerning the structure and function of feeding limbs in extinct and extant hoplocaridans is assessed. There is no evidence for a filter-feeding ancestor of the Hoplocarida. The lack of specialized endites or exopods in extinct and extant forms, the simple setal structure and arrangement in larval and adult stomatopods and a consideration of functionally possible intermediate forms indicate that stomatopods probably arose from simple raptatory ancestors.

The anatomy and function of the proventriculus of *A. laevis* is described in detail. The cardiac stomach lacks masticatory ossicles. Mastication is achieved by the actions of the molar processes of the mandibles together with contractions of the gastric mill. The breakdown of food is aided by digestive juices pumped into the cardiac stomach from the digestive gland. The posterior cardiac plate is a complex filtratory structure through which all macerated food passes before entering the pyloric stomach. The dorsal pyloric stomach is vestigial and does not provide direct communication with the midgut. Finely suspended material from the cardiac stomach flows through the ampullae directly into the digestive gland. This posterior

flow is a result of contractions of gastric muscles investing the wall of the cardiac stomach. Although partial filtration of material occurs during posterior flow, the material in both the upper and lower ampullary chambers is admixed in the post-ampullary chamber before passage into the digestive gland. The ampullae act primarily as a mechanism to filter digestive fluids flowing forwards from the digestive gland and to pump these into the cardiac stomach. Partially digested food particles are thus prevented from passing anteriorly into the cardiac stomach. The digestive cycle from ingestion to defaecation is phasic, characterized by discrete sequences of ampullary forward pumping, posterior flow from the cardiac stomach to the digestive glands and transfer of unassimilated particles into the midgut. The entire process occupies between 24 and 48 h in experimental animals. Indigestible fragments stored in the folds of the cardiac stomach are regurgitated when all digestible material has been pumped into the digestive gland. The structure and function of the proventriculus in the Hoplocarida is uniquely different from those of other Malacostraca.

A. fasciata, *O. nepa*, *H. stephensoni*, *O. cultrifer* and *G. graphurus* are generally similar in proventricular structure to *A. laevis*. Minor differences in the structure of the ossicles of the cardiac stomach, cuticular processes and relative proportions of the cardiac and pyloric regions are related to trophic specializations and the size of the animal.

Histological, histochemical and transmission electron microscope investigations of the digestive gland and midgut of *A. laevis* indicate that the digestive gland is the sole source of digestive enzymes and the major site of absorption and storage of the products of digestion. E-, R- and B-cells are present in the epithelial lining of the digestive gland. No F-cells were found. Secretion is holocrine, correlating the intermittent feeding and digestive cycle in stomatopods.

The diagnostic characters of the Eumalacostraca and the available information on hoplocaridan evolutionary relationships are reviewed in the light of the information obtained in the present study. The removal of the Hoplocarida from the Eumalacostraca is supported and a polyphyletic origin of the Phyllocarida, Hoplocarida and Eumalacostraca is proposed.

1. Introduction

Recent palaeontological studies (Schram 1969*a*, *b*, 1973) have suggested that the Eumalacostraca are polyphyletic and that the Hoplocarida are not an offshoot of some early caridoid form as stated by Siewing (1956, 1963) and Brooks (1962). The question of polyphyly in the Malacostraca has arisen several times in the history of crustacean phylogenetic theory. Claus (1885) was first to propose an independent origin for the Stomatopoda and later workers (Grobben 1892, 1919; Haeckel 1896; Giesbrecht 1913; Giesbrecht & Balss 1933; Balss 1938; Siewing 1956, 1963; Glaessner 1957; Brooks 1962, 1969*b*; Schram 1969*a*, *b*, 1973; Burnett & Hessler 1973; Reaka 1975*a*, *b*) have been divided on the issue. Most agreement lies with the monophyletic theory of Siewing (1956, 1963). Burnett & Hessler (1973) proved some of Siewing's evidence to be erroneous but their conclusions were in concurrence with his theory and in disagreement with that of Schram (1969*a*, *b*).

One reason underlying such divergent opinion is a lack of information concerning functional mechanisms and processes in Stomatopoda. The assessment of the morphological characters of stomatopods has been based largely on comparisons with caridoid morphology, without consideration of functional processes. Detailed functional information is essential, particularly during an attempt to relate such trophically dissimilar groups as the Phyllocarida and the Hoplocarida.

In this study the processes of feeding and digestion in stomatopods have been investigated, with greatest emphasis on proventricular structure and function. Particular attention has been paid to the musculature associated with the treatment of food in the proventriculus and on the flow relationships between the proventriculus, digestive glands and the midgut. The results emphasize the complexity of the system in stomatopods and its contrast with the functional processes and muscular configurations of other malacostracan groups. Throughout this study it was found necessary to avoid the use of existing terminology and adopt more representative terms. This procedure has avoided the implication of homology in structure that Siewing (1956) proposed in his study of malacostracan internal morphology.

The Stomatopoda is a relatively small group, comprising about 350 extant species divided into six families (Manning 1977). Morphologically, these display a conservatism related to the ubiquitous predatory habits of the group. All extant hoplocaridans are highly specialized carnivores that utilize their enlarged second maxillipeds to capture or immobilize their prey. The two major families, the Squillidae and the Gonodactylidae, differ mainly in the morphology and functional mechanism of their raptorial appendages. Representatives of these families have been compared in the present investigation. Recent studies (Caldwell & Dingle 1975, 1976; Dingle & Caldwell 1978) refer to these trophic habits as 'spearing' in squillids and 'smashing' in gonodactylids, depending on whether the limb is used with the dactyl extended or with it folded onto the propodus. There have been no studies of the morphological differences in other mouthparts or of differences in proventricular structure between the two major families. Such differences give clues to the patterns and processes underlying trophic specialization and allow more meaningful comparisons to be made with other Malacostraca.

The Phyllocarida (Cannon 1927; Rowatt 1947), Syncarida (Cannon & Manton 1929), Peracarida (Dennell 1937) and Eucarida (Kaestner 1970) each include species of differing dietary requirements ranging from detritivorous and/or filter-feeding forms to omnivorous and often carnivorous forms. Such differences on a species level are usually correlated with modifications of the mouthparts and proventriculus (see, for example: Barnard 1924; Cannon 1927; Cannon & Manton 1929; Nicholls & Spargo 1932; Dennell 1937; Rowatt 1947; Hassall 1977; Kunze & Anderson 1979). Locomotory adaptations show similar divergences in relation to habits (Hessler 1981). The absence of major lines of trophic diversification within the Stomatopoda poses fundamental questions about the evolution of the group.

Fossil evidence indicates there has been little morphological divergence in the Stomatopoda since the Jurassic (Holthuis & Manning 1969). The systematics of the group are based on differences in body armature, particularly telson armature, which are difficult to interpret in a functional or an evolutionary sense. The morphological characteristics that distinguish the Hoplocarida from other Malacostraca have yielded several divergent interpretations (see, for example: Schram 1969*a*, *b*; Burnett & Hessler 1973) due to difficulties in establishing which characters are primary and which are secondary specializations of stomatopods. Other characters such as the presence of a three-segmented protopod on the pereiopods and a triflagellate antennule have defied interpretation and remain enigmatic.

The stomatopod proventriculus cannot be interpreted in an evolutionary context on morphology alone. Previous descriptions (Petricevic 1915; Reddy 1935; Siewing 1956) have not distinguished specializations that reflect the carnivorous habits of the group. Reddy (1935) and Siewing (1956) both attempted to relate the morphology in stomatopods to proventricular

structure in other, non-carnivorous, malacostracans. Neither interpretation is satisfactory in the light of the functional analysis presented in this study. All descriptions and interpretations of functional mechanisms are based on observations and experiments on living animals. Most studies on proventricular function in other malacostracan groups have been based on morphological data from preserved specimens; few include observations of function in the living animal (Martin 1964; Schaefer 1970; Powell 1974).

2. Materials and methods

The six species investigated were collected from several localities along the northern and eastern Australian coastline. The southernmost occurring species, *Alima laevis* (Hess), was collected from Port Jackson, New South Wales. *Anchisquilla fasciata* (de Haan), *Oratosquilla nepa* (Latreille) and *Harpiosquilla stephensoni* Manning were collected from trawls in the Gulf of Carpentaria and Moreton Bay, Queensland. *Odontodactylus cultrifer* (White) was found only in Moreton Bay. The coral-inhabiting species, *Gonodactylus graphurus* Miers, was collected near Townsville, Heron Island and One Tree Island on the Great Barrier Reef, Queensland.

The structure of the mouthparts and the feeding mechanisms were studied by means of techniques previously described (Kunze & Anderson 1979). Skeletal structures were examined in specimens treated with potassium hydroxide solution (50 g/l) and stained with alizarin red S or methylene blue and eosin. Portions of the proventriculus were examined by scanning electron microscopy by means of the methods of Kunze & Anderson (1979). The musculature was studied in fresh and in fixed specimens. Serial sections were stained with Milligan trichrome (Humason 1972) or azan. Hand-cut serial sections were prepared from decalcified specimens embedded in gelatin. The gelatin blocks were hardened for several days in 70 % (by volume) alcohol before being sectioned. Sections were cleared with increasing concentrations of glycerol and mounted in glycerine jelly.

To observe the movements of the proventriculus, animals were dissected live in cool (10 °C) saline solution (Powers 1973). In cases where large portions of the lateral and dorsal exoskeleton were removed, animals were initially anaesthetized with 3 % (by mass) procaine hydrochloride (Oswald 1977). Several vital stains, including methylene blue, carmine, indian ink, and congo red, were used to observe the passage of material through the proventriculus. Further details about this technique are mentioned in § 6*e*.

Tissue components of the digestive glands and midgut were identified by means of periodic acid–Schiff (PAS), Alcian blue 8GS and mercuric bromophenol blue staining methods described by Barker & Gibson (1977). Glycogen and lipid food reserves were identified in tissues fixed and stained by techniques also described by Barker & Gibson (1977). Histochemical methods used were the Gomori methods for acid and alkaline phosphatases (Humason 1972). Sites of iron absorption were localized in animals fed saccharated iron(II)carbonate by the technique of Nicholls (1931). Small tissue blocks were fixed, stained and sectioned for transmission electron microscopy following the procedure of Egan & Anderson (1979).

3. The functional morphology of the mouthparts

There have been no descriptions of the mouthparts and limbs of stomatopods since those of Giesbrecht (1910, 1921) and Balss (1927, 1938), apart from brief accounts by Holthius &

Manning (1969) and Kaestner (1970). The early descriptions lacked functional interpretation, and provided no comparative information on setation or armature. Giesbrecht (1921) gave a detailed account of the skeletal morphology of *Squilla mantis* (L.), mentioning the mouthparts in relation to their surrounding endophragmal skeleton.

Burrows (1969) gave detailed descriptions of the structure and musculature of the raptorial appendages in relation to the mechanics and neural control of the strike response in *Squilla empusa* Say and *Hemisquilla ensigera* (Owen). Recent work on agonistic behaviour of squillid and gonodactylid stomatopods (Caldwell & Dingle 1975, 1976; Dingle & Caldwell 1978) shows that differences in the morphology of the raptorial limbs may be associated with differences in feeding habits. The nature of these morphological differences, particularly in relation to feeding appendages other than the raptorial claws, remains unclear. The relationship between mouthparts, diet and proventricular structure in different species is also unknown.

In this section a detailed description of the feeding appendages of *Alima laevis* is given and comparisons are made with the mouthparts and diets of other squillid and gonodactylid stomatopods. A description of the mandibular mechanism and its associated musculature in *A. laevis* is included as a basis for comparison with mandibular mechanisms of other Crustacea, described by Manton (1964, 1977). The functions of the other mouthparts are described later in §4.

(*a*) *The mouthparts of Alima laevis* (*Hess*)

The mouthparts of stomatopods comprise the mandibles, maxillules, maxillae and five pairs of maxillipeds formed by thoracopods 1 to 5 (figure 1).

The labrum forms the anterior wall and ventral lip to the pre-oral cavity. It is not a clearly demarcated structure, being fused to the epistome on the ventral surface of the mandibular segment and continuous with the ventral cuticle of the proventriculus at its inner, dorsal margin (figure 1, lb). There is no oesophagus in stomatopods. Petricevic (1915) regarded the ventral posterior portion of the cardiac stomach as homologous with the oesophagus but there is no morphological or functional justification for such a conclusion. Laterally, the labrum fuses with the cuticle adjacent to the ventral process of the mandibular endophragm (figure 2, v pr). The labrum is not calcified on its ventral surface but is heavily sclerotized and has a well developed musculature (see §5*c*).

(i) *The mandibles*

The masticatory surfaces of the mandibles exhibit an inverted L shape and lie behind the labrum. The molar process of each mandible extends medially above the labrum and penetrates the posterior ventrolateral corners of the proventriculus (figure 1). The mandible body (or corpus mandibulae) (figure 8*f*, *g*, mb b) is a massive structure extending dorsally on either side of the mandibular endophragm. The mandible has two articulations. Dorsally, a rounded protuberance of the mandible body forms a ball and socket articulation with the posterior dorsal tubercle of the mandibular endophragm (p d t, figure 2). Anteroventrally, the rounded protuberance on the lower anterior margin of the mandible body articulates with the invagination of the mandibular endophragm immediately below the posterior ventral tubercle (p v t, figure 2). These two articulations allow promotor–remotor rolling movements and a limited range of abduction–adduction. The remaining anterior, posterior and ventral margins of the mandible that border the mandibular foramen are connected to the surrounding skeleton by flexible cuticle.

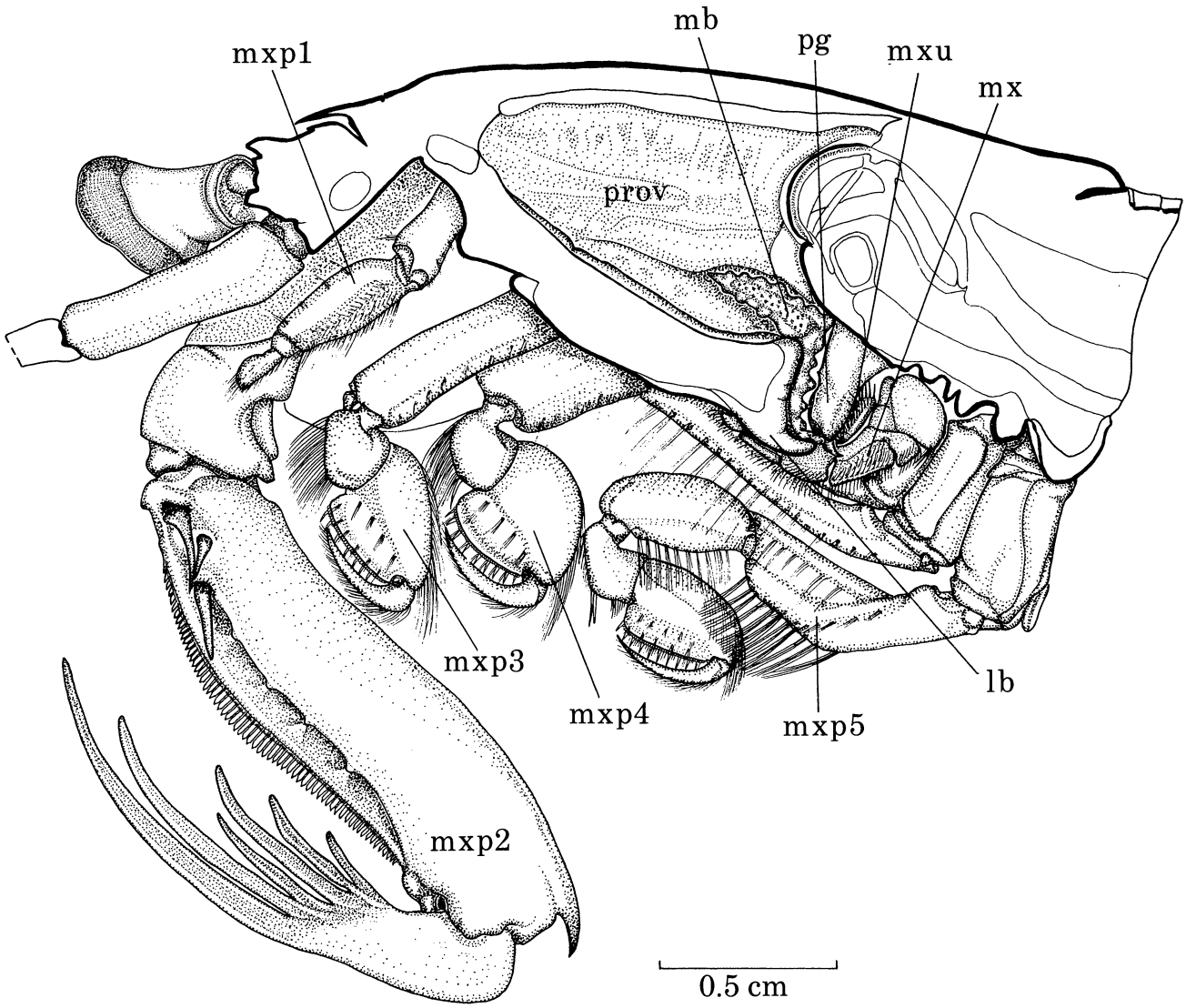


FIGURE 1. *A. laevis*: median view of the mouthparts and proventriculus exposed by sagittal section.

The incisor process has a single medial row of seven sharp teeth, increasing in size dorsally. The molar process bears two rows of teeth, eight dorsally and six ventrally. Between the two rows is a curved depression serving as a grinding plate (figure 8*f*). There is no mandibular palp in *A. laevis*.

(ii) *The mandibular musculature and mechanism*

The mandibular mechanism of stomatopods is strikingly different from those of the Syncarida, Peracarida and Decapoda described by Manton (1964). Stomatopods have retained well developed molar processes, unlike other large-food-feeding malacostracans such as *Ligia oceanica* Roux, *Astacus fluviatilis* (*Potamobius astacus* L.) and *Carcinus maenas* L. (Manton 1964). Associated with this feature is the dual use of transverse biting movements of the incisor

processes and rolling promotor–remotor movements of the molar processes. It is possible to identify many of the characteristic mandibular muscles that are found in Branchiopoda, Leptostraca, Syncarida, Peracarida and Decapoda. These muscles are listed below, following the terminology employed by Manton (1964).

(1) The anterior mandibular promotor (muscle 3) originates from the dorsal body wall, lateral to the longitudinal trunk muscles. It inserts on the arthrodial membrane adjacent to

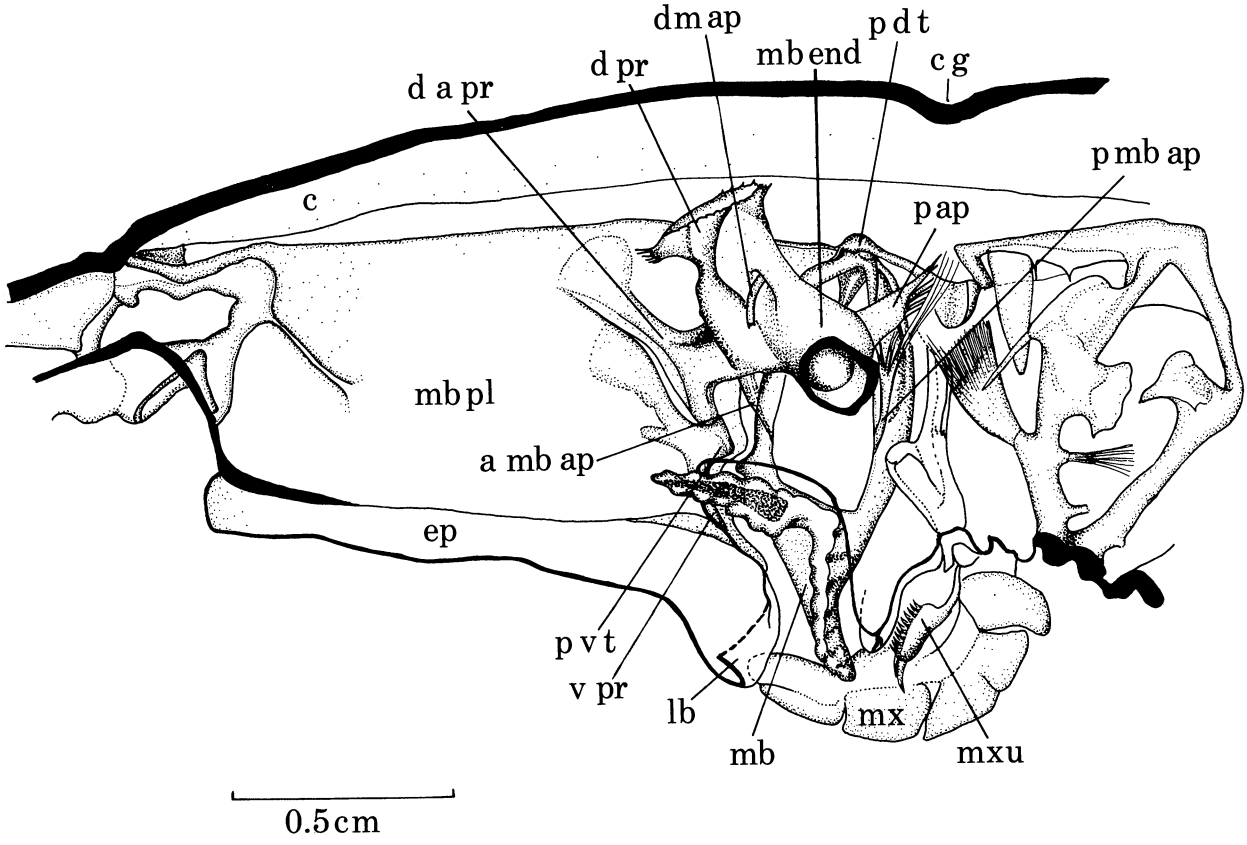


FIGURE 2. *A. laevis*: median view of the cephalothoracic skeleton exposed by sagittal section, showing endophragmal structures for muscle attachment.

the upper anterior margin of the mandible (figures 3*b*, 8*g*). Contraction of muscle 3 results in a slight medial rotation of the molar processes and abduction of the incisor processes.

In the anostracan branchiopod *Chirocephalus diaphanus* Prevost, anaspidacean syncarids and mysids (Manton 1964), contraction of muscle 3 causes a promotor roll similar to the movement of a trunk limb.

(2) The mandibular promotors (muscles 5b, 6). Muscle 5b originates from the ventral surface of the mandibular endophragmal 'bridge', which spans the space between the mandibles and inserts along the anterior lateral wall of the mandible body (figures 3*a*, *b*, 4*a*, *b*, 6, 8*g*). Contraction of muscle 5b effects a promotor roll. The relative position of the axis of swing (figure 3*b*, x) causes a translation of this movement into a medial swing of the molar process with no accompanying abduction of the incisor process.

In *Chirocephalus*, anaspidaceans and mysids, muscle 5b effects a promotor roll causing abduction of the incisor processes and separation of the molar processes (Manton 1964).

Muscle 6 originates from the lateral surface of the anterolateral wing of the mandibular endophragm and inserts on the dorsal anterior margin of the mandible body (figures 3*b*, 4*a*, 5, 6, 8*g*). Contraction of these muscles causes medial movement of the molar processes without significant abduction of the incisor processes.

Muscle 6 is relatively smaller in *Chirocephalus* and *Hemimysis lamornae* (Couch) and 'promotes movements at right angles to the main mandibular roll' (Manton 1964). In *Anaspides tasmaniae* Thomson and *Paranaspides lacustris* Smith, this muscle assists in the promotor roll providing abduction of the incisor processes.

(3) The anterior mandibular remotor (muscle 2) originates anterior to muscle 3, on the dorsolateral cephalic margin where the carapace fuses to the lateral wall (figures 3*b*, 4*a*, 5, 6, 8*g*). It inserts on the anterior mandibular apodeme (figures 5, 6, a mb ap). Contraction of muscle 2 produces a remotor roll of the mandible body. This results in a posterolateral swing of the molar processes accompanied by a slight dorsomedial movement of the incisor processes. There is no pronounced adduction of the incisor processes.

In anaspidaceans and mysids, muscle 2 functions in increasing the strength of the remotor roll, thus effecting grinding by the molar processes and biting by the incisor processes. Muscle 2 is absent in *Chirocephalus* (Manton 1964).

(4) The mandibular remotors (muscles 4, 5a, 5c) function mainly as adductors of the incisor processes. The posterior mandibular remotor (muscle 4) originates from the undersurface of the carapace, medial to the dorsal longitudinal muscles (figure 3*b*) and inserts on the posterior mandibular apodeme (figures 2, 5 and 6, p mb ap). Contraction of muscle 4 causes adduction of the incisor processes without rotation of the molar processes.

In *Chirocephalus*, anaspidaceans and mysids, muscle 4 provides a remotor roll similar to a trunk limb resulting in grinding of the molar processes and biting by the incisor processes (Manton 1964).

Muscle 5a originates from the mandibular endophragmal bridge, posterior to the origins of muscle 5b, and inserts over the posterior lateral wall of the mandible body (figures 3*a*, 4*b*, 6, 8*g*). Contraction of this muscle also effects adduction of the incisor processes. The molar processes are swung laterally by the remotor roll. This is because the axis of swing lies perpendicular and posterior to the molar process and parallel to the incisor process (figure 3*b*). In *Chirocephalus* and anaspidaceans the molar process partially overlaps the axis of swing and lies on the same side of the axis as the incisor process. In these animals muscle 5a functions similarly to muscle 4 (Manton 1964).

The transverse mandibular remotor (muscle 5c) is paired in stomatopods, with each muscle of the pair arising from the upper surface of the median bridge of the mandibular endophragm. Each inserts on the posterior margin of the mandible (medially facing) (figures 3*b*, 4*b*, 6). Contraction of these muscles causes movements similar to those of muscle 4, i.e. adduction of the incisor processes. The action of this muscle is similar in *Chirocephalus*, anaspidaceans and mysids. In these animals, however, the transverse muscles, like muscles 4 and 5a, also effect grinding of the molar processes (Manton 1964).

In summary, the mandibular musculature of stomatopods may be divided into the following four groups: muscles that cause a promotor roll (muscle 3); muscles that cause a promotor roll but effect only a medial swing of the molar processes (muscles 5b, 6); muscles that cause

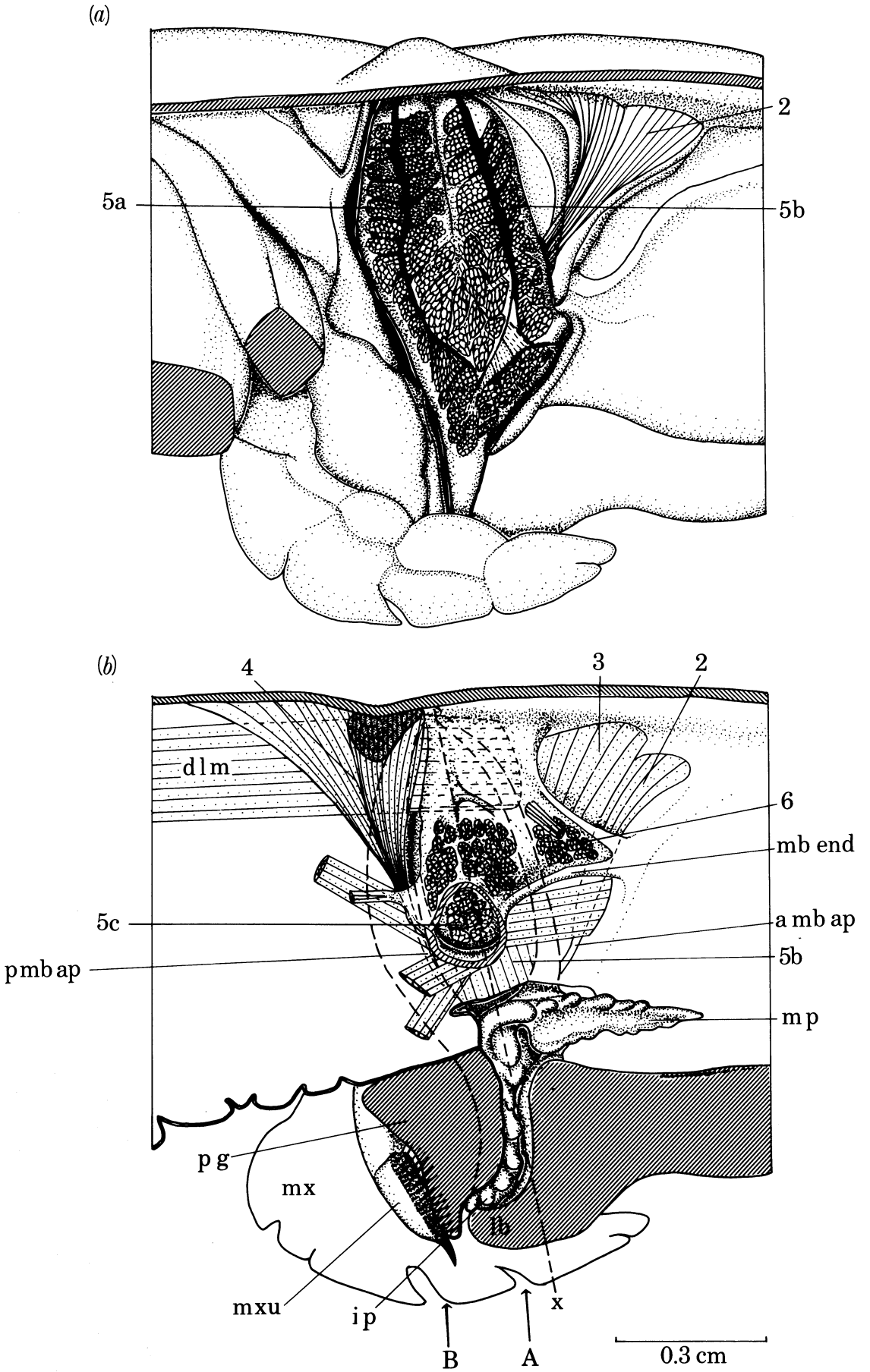


FIGURE 3. (*a*) Lateral external view of the mandibular musculature of *A. laevis*. (*b*) Median view of the mandibular musculature of *A. laevis* exposed by sagittal section. A, B, arrows indicate planes of section corresponding to those in figure 4*a*, *b*.

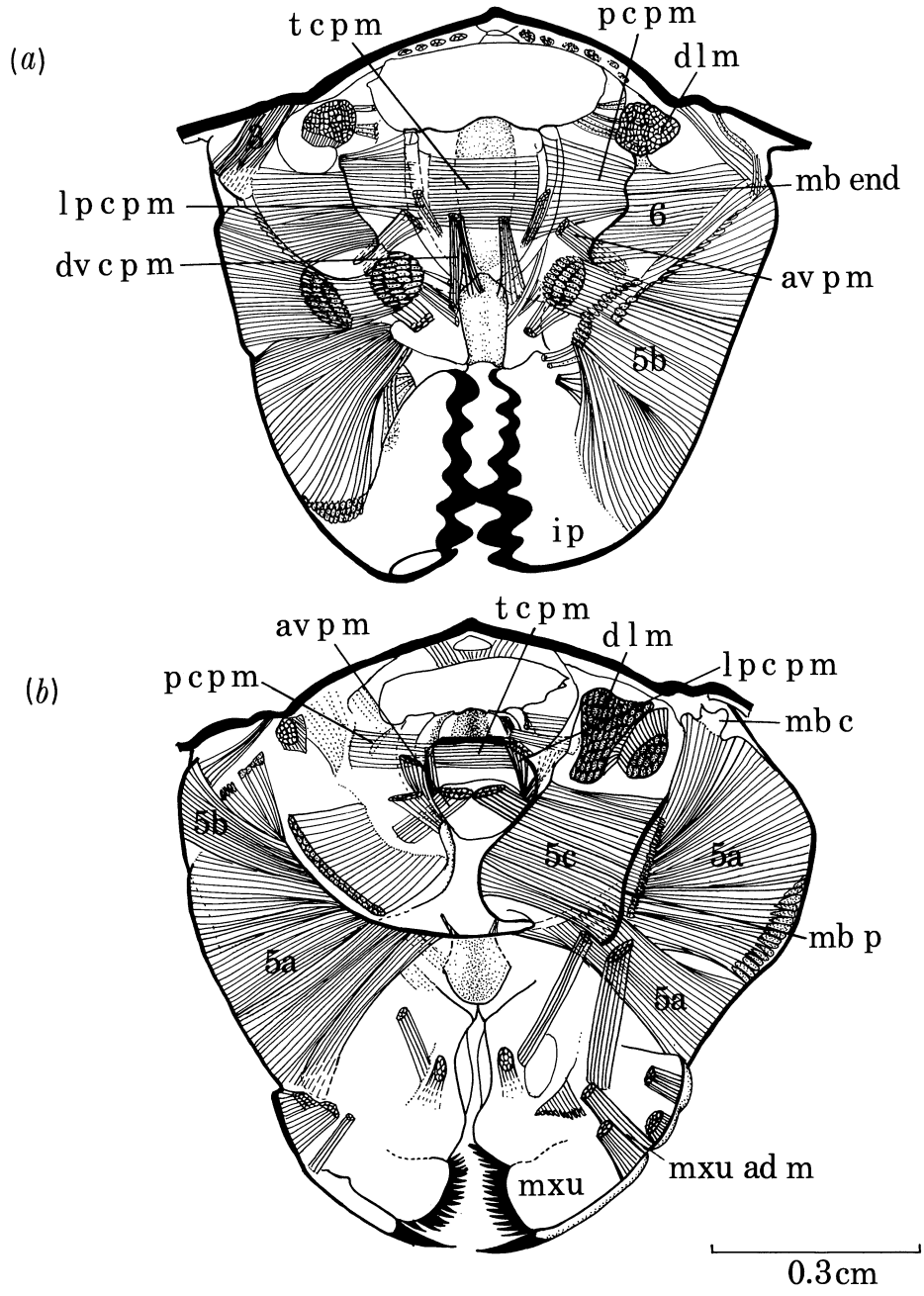


FIGURE 4. Posterior views of sequential thick transverse sections of the cephalothorax of *A. laevis*, showing mandibular and proventricular musculature; (*a*) is anterior to (*b*), corresponding to levels A and B, respectively, in figure 3*b*. The right half of (*b*) is more posterior than the left half of the figure.

a remotor roll (muscle 2) and; muscles that cause a remotor roll but secondarily effect adduction of the incisor processes (muscles 4, 5a, 5c).

The most significant feature of the mandibular arrangement in *A. laevis* is the replacement of the transverse mandibular tendon by a heavily calcified endophragmal skeleton. A detailed description of the endoskeleton was given by Giesbrecht (1921). Associated with the loss of the transverse tendon are changes in the origins of muscles 5c and 6. In species with a trans-

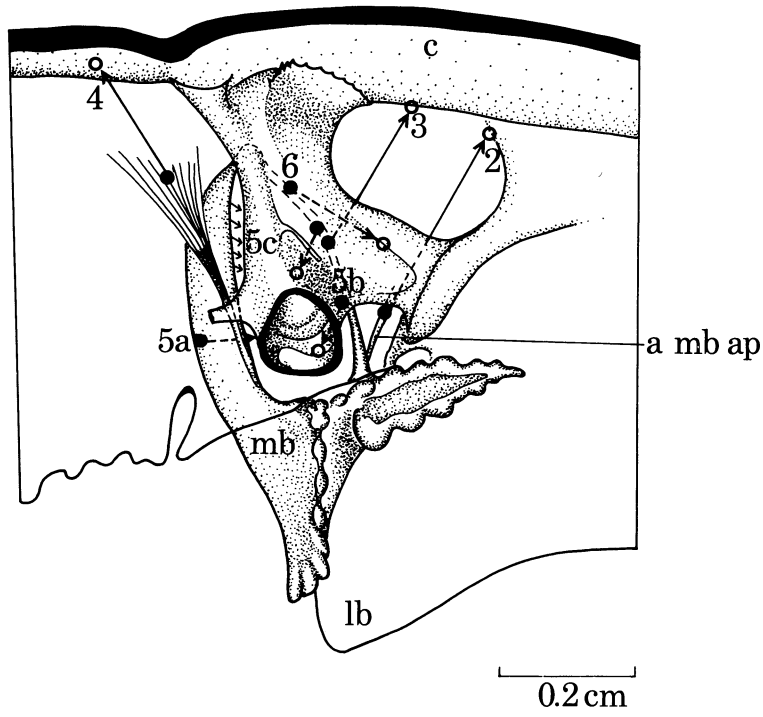


FIGURE 5. *A. laevis*: median sagittal view of the mandibular endophragm and mandible after removal of the proventriculus (right side is anterior).

verse mandibular tendon, such as *Chirocephalus*, *Nebalia bipes* (*O. Fabricius*), *Paranaspides* and *Anaspides*, muscle 5c traverses the space between the posterior mandibular margins (Manton 1964). In *A. laevis* there is an extensive intervening endophragmal plate from which the paired transverse mandibular muscles arise. Muscle 6 is enlarged and has broad origins on the endophragmal skeleton compared with a smaller muscle 6 with tendinous origins in the above four species.

The mandibular mechanism does not correspond to that of *Anaspides*, *Ligia* or the decapods examined by Manton (1964). The musculature is similar to *Anaspides*, *Paranaspides* and *Hemimysis* in that all these species possess muscles 2, 3, 4, 5a, 5b, 5c and 6. In this respect stomatopods may be grouped with the less advanced Malacostraca. Although stomatopods are large-food feeders, they do not possess the more specialized skeletomuscular arrangements of other large-food feeding malacostracans such as *Ligia*, *Astacus* and *Carcinus*. These species have transverse biting mechanisms, although isopods and decapods have attained them in different ways. Characteristic of both *Ligia* and the decapods examined by Manton (1964) is the loss

of several structures, thus allowing for a wider mandibular gape and powerful transverse biting movements. The major features are the disappearance of the transverse mandibular tendon and muscles 5b and 5c. In *Ligia* the other major change has been a tangential shift in the axis of swing from an oblique position, as in mysids and anaspidaceans, to a horizontal position. In *Astacus* and *Carcinus* an oblique axis of movement is retained but there is no strong

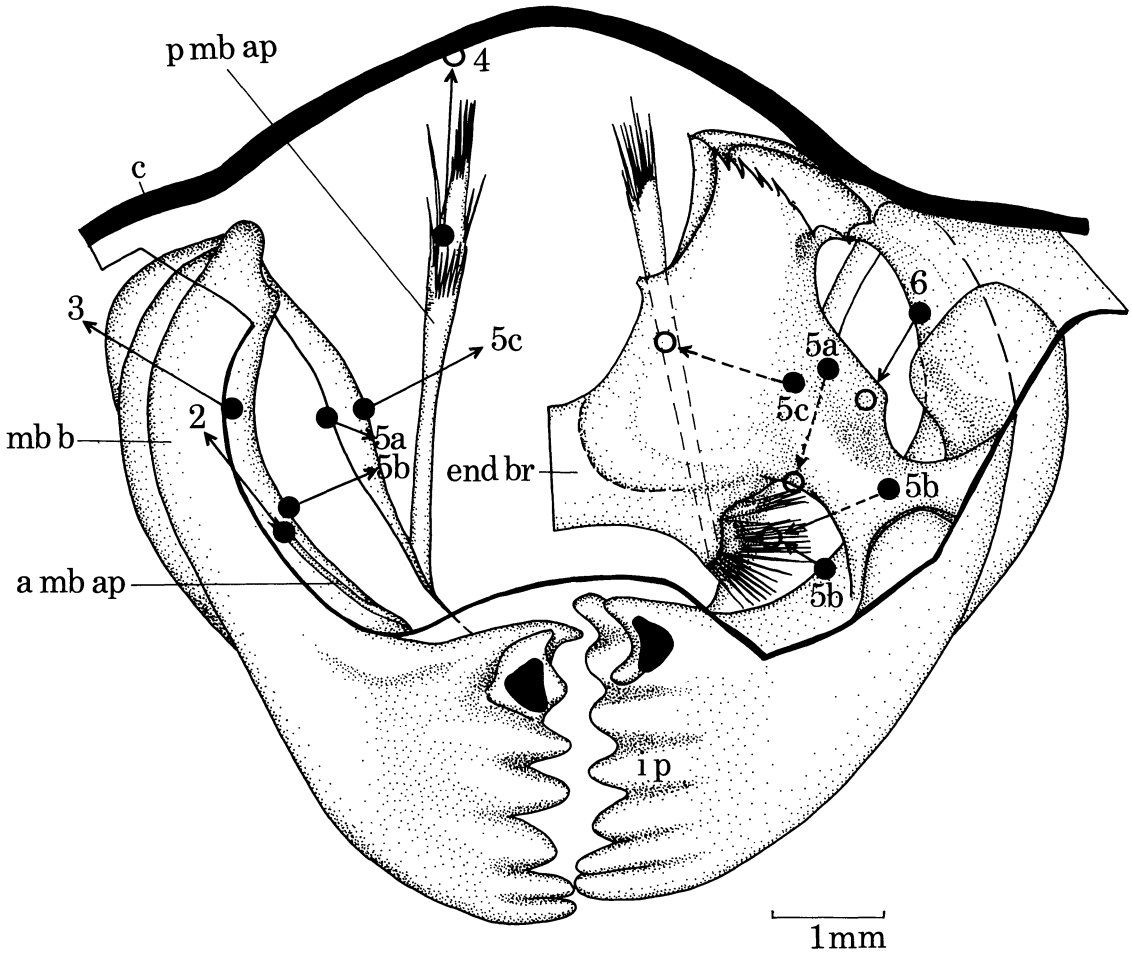


FIGURE 6. *A. laevis*: anterior view of a transverse section of the mandibular skeleton, left half with endophragm removed. Arrows indicate regions of origin (O) and insertion (●) of the mandibular muscles.

dorsal mandibular articulation and no freedom of movement at the base of the axis (Manton 1977, pp. 80–81). The axis of mandibular movement in stomatopods is almost vertical (as in *Chirocephalus* and *Nebalia*) and there is a strong dorsal articulation. Manton (1964) stated that such an arrangement is best suited to grinding and squeezing actions. This study supports Manton's conclusion. Although *A. laevis* feeds on large, hard items (see §3*c*), the incisor processes only grip the food while it is torn apart by the maxillipeds (see §4). Large fragments of food pass into the proventriculus, within which the molar processes of the mandibles serve as the major masticatory structures. Modifications in musculature can be recognized that strengthen the adductor movements of the incisor processes and the promotor movements

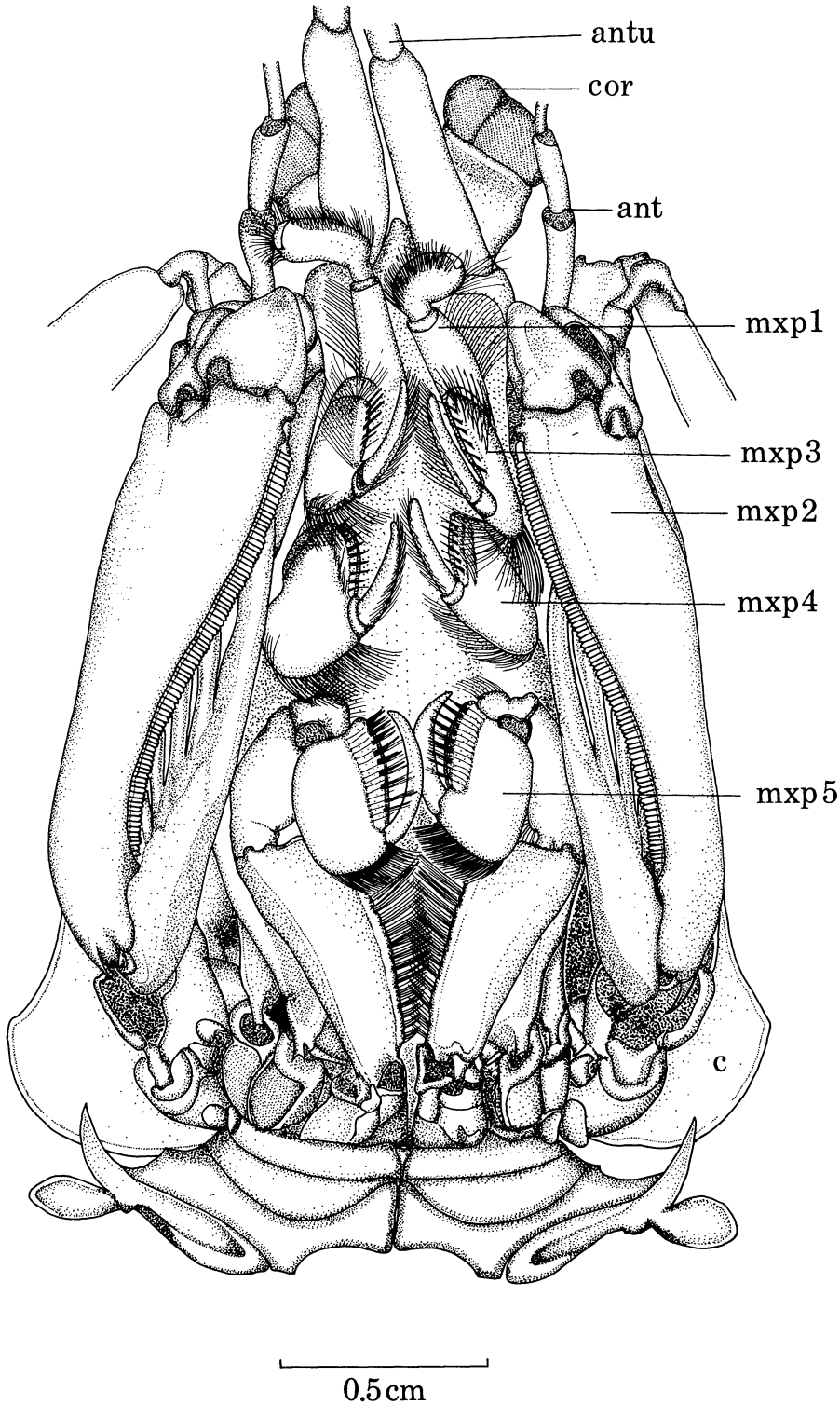


FIGURE 7. *A. laevis*: ventral view of the cephalothorax, showing the arrangement of the maxillipeds. The second maxillipeds are laterally displayed to expose the other maxillipeds.

of the molar processes. In *Chirocephalus*, *Hemimysis* and *Paranaspides*, muscle 4 provides mandibular movements similar to those of a trunk limb: in *A. laevis* it is large and functions as a powerful adductor muscle for the incisor process. Muscles 5b and 6 are also enlarged in comparison with *Chirocephalus*, *Hemimysis* and *Paranaspides*. Both serve as powerful promotors of the molar processes. A powerful transverse adductor action is thus possible by means of the less advanced muscular complement found also in *Chirocephalus*, mysids and anaspidaceans. This allows for the retention and further strengthening of promotor–remotor rolling movements serving a powerful grinding action of the molar processes.

(iii) *The paragnaths*

These lie behind the mandibular incisor processes (figure 1, pg). When the mandibles are held laterally the paragnaths fit tightly against the labrum, sealing off the preoral cavity. A row of simple setae borders the ventral and medial margins of the paragnaths.

(iv) *The maxillules*

The maxillules lie behind the paragnaths, with their spinose margins projecting medioanteriorly between the medial surfaces of the paragnathal lobes (figure 1, mxu). The coxa and basis of the maxillule each have a well developed endite (figure 8*h*). There is a small, unsegmented palp on the medioventral margin of the distal endite, regarded by Holthuis & Manning (1969) to be the vestige of the endopod. The proximal endite bears on its oral surface three adjacent rows of sclerotized, stout spines. The distal endite extends orally as a single, large-tooth with a small, tooth-like spine adjacent to it, and two and three setae along the ventral margin (figure 8*h*, d e).

(v) *The maxillae*

The maxillae lie behind the maxillules and curve ventrally and anteriorly to extend beneath the labrum. Each consists of four segments (figure 8*i*). The first is cylindrical and supported by five calcified plates. On the medioposterior surface is a cup-shaped endite bearing three rows of simple setae on the anterior, median and posterior margins. The long, fine setae brush over the median posterior surface of the proximal endite spines of the maxillule, toward the mouth. The second segment is flattened and is supported by three calcified plates on the aboral surface. Arising from the medial surface are two endites, each bearing brushes of long, fine, simple setae. Another row of shorter, stouter setae borders the medial edge of the second segment adjacent to the endites. These setae brush over the spines of the maxillule. The third and fourth maxillary segments are each supported by two calcified plates on their posterior surface. The medial margins bear dense brushes of simple setae, which, together with the endite setae of the second segment, form a screen over the labrum, paragnaths, mandibles and maxillules, preventing the escape of food particles. The lateral margins of the third and fourth segments of the maxilla bear finer rows of simple setae, which assist in brushing material medially.

(vi) *The maxillipeds*

According to Holthuis & Manning (1969), the maxillipeds each comprise seven segments: a trisegmented protopod consisting of precoxa, coxa and basis and an endopod consisting of a fused ischiomerus (usually termed merus), carpus, propodus and dactylus (the latter

forming a subchela). A precoxa is, however, not clearly defined on any maxilliped although it is well developed on each pereiopod. There are no exopods, but each maxilliped carries a respiratory epipod on the coxa (Burnett & Hessler 1973).

(1) *First maxillipeds.* These, which lie dorsal to the other maxillipeds, extending along the mandibular pleurite in close apposition with the undersurface of the carapace, differ from them both morphologically and functionally (figure 1, mxp1). Anteriorly, they extend to the level of the cornea. The coxa and basis are slender and elongate, articulating at an angle of 45° (figure 8*a*), which allows great mobility of the limb during cleaning activity. The basis bears, on its ventral surface, two rows of fine simple setae and a sparser covering of similar setae on the dorsal surface. These, together with similar rows of setae on the merus and carpus, brush ventrally along the lateral cephalic surface. The merus is similar in shape to the basis, but shorter, forming a relatively inflexible articulation with the basis. The merus–carpus articulation sweeps through an arc of 90°. The rectangular carpus bears a dense brush of simple setae on its ventral surface, those of the medial side being shorter than those on the lateral side. Dorsally, it bears a row of long, simple setae. The subchela is very much reduced in comparison with those of the other maxillipeds. The dactylus is almost vestigial, represented by a small tooth articulating on the mid-dorsal surface of the propodus. The rounded propodus has its distal margin produced into a beak onto which the dactyl closes. Its setation is specialized for cleaning. The dorsal surface bears a row of long simple setae and the proximal half of the ventral surface bears a dense brush of shorter, stouter, simple setae. The distal half of the ventral surface bears a clump of distally serrate setae. The shaft of each seta is naked for two-thirds of its length, with the terminal one-third bearing a cup-shaped brush of setules. The setules are perpendicular to the long axis of the seta and directed ventrally. The flexibility of movement of the first maxillipeds enables the animal to brush the eyes, antennules, antennae, most of the cephalic pleurites and ventral parts of the thorax and abdomen. The small subchelae are used to pick pieces of debris from the body.

(2) *Second maxillipeds.* The raptorial appendages are enlarged and heavily armoured (figure 8*b*). The propodus and dactylus form a 'jack-knife', which, when folded, fits into a groove on the ventral surface of the merus. All segments are heavily calcified, providing lateral and ventral protection for the cephalic segments and other mouthparts when the merus, propodus and dactylus are folded under the carapace (figure 7). The coxa and basis are short, stout segments containing powerful musculature for the remainder of the limb. The basis has a limited lateromedial articulation with the coxa and is fused to the merus. The enlarged merus serves as the muscular powerhouse for the raptorial limb. Its dorsal anterior margin is deeply concave, allowing retraction underneath the antennal protopod. The musculature and associated endophragma of the merus, carpus and propodus, described by Burrows (1969) for *Squilla empusa* and *Hemisquilla ensigera*, are similar in *A. laevis* and require no description. The carpus articulates with the merus by two ball and socket joints, allowing the propodus to be moved in an arc of almost 150°. When folded, the carpus fits into the ventral groove of the merus. The articulation of the carpus with the propodus is by a single ball and socket joint, allowing only limited dorsoventral and lateral movement of the latter.

The rectangular propodus is almost as long as the merus and slightly concave on its medial face. On the distoventral margin is a sharp spine. The dorsal surface is heavily sculptured, with six depressions separated by calcified ridges, which accommodate the spines of the dactylus when it is folded onto the propodus. On the distal margins of the anterior two ridges

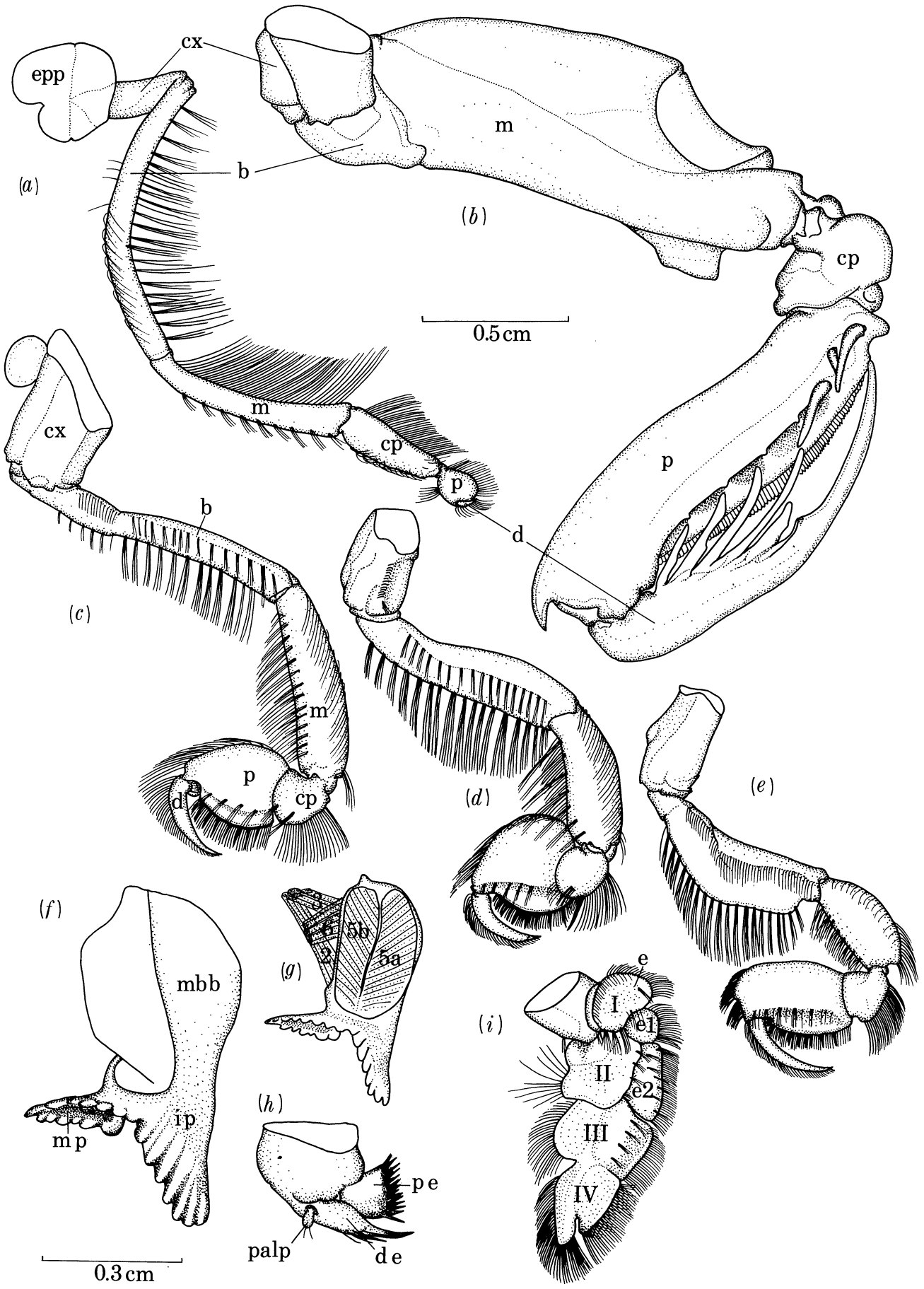


FIGURE 8. *A. laevis*: (*a*) first maxilliped; (*b*) second maxilliped; (*c*) third maxilliped; (*d*) fourth maxilliped; (*e*) fifth maxilliped; (*f*) mandible; (*g*) mandible, showing mandibular muscles; (*h*) maxillule; (*i*) maxilla.

are two articulating spines which have muscle attachments. Along the lateral margin of the dorsal propodal surface is a row of about 60 flexible teeth which, together with the dactylar spines, serve for holding prey. The propodus has well developed musculature responsible for dactylar protraction and retraction. The articulation with the dactylus is via a single ball and socket joint that allows it to be swept in an arc of 120°.

The dactylus forms the terminal spear to the raptorial limb. It is produced into seven sharp spines which curve anterodorsally. It is heavily calcified, particularly on the proximal ventral surface, which may be used during the strike response, often during agonistic interactions (Dingle & Caldwell 1978).

(3) *Third, fourth and fifth maxillipeds.* These share a common structure (figure 8*c*, *d*, *e*). Their coxae are arranged transversely in a row between the coxae of the two raptorial limbs, to which they lie medial and slightly ventral (figure 7). The basis of each is reflexed anteriorly with respect to the coxa and is longer than that of the next posterior maxilliped (figure 8*c*, *d*). The size of the merus shows a similar gradation. The sequential shortening of basis and merus, coupled with the anterior basal reflexion, results in the subchelae being held in the same horizontal plane underneath the epistome. The compressed limb-base attachments allow the third, fourth and fifth maxillipeds to seal off the oral area completely, thus preventing the escape of food from the dorsal anterior mouthparts and protecting the more delicate maxillae, maxillules and paragnaths. The third to fifth maxillipeds bear extensive setation along the ventral surfaces of the basis, merus, carpus, propodus and dactyl. The setation of the basis and merus increases in density from the third to fifth maxillipeds. The basal and meral setae of the third and fourth maxillipeds form a lateral screen, while those of the fifth maxillipeds form a ventral screen (figure 7).

The flexible articulation of the basis with the coxa is by a double ball and socket arrangement. The basal–meral articulation is very limited. The carpi of the third, fourth and fifth maxillipeds are almost identical. Each is a small, almost triangular segment with a free articulation with the merus. On the ventral surface is a dense brush of simple setae. Distally, there are two sharp spines surrounded by shorter stout setae. On the mediodistal surface is a row of short, dense, simple setae. The articulation of the carpus with the propodus is limited to minor dorsoventral and lateromedial movements.

The propodi of the third and fourth maxillipeds are oval, with a row of ventrally directed setae on their dorsal surface. On the ventral margin is a row of flexible teeth similar to, but less robust than, those of the raptorial limb. Lateral to this row of teeth is a row of four or five spines, each surrounded by several simple setae. The propodus of the fifth maxilliped is more rectangular, with the distal margin bearing a dense brush of short setae which sweep across the long setae of the basis of the same limb.

The dactyli of the third to fifth maxillipeds are heavily calcified, curved teeth, each with a ventral border of setae. Each dactylus articulates through 45–60° with the propodus and, when flexed, slides against the medial surfaces of the ventral propodal teeth.

(*b*) *Comparisons with other squillid and gonodactylid stomatopods*

In addition to *Alima laevis*, five other species were examined to assess the degree of morphological variation of the mouthparts within and between the families Squillidae and Gonodactylidae. The squillids were *Anchisquilla fasciata*, *Oratosquilla nepa* and *Harpiosquilla stephensoni*; the gonodactylids were *Odontodactylus cultrifer* and *Gonodactylus graphurus*.

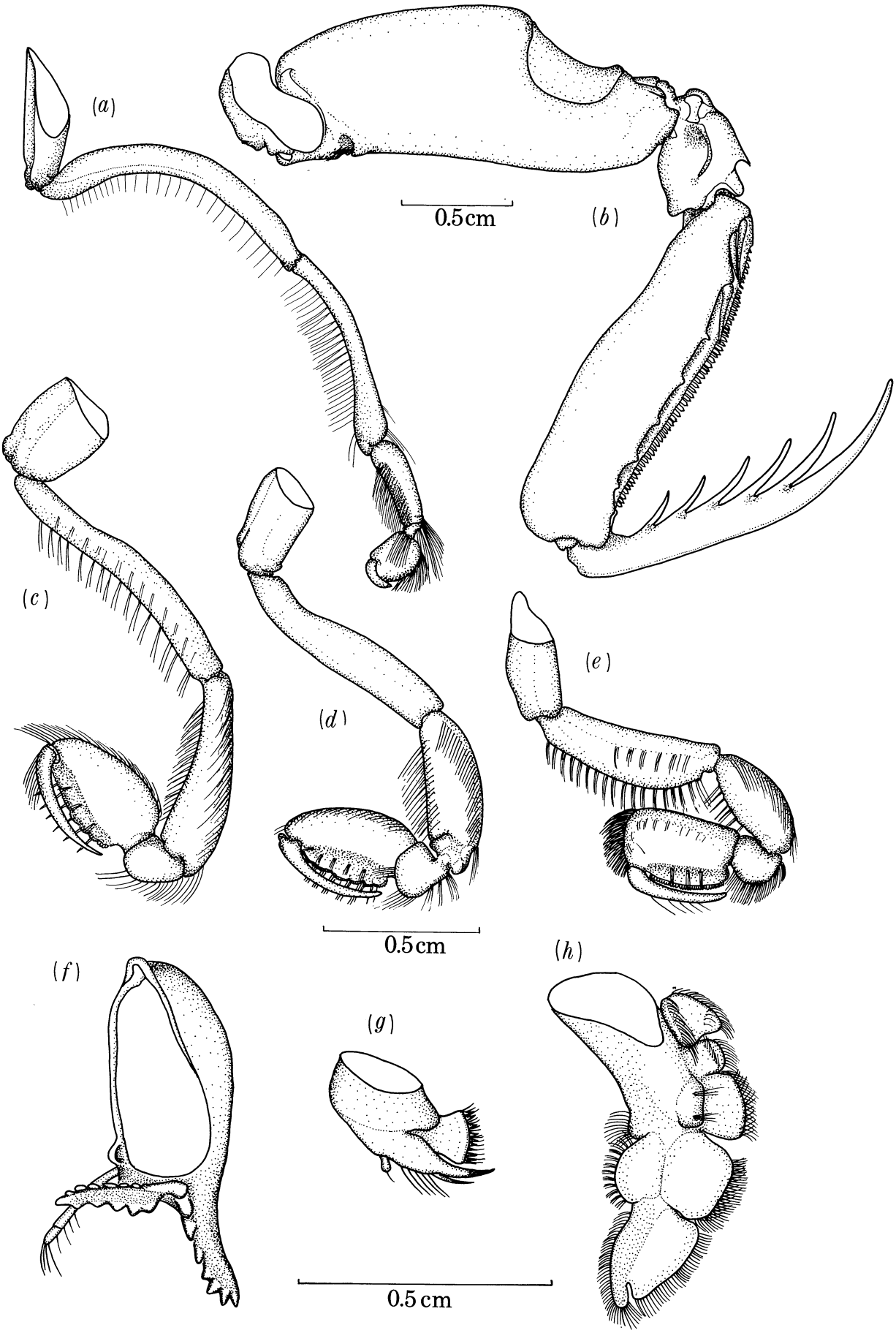


FIGURE 9. *A. fasciata*: (*a*) first maxilliped; (*b*) second maxilliped; (*c*) third maxilliped; (*d*) fourth maxilliped; (*e*) fifth maxilliped; (*f*) mandible; (*g*) maxillule; (*h*) maxilla.

(i) *Mandibles*

The number, relative size, and shape of the teeth on the incisor process and ventral row of the molar process are similar in *A. laevis*, *A. fasciata* and *O. nepa* (figures 8*f*, 9*f*, 10*f*). The posterior four teeth on the dorsal row of the molar process in *A. fasciata* and *O. nepa* are blunter and more closely spaced.

The mandibles of *H. stephensoni* (figure 11*f*) contrast with those of the above three species in a number of respects. The ventral part of the incisor process is more posteriorly curved, so that the three lower teeth occlude horizontally, not vertically. The molar process is relatively longer and narrower, with the anterior teeth much smaller and the lower posterior two teeth enlarged. The depression between the dorsal and ventral rows of teeth on the molar process is also relatively shallower.

The mandibles of *O. cultrifer* and *G. graphurus* are generally more robust than those of the squillids investigated (figures 12*f*, 13*h*). The molar process terminates in two teeth (one in squillids) and the depression between the upper and lower rows is more deeply excavated. The dorsal and ventral teeth are relatively larger and more rounded, with the posterior three dorsal teeth fused into a single cutting edge. A mandibular palp is present in all species except *A. laevis*.

(ii) *Maxillules*

The maxillules of *A. fasciata* (figure 9*g*), *O. nepa* (figure 10*g*) and *H. stephensoni* (figure 11*g*) are similar to those of *A. laevis*. Those of the gonodactylids investigated differ only slightly. In *O. cultrifer* and *G. graphurus* (figures 12*g*, 13*g*) the spines on the proximal endite are relatively longer, more robust and less densely arranged. Ventrally, the proximal endite bears two long, spine-like setae adjacent to the terminal tooth (one in squillids).

(iii) *Maxillae*

The maxillae of *A. laevis*, *A. fasciata* and *O. nepa* are similar (figures 8*i*, 9*h*, 10*h*). In *H. stephensoni*, the fourth maxillary segment is rectangular and more elongate and bears an additional row of fine setae along the midline (figure 11*h*).

In *O. cultrifer* and *G. graphurus* (figures 12*h*, 13*f*) the second, third and fourth segments are relatively broader and rounder than those of the squillids investigated. The setation along the lateral and median margins is also relatively sparse in comparison with that of squillids.

(iv) *First maxillipeds*

Although the first maxillipeds are principally cleaning appendages, they are frequently used during feeding to brush material towards the other maxillipeds and so will be included herein.

The first maxillipeds of the squillids examined are similar. In *A. fasciata* (figure 9*a*) and *H. stephensoni* (figure 11*a*) the subchela is relatively larger and the dactyl and propodal 'beak' relatively longer than in *A. laevis* (figure 8*a*) and *O. nepa* (figure 10*a*).

The first maxillipeds of *O. cultrifer* (figure 12*a*) differ from those of the above squillid species in the following characters: the subchelae are larger and more elongate dorsoventrally; the propodal beak is more prominent and bears a row of short, fine setae around its margin; and the dactylus is relatively shorter and broader, with a dense brush of setae on its ventral surface.

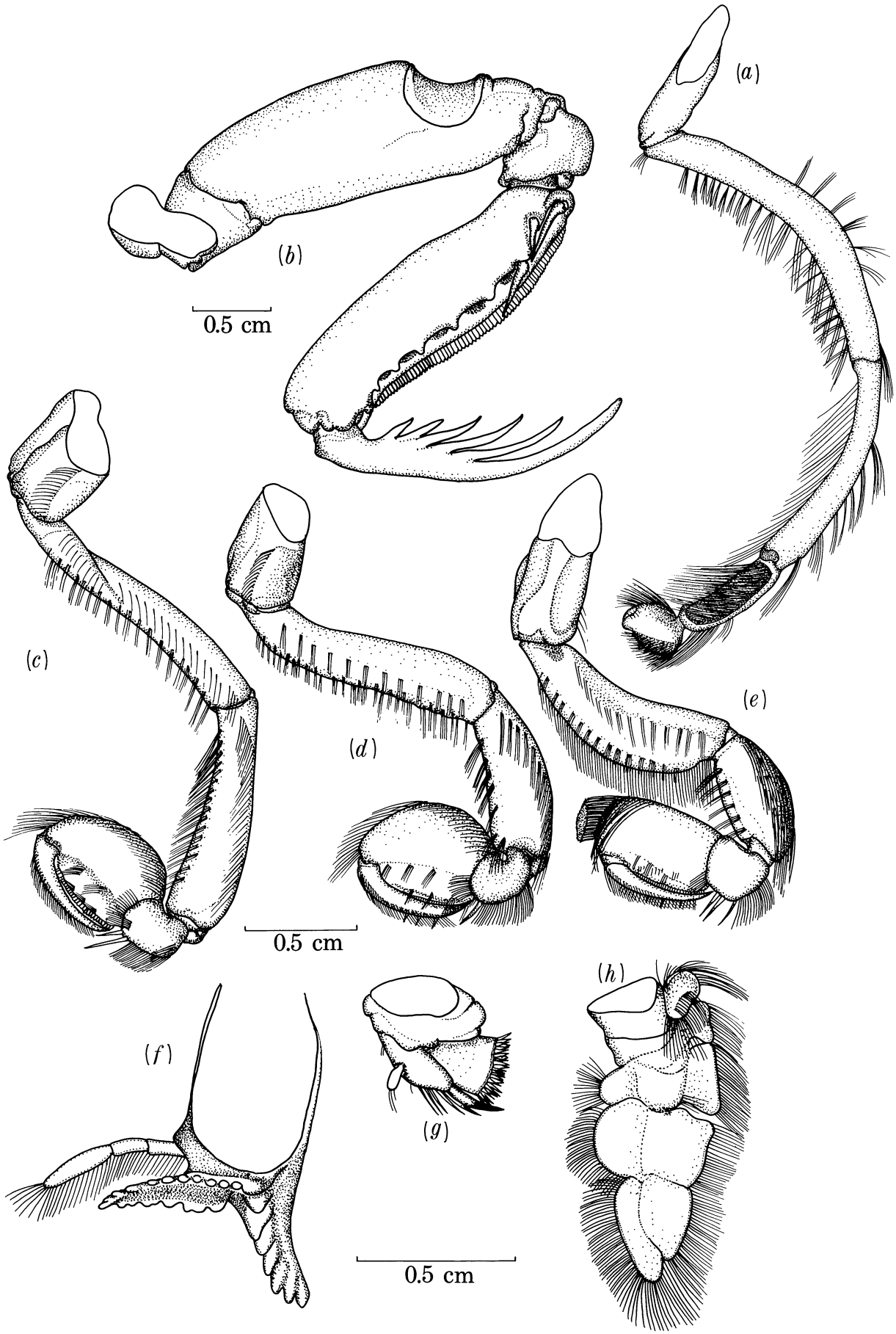


FIGURE 10. *O. nepa*: (*a*) first maxilliped; (*b*) second maxilliped; (*c*) third maxilliped; (*d*) fourth maxilliped; (*e*) fifth maxilliped; (*f*) mandible; (*g*) maxillule; (*h*) maxilla.

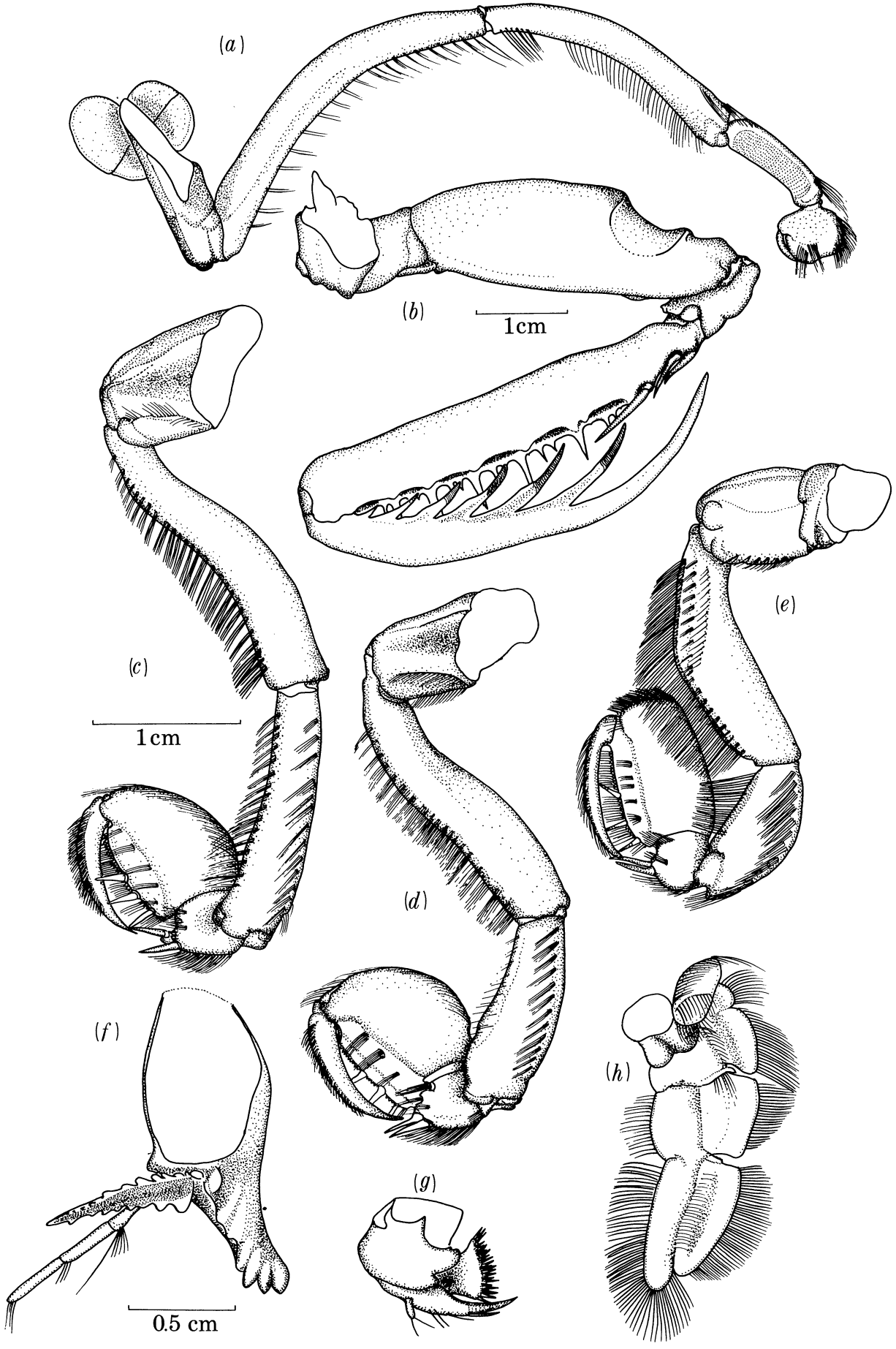


FIGURE 11. *H. stephensoni*: (*a*) first maxilliped; (*b*) second maxilliped; (*c*) third maxilliped; (*d*) fourth maxilliped; (*e*) fifth maxilliped; (*f*) mandible; (*g*) maxillule; (*h*) maxilla.

The first maxilliped of *G. graphurus* (figure 13*b*) differs from that of *O. cultrifer* in having a shorter carpus and dactylus.

(v) *Second maxillipeds*

The second maxillipeds of the other species examined differ in a number of respects from those of *A. laevis* (figure 8*b*). In *A. fasciata* the dactylus and the toothed propodal margin are narrower (figure 9*b*). The dactylar spines are spirally grooved, forming barbs similar to those described for *Squilla empusa* (Caldwell & Dingle 1976). Barbed dactylar spines are also present in *O. nepa* and *H. stephensoni* (figures 10*b*, 11*b*).

The raptorial limb of *O. nepa* (figure 10*b*) is morphologically intermediate between *A. laevis* (figure 8*b*) and *A. fasciata* (figure 9*b*).

In *H. stephensoni* the propodus and dactylus are narrow and elongate. The marginal propodal teeth are replaced by a row of long, sharp, barbed spines interspaced with paired shorter spines (figure 11*b*). The proximal ventral curvature of the dactylus is a feature of male *H. stephensoni*. The second to fifth dactylar spines are enlarged proximally, forming a ridge midway along each spine. Distal to the ridge each spine is serrated.

The raptorial limbs of gonodactylids (figures 12*b*, 13*a*) differ from those of squillids. In *O. cultrifer* the merus is enlarged, muscular and the basal articulation located subterminally on the lower medial surface (figure 12*b*). In squillids this articulation is along the anterior margin of the merus (figures 8*b*, 9*b*, 10*b*, 11*b*). The gonodactylid basi-meral articulation allows for wider lateral extension and greater lateromedial flexibility. In *O. cultrifer* the propodus is short, rounded and distally calcified (figure 12*b*). The musculature associated with dactylar protraction–retraction is reduced and the marginal teeth and spines are absent. Instead, there is a single depression along the ventral surface, into which the dactylus is folded. Ventrally, the dactylus is heavily calcified, forming a large 'elbow' used in the strike response (figure 12*b*). Distally, it is tapered with small ridges along the upper surface and the spines reduced. In *O. cultrifer* there are three tooth-like dactylar spines (figure 12*b*), absent in *G. graphurus* (figure 13*a*).

The raptorial limb of *G. graphurus* exemplifies the more specialized gonodactylid construction, amplifying certain of the characters of *O. cultrifer*. The basi-meral articulation is ventral, on the lower third of the merus and located one-third along its length, not subterminally (figure 13*a*). This shift places the merus more lateral to the body, allowing a wider lateral spread of the raptorial limbs. The upper distal concavity of the merus (absent in *G. graphurus*) is thus not required to permit retraction of the limb against the antennal peduncle. The mid-ventrolateral portion of the merus is deeply excavated to accommodate the shortened propodus. The heavily calcified propodus bears six or seven denticles along its upper distal surface (figure 13*a*). The dactylar elbow is larger and more calcified in *G. graphurus* than in *O. cultrifer*.

(vi) *Third, fourth and fifth maxillipeds*

Maxillipeds 3–5 are similar in *A. fasciata* (figure 9*c*, *d*, *e*) and *A. laevis* (figure 8*c*, *d*, *e*). Those of *O. nepa* have fewer, broader teeth along the ventral propodal margins, with spaces between the teeth for the lateral spines (figure 10*c*, *d*, *e*). In *O. nepa* the dactyli are more robust.

In *H. stephensoni* the row of propodal teeth on each maxilliped is restricted to the distal third of the lower margin (figure 11*c*, *d*, *e*). The proximal two-thirds bears three articulated spines, interspaced with paired teeth.

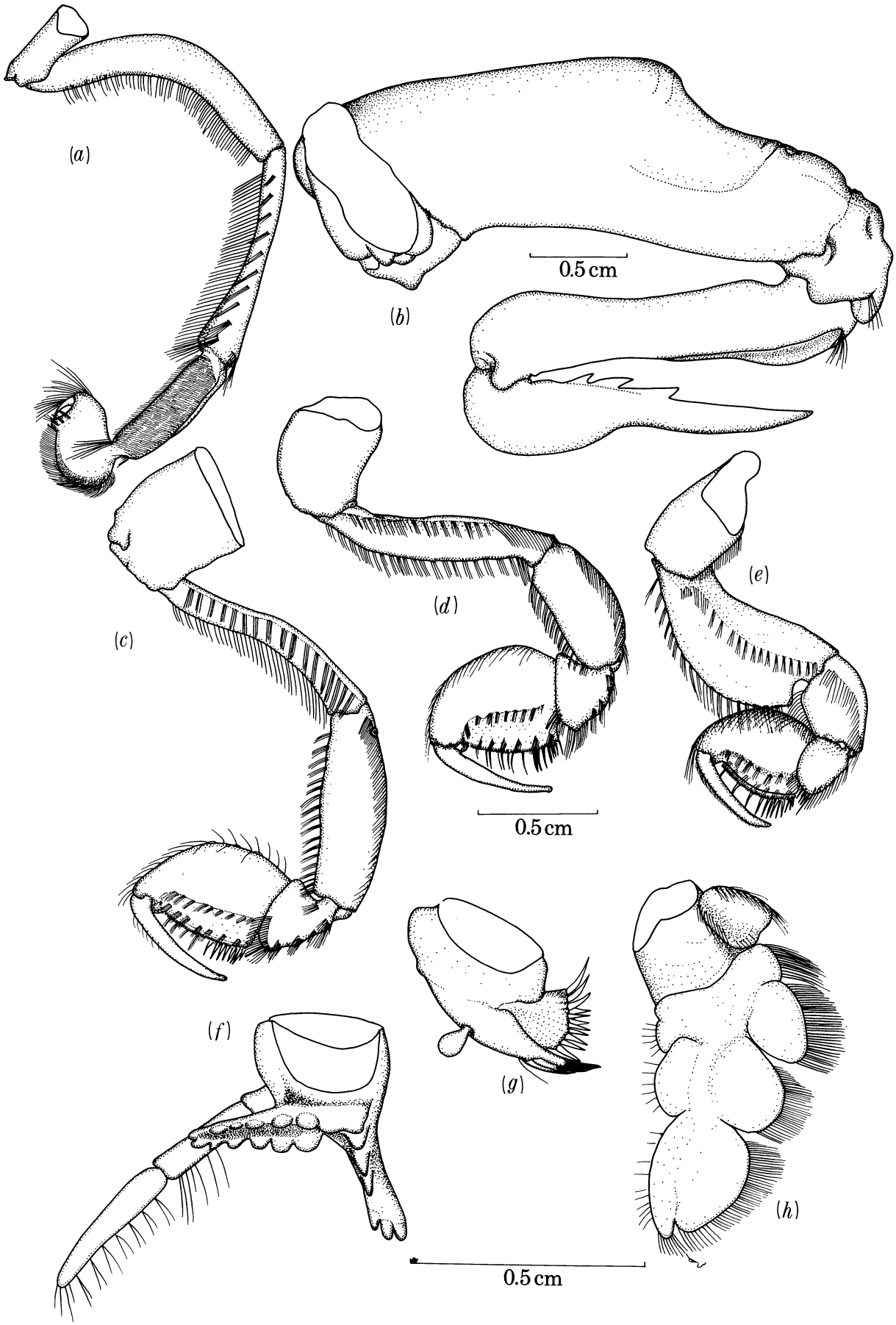


FIGURE 12. *O. cultrifer*: (*a*) first maxilliped; (*b*) second maxilliped; (*c*) third maxilliped; (*d*) fourth maxilliped; (*e*) fifth maxilliped; (*f*) mandible; (*g*) maxillule; (*h*) maxilla.

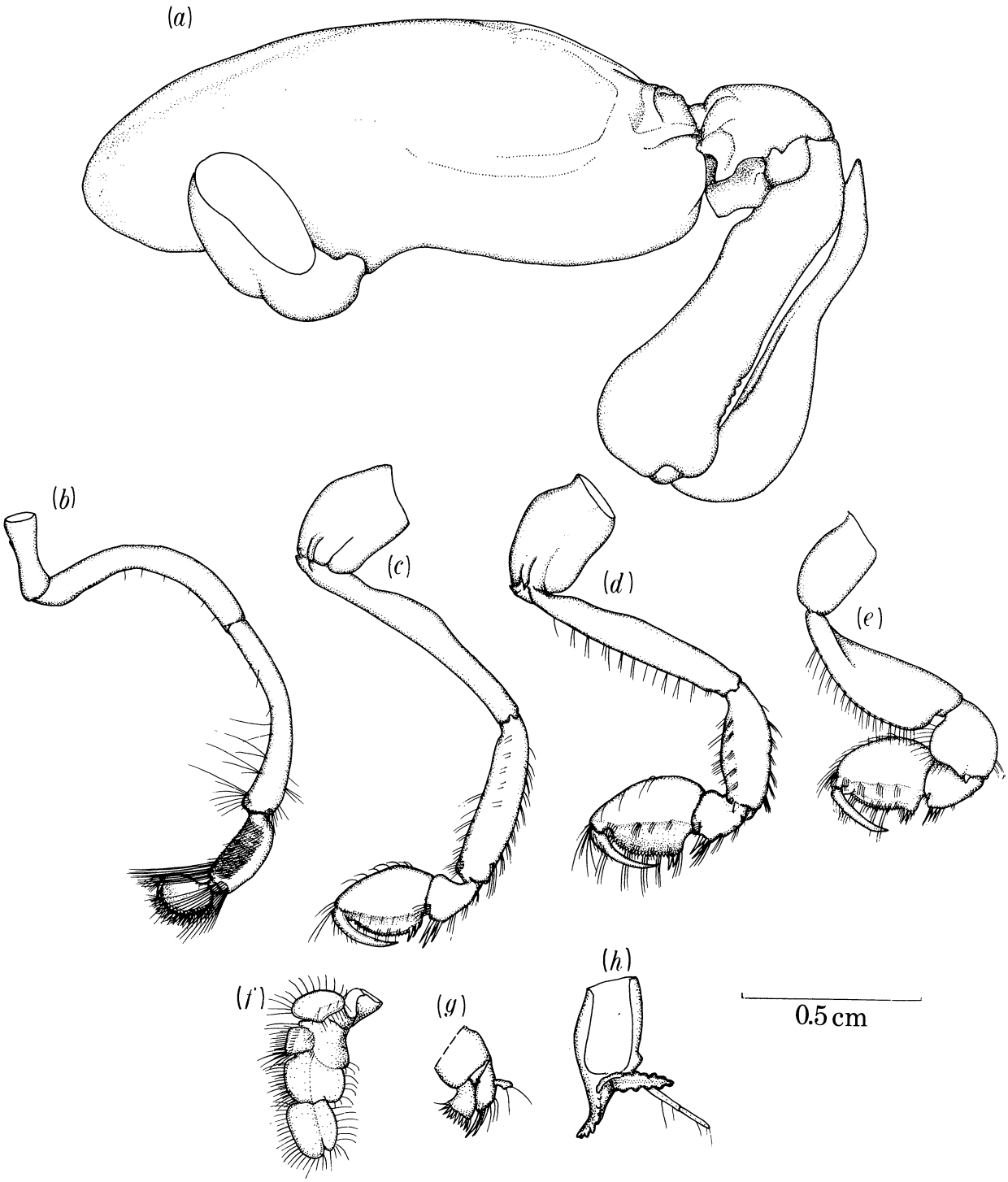


FIGURE 13. *G. graphurus*: (*a*) second maxilliped; (*b*) first maxilliped; (*c*) third maxilliped; (*d*) fourth maxilliped; (*e*) fifth maxilliped; (*f*) maxilla; (*g*) maxillule; (*h*) mandible.

In *O. cultrifer* (figure 12*c*, *d*, *e*) the lower mesial region of the propodus is flatter, the propodal teeth narrower and the lateral spines closely spaced along the proximal third of the lower margin. The propodi and dactyli are narrow and not as heavily calcified. The dactyli are relatively shorter and do not over-reach the propodus when closed. In *O. cultrifer* there is more than 75 % overlap along the lateral propodal surfaces when maxillipeds 3–5 are retracted (30–40 % in squillids). Generally, the maxillipeds are more compressed towards the mouth in the two gonodactylids. The propodus of the fifth maxilliped in *O. cultrifer* is curved and lacks the distal brush of short setae. Instead, there is a row of six to eight small, spinose setae. The carpi bear several spines and the meri are relatively shorter and broader than those of squillids (figure 12*c*, *d*, *e*).

In *G. graphurus* there are fewer ventral propodal spines, the dactyli are relatively shorter, and there is a further reduction in setation (figure 13*c*, *d*, *e*).

A summary and functional interpretation of the interspecific differences in mouthpart structure are given in §3*d*.

(*c*) *Gut contents*

Few published studies of stomatopod feeding include an analysis of gut contents. Predation on crustaceans, fish and molluscs has been reported by many workers and cannibalism is a well documented phenomenon (Schmitt 1965; Senta *et al.* 1969; Dingle & Caldwell 1969; Camp 1973). Camp (1973) analysed the foreguts of two gonodactylid and six squillid species. He identified a variety of major food items, including crustaceans, polychaetes, fishes, echinoderms and molluscs. Based on this wide range of occasional food items, Camp suggested that stomatopods probably augment normal food supplies by scavenging.

This study confirms Camp's suggestion. The gut contents of the six species investigated were qualitatively analysed for identification of major food items. Attempts to quantify the amount of each food item present proved impossible, due to the degree of maceration that had occurred and the variation in gut fullness. Where possible, at least ten individuals of each species were examined. For *H. stephensoni*, *O. cultrifer* and *G. graphurus* only a few individuals were obtained, many with their guts empty. Observational evidence of dietary preference of animals maintained in aquaria proved indicative of the diets of each species.

(1) *A. laevis*. All the 15 foreguts of this species examined contained remains of palaemonid crustaceans. Polychaete worms were present in two individuals. Scavenged items (present in three individuals) included parts of fish, small bivalve and gastropod molluscs, and detrital material which contained diatoms, sponge spicules and shell fragments.

(2) *A. fasciata*. The major prey of *A. fasciata* (present in eight of the ten individuals examined) was small cephalopods. Minor prey were unidentified decapod crustaceans. Some fish remains (scales and bones) were present in foreguts of individuals that had ingested squid. The fish probably represent prey ingested by the squid. *A. fasciata* maintained in aquaria ate prawns and squid; no preference for either was observed.

(3) *O. nepa*. The guts of eight of the ten individuals examined contained palaemonid crustaceans, and two contained squid. Some fish remains were also present. *O. nepa*, maintained in aquaria, fed on prawns and squid, showing a preference for the former.

(4) *H. stephensoni*. Only five individuals with partially full guts were obtained. Fish were the most common food item. Crustacean remains were found in two individuals, but probably represent the diet of the fish, as the sizes of the fragments of antennae and setae were not commensurate with the large size of *H. stephensoni*.

(5) *O. cultrifer.* Only three individuals were obtained that did not have empty guts. These had eaten bivalves, gastropods and some crustaceans. *O. cultrifer* maintained in aquaria showed a preference for gastropod molluscs but occasionally would also eat prawns.

(6) *G. graphurus.* All of the foreguts of the five individuals examined contained shell fragments of gastropod and bivalve molluscs, often very large pieces occupying the length of the proventriculus. Individuals maintained in aquaria fed occasionally on pieces of squid. Feeding was more successful when live molluscs, usually *Austrocochlea constricta*, were placed in the aquaria. *G. graphurus* also preyed upon brachyuran crabs (*Naxia* sp.) which were maintained in aquaria.

A summary of the major food types is given in table 1.

TABLE 1. SUMMARY OF FOOD TYPES IN THE FOREGUTS OF SQUILLID AND GONODACTYLID STOMATOPODS

species	major prey items	minor prey items
A. laevis	palaemonid crustaceans	polychaete worms
A. fasciata	cephalopod molluscs	decapod crustaceans
O. nepa	palaemonid crustaceans	cephalopod molluscs
H. stephensoni	fish	—
O. cultrifer	gastropod and bivalve molluscs	crustaceans
G. graphurus	gastropod and bivalve molluscs	crabs

(*d*) *Conclusions concerning mouthparts*

The mouthparts of *A. laevis* serve to illustrate the general morphology and arrangement of mouthparts in stomatopods. The mandibles retain well developed incisor and molar processes used in biting and in intraproventricular grinding actions respectively. The mandibular mechanism differs from those of trophically similar malacostracans, such as *Ligia*, *Astacus* and *Carcinus* (Manton 1964). Stomatopod mandibles retain a similar muscular complement to those of less advanced crustaceans such as *Chirocephalus*, anaspidaceans and mysids (Manton 1964). The differential development of promotor and remotor muscles, operating either side of a near vertical axis of mandibular swing, characterizes the stomatopod mandibular mechanism and distinguishes it from mandibular mechanisms in the 'less advanced' crustaceans. An extensive mandibular endophragm provides structural support for the enlarged muscles and replaces the transverse mandibular tendon found in *Chirocephalus*, anaspidaceans and mysids.

The maxillules are small, with strong spines and setae which aid in ingestion. The maxillae are also small and screen the pre-oral cavity.

The five pairs of maxillipeds are specialized for different functions. The small, first maxillipeds are long, flexible appendages used mainly in cleaning. The second maxillipeds are large, powerful appendages used in prey capture. The third, fourth and fifth maxillipeds are morphologically similar. Their propodi and dactyli are modified as subchelae which bear strong spines and setae used in the manipulation and collection of food. The setation of maxillipeds 3–5 forms an interlocking mesh when the limbs are retracted, holding food material within the oral field.

(i) *Trends within the* Squillidae

A. fasciata and *O. nepa* are similar in mouthpart structure, habitat and prey items. They exhibit modifications related to feeding habits slightly different from that of *A. laevis* (see §4). *A. laevis* is also a scavenger, as indicated by gut analysis and observations of animals in aquaria. *O. nepa* and *A. fasciata* will not normally scavenge unless starved. Correlated with these differences are a number of specializations of *A. fasciata* and *O. nepa*. Their mandibles have more robust grinding surfaces. The raptorial dactylus is streamlined and the dactylar spines are barbed. The spines on maxillipeds 3–5 are also more robust than those of *A. laevis*.

H. stephensoni, a much larger species, exemplifies a more extreme specialization of the squillid construction. In addition to modifications related to its large size, there are further modifications for the capture of large, moving prey and an increase in masticatory efficiency. There is horizontal occlusion of the mandibular incisor processes and an increase in the relative length of the molar processes. The propodi of the raptorial limbs have barbed spines and are relatively larger than the propodi of other squillids examined. There is a further streamlining of the dactyli and specialization of the dactylar spines. Finally, the spines on the propodi of the third and fourth maxillipeds are more robust in *H. stephensoni*.

(ii) *Comparisons between* Gonodactylidae *and* Squillidae

The mouthparts of gonodactylids contrast with those of squillids in a number of respects correlated with differences in prey and modes of prey capture (see §4). In gonodactylids, the grinding surfaces of the mandibles are more robust, the setation of the maxillules is highly sclerotized and there is a reduction in the setation of the maxillae in comparison with corresponding structures in squillids. The reduction of the dactyli of the first maxillipeds in gonodactylids may be related to the reduced role these limbs play in feeding in comparison with their role in squillid feeding. The second maxillipeds in the gonodactylids studied are specialized as smashing implements with a corresponding reduction in the dactyli and the development of a specialized basis–merus articulation. In *O. cultrifer* and *G. graphurus* maxillipeds 3–5 are less robust and are compressed towards the mouth compared with those of squillids. The fifth maxillipeds lack the characteristic propodal setation of squillids, and setation, in general, is reduced in the two gonodactylids.

(iii) *Trends within the* Gonodactylidae

Although only two species of gonodactylids were examined, observations made of other members of this family (for example, *Gonodactylus platysoma* Wood-Mason, *G. falcatus* (Forskål) and *Odontodactylus scyllarus* (L.)) but not included herein suggest that *G. graphurus* represents an extreme trend in gonodactylid specialization.

A number of features of the mouthparts of *O. cultrifer* are amplified in *G. graphurus*. There is further reduction in setation. The dactyl of the first maxillipeds is almost vestigial. The basis–merus articulation of the raptorial limb is more specialized and the upper meral concavity is reduced. These two features are related to the greater lateral displacement and increased lateromedial flexibility of the raptorial limbs in *G. graphurus*. This specialization, although associated with movements during prey capture (see §4), cannot be divorced from an additional association with behavioural responses during agonistic encounters. Meral

display is a significant component of behaviour in species of *Gonodactylus* and involves the lateral spread of the raptorial appendages (Caldwell & Dingle 1975; Dingle & Caldwell 1969).

In *G. graphurus*, the raptorial limb is relatively larger and more calcified than that of *O. cultrifer* and there are no spines on the dactyl. Also, maxillipeds 3–5 are further reduced in length as compared with those of *O. cultrifer*. The possible functional significance of these features is discussed in §4.

4. Feeding mechanisms

Feeding mechanisms in stomatopods have attracted only cursory attention. General descriptions of feeding have been given by Giesbrecht (1910), Balss (1927, 1938), Reddy (1935) and Kaestner (1970). More detailed accounts of prey capture are included in relation to neurological and neurophysiological aspects of prey capture (Schaller 1953; Burrows 1969; Kelly 1976) and to studies on feeding behaviour and agonistic interactions (Caldwell & Dingle 1975, 1976; Dingle & Caldwell 1978).

Little is known about how food is manipulated and passed into the proventriculus. Furthermore, morphological differences in the other feeding appendages, apart from the raptorial limbs, have not been described or evaluated in a functional sense. The presence of five pairs of subchelate appendages is a unique feature of the Stomatopoda. A functional interpretation of this configuration has never been attempted and no comparisons have been made with the feeding mechanisms of other malacostracan groups.

In this study, feeding mechanisms were analysed from Super 8 cine films and by observations of animals in aquaria. Pieces of food material (prawn, squid, mussel) and live prey (shrimps, snails) were introduced into the aquaria and the stomatopods were filmed from a lateral and ventral aspect while feeding. The feeding behaviour of *Harpiosquilla stephensoni* was observed during a brief visit to the University of Queensland. All other species studied were maintained in aquaria for several months. Details of movements of the mandibles, maxillules and maxillae were observed by means of a dissecting microscope. Each animal was held down on its dorsal surface and food was placed between the maxillipeds. Vital dyes were used to distinguish the passage of food material.

(*a*) *Prey capture*

The prey-capture strike of stomatopods is one of the fastest animal movements known, the time taken from rest to the moment prey is struck being 4–8 ms, at 15 °C (Burrows 1969). According to Burrows, this rapid movement is possible through a specialized arrangement of joints and tendons for muscle insertion. The muscles themselves are not specialized and can be used in both fast and slow movements. The mechanism, according to Burrows, involves a click joint between the merus and propodus that allows the extensor muscles to reach a peak tension. Relaxation of the flexor muscles releases the stored energy, causing the limb to snap open.

Burrows (1969) studied *Squilla empusa* and the gonodactylid *Hemisquilla ensigera* and found the strike mechanism to be similar in both. *H. ensigera* is intermediate in raptorial limb morphology between the squillids and gonodactylids examined in this study. In *H. ensigera*, the basis–merus articulation is terminal and the merus is grooved inferiorly throughout its length (Manning 1968). Prey capture can involve either smashing or spearing, the latter being the more common (Burrows 1969).

The method of prey capture is similar for *A. laevis*, *A. fasciata*, *O. nepa* and *H. stephensoni*. The movement involves a ventral anterior swing of the propodus of the raptorial limb around the carpus, accompanied by a ventral swing of the dactylus (figure 14*a*). The dactylus is approximately 45° ventral to the propodus at the onset of the lunge. The actual strike involves an anterior swing of the propodus until it reaches an angle of 60–120° with the body. The dactylus

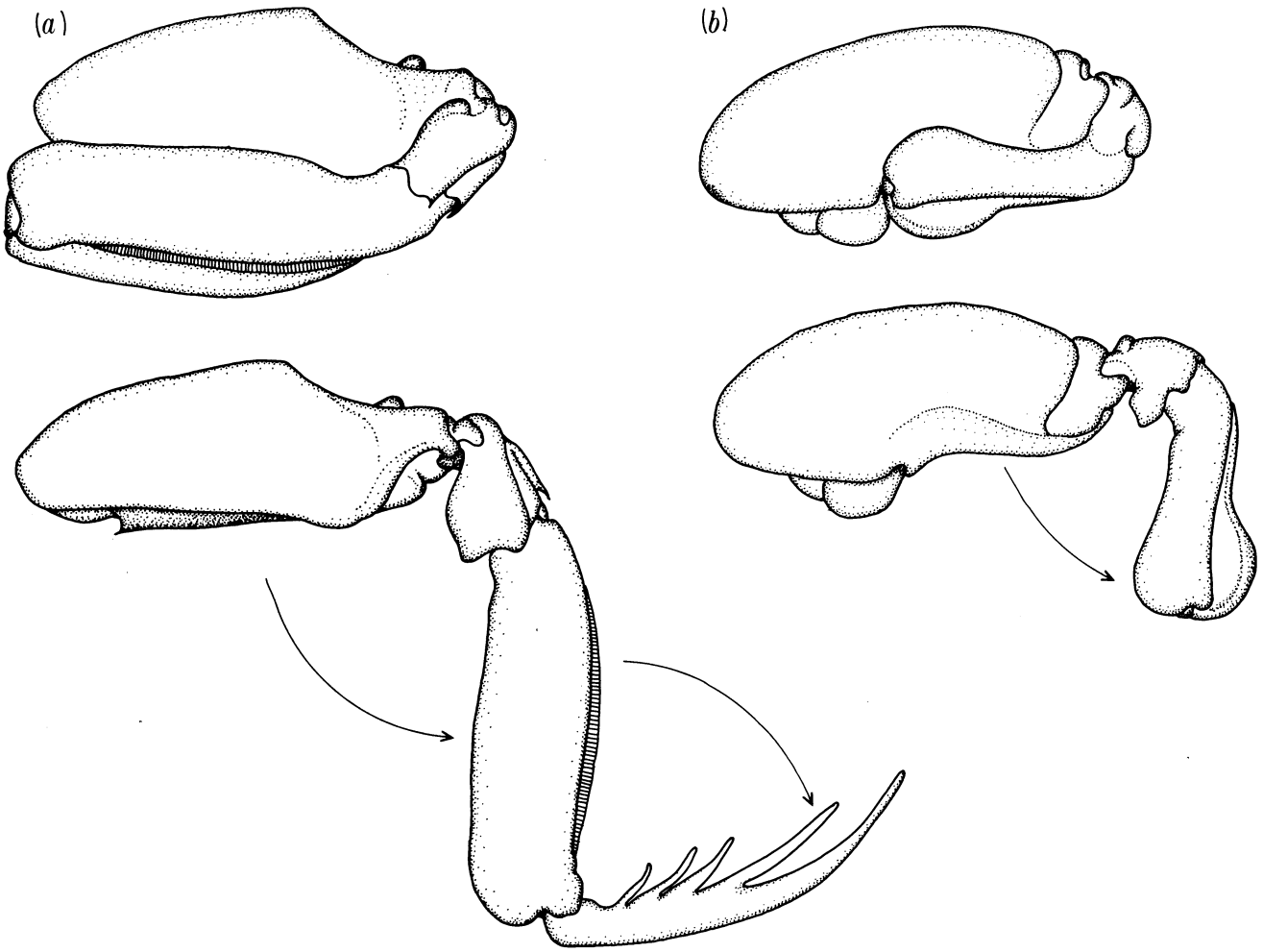


FIGURE 14. Right raptorial limbs in (*a*) *A. fasciata* and (*b*) *G. graphurus*, illustrating the differences in the prey-capture strike of squillid and gonodactylid stomatopods, respectively. Arrows indicate the direction of movement.

is further extended during the lunge and then snapped onto the ventral propodal margin. The capture strike can involve one or both raptorial limbs. In *A. laevis*, *A. fasciata* and *O. nepa*, one raptorial limb was mainly used.

Immediately following capture, prey held between the propodus and dactyl is brought back towards the other maxillipeds by a posterior swing of the propodus about the carpus. As a result, the food material is pressed against the more dorsally placed third, fourth and fifth maxillipeds.

Among the squillids examined, only *H. stephensoni* shows slight differences: prey is attacked when further away from the animal. In this respect *H. stephensoni* is similar to *Harpiosquilla harpax* (de Haan), which Dingle & Caldwell (1978) found to be more capable of catching and consuming fish than the four other species they investigated. This seems to be related to the longer raptorial appendage allowing a greater 'reach'. The presence of heavy, sharp spines on the anterior margin of the propodus in both *H. harpax* and *H. stephensoni* is also significant.

The prey-capture strike in *O. cultrifer* and *G. graphurus* does not involve dactylar extension. The propodus is swing from a horizontal position, within the groove of the merus, in an arc of 90–130°. Prey is struck with the enlarged, heavily calcified 'elbow' on the proximal ventral region of the dactyl (figure 14*b*), which serves to immobilize rather than capture prey. Prey may be struck several times, often in rapid succession. Once immobilized and/or dismembered, prey is grasped and held by the third, fourth and fifth maxillipeds, which further manipulate it before ingestion.

(*b*) *Food manipulation*

Subsequent to capture or immobilization, the food is fragmented by the third, fourth and fifth maxillipeds. The movements of the maxillipeds are rapid and uncoordinated. Food is never macerated by the maxillipeds.

Initially, prey is grasped between the medial faces of the last three pairs of maxillipeds, whose subchelae are used to pull pieces of flesh. The actions of these limbs are similar to those of the raptorial limb of squillids. The propodus is moved ventrally and the dactylus extended at an angle of 45–75° with the propodus. Food is hooked by the dactylus, which is then closed onto the propodus. The subchela is then moved dorsally and slightly laterally via an anterior swing around the coxa–basis articulation and a posterior swing around the carpus–merus articulation. The sequence of movements of the third, fourth and fifth maxillipeds is random. One or more limbs may be extended at a time on either or both sides of the animal. Food material is not usually held by the subchelae once it is transferred to the other maxillipeds. The dactyli are used as hooks. The movements of the maxillipeds position the food under the more dorsal mouthparts. The rapid movements of the maxillipeds occur in bursts of activity lasting 3–5 s interspersed with longer periods during which the food is held between the medial propodal surfaces and pressed posterodorsally against the maxillules and mandibles. The maxillae are usually held laterally. The maxillules push food between the incisor processes of the mandibles, which then adduct. The propodi of the maxillipeds are then pulled anteriorly and medially while the dactyli are firmly hooked onto the food mass. By this action the food is torn into smaller fragments, which are held by the mandibles and rapidly ingested. The manipulative movements continue (posterodorsal movements of the propodus), pushing more food between the incisor processes.

When feeding on smaller morsels, such as polychaetes or small carids, the whole animal is pushed between the mandibles by repetitive, simultaneous posterodorsal movements of the third, fourth and fifth maxillipeds and ingested in three or four fragments. Often, the entire animal is pushed into the foregut without any fragmentation.

The first maxillipeds are occasionally used to move food material from underneath the carapace towards the mouthparts, particularly when large food masses are held. The movement of the first maxillipeds is a ventral swing of the merus and carpus while the food is hooked by the minute dactylus.

In the two gonodactylids investigated, the movements of the third, fourth and fifth maxillipeds are slightly different. They are closely compressed, with 50–75% lateral overlap by adjacent maxillipeds, whereas, in the squillids examined, the maxillipeds are in a longitudinal arrangement with much less overlap. The gonodactylids use their maxillipeds to 'pick' at the flesh of immobilized prey such as molluscs and hard-shelled crustaceans. The limbs are extended beneath the raptorial limbs, which are held laterally, and food is grasped by the dactylus onto the propodus. The high degree of overlap allows all three pairs of maxillipeds to be inserted into a small gastropod shell or inside the exoskeleton of a crab. Pieces of flesh are torn away and passed towards the maxillules. Material may also be held between medial faces of the coxae, allowing more food to be collected by means of the propodus and dactylus.

The rapid manipulative and tearing movements typical of the squillids are less common in the gonodactylid feeding mechanism. The actions of the third to fifth maxillipeds are similar to those of the second maxillipeds, except that the movements are not as rapid or as powerful. The arrangement and articulations of the limb segments are similar.

(*c*) *Ingestion*

The mouthparts involved in ingestion are the mandibles and maxillules. The maxillae function mainly as a screen underneath the maxillules, preventing food from moving out of the oral region during ingestion.

While the maxillipeds push food towards the dorsal mouthparts, the maxillae are moved apart and the maxillules are moved posteroventrally. The maxillules are then brought medially around the food mass with an anterodorsal swing, pushing it between the incisor processes of the mandibles.

The arrangement and movements of the mouthparts associated with ingestion are similar in all species investigated.

(*d*) *General considerations concerning the evolution of the predatory feeding mechanism of* Stomatopoda

The belief that the original hoplocarids (Palaeostomatopoda) evolved from marine filter feeders that used their thoracopods as food strainers (Holthuis & Manning 1969; Schram 1969*a*, *b*; Caldwell & Dingle 1975) has not been critically examined in relation to feeding mechanisms of extant forms. In the light of the evidence presented herein, such a belief is without firm basis.

(i) *Palaeontological evidence*

The Hoplocarida is divided into two major groups, the Palaeostomatopoda and the Stomatopoda. The extinct Palaeostomatopoda are distinguished from the Stomatopoda by the presence of subchelate thoracic appendages of subequal size. Additional features of palaeostomatopods are the presence of a telson with a fixed median spine and styliform furca (Brooks 1969*b*).

According to Schram (1969*a*), the Hoplocarida contains a third (extinct) group, the Aeschronectida, which includes *Aratidecthes* Schram and *Kalidecthes* Schram. These were supposedly 'natant, filter-feeding types, quite distinct from the burrowing and lurking carnivorous hoplocaridans'. The aeschronectids presumably arose from the so-called Hoplostraca erected by Schram (1969*a*) to include *Sairocaris* Rolfe and *Kellibrooksia* Schram. There is, however, no indication of the form of the thoracic limbs in either of these genera.

Schram (1969*b*) derives the Palaeostomatopoda from the Aeschronectida. The latter are characterized by the possession of a carapace covering the whole thorax, with the strong development of lateral wings. The thoracic appendages were unmodified, without chelae or subchelae. The endopods of the thoracopods comprised four segments.

There is no evidence of cephalic kinesis in aeschronectids, and the abdominal gills, according to Schram (1969*b*), are different from those of Stomatopoda. The carapace covers the whole thorax, extending ventrolaterally over the limb bases.

The main feature that Schram used to link the Aeschronectida with Hoplocarida is the so-called three-segmented protopod and four-segmented endopod. Schram's (1969*b*) diagnosis of the Hoplocarida places the onus on the triflagellate first antenna and the arrangement of the segments of the thoracopods. The previous diagnosis of the Hoplocarida given by Moore (1969), based mainly on Calman (1909), seems preferable until further palaeontological studies confirm Schram's (1969*b*) tentative groupings.

The distinctive carapace morphology and lack of evidence for cephalic kinesis might equally be used to link aeschronectids, such as *Aratidecthes*, with the early caridoid malacostracans such as the Mysidacea. In *Aratidecthes* the structure of the first antenna is unknown and the protopods of the thoracopods are concealed by the overhanging carapace.

Schram (1969*b*) speculated that the shielding of the leg base in *Kalidecthes richardsoni* Schram might be correlated with a possible ventral food channel directing food orally. This speculation was based on the presence of setiferous thoracopods, with the inference that *K. richardsoni* was a nektonic detrital or filter feeder.

Detritivory or omnivory is a possible ancestral feeding mechanism for extant Hoplocarida. Filter feeding, as defined by Marshall & Orr (1960) and Manton (1977), requires specializations that are not evident in any extinct or extant hoplocarid or hoplostracan. These specializations are: the presence of a filter; a mechanism to generate a water current through the filter; a means of removing food from the filter and transferring it to the mouth; and an exit for the filtered water (Marshall & Orr 1960).

(ii) *Ontogenetic evidence*

Hoplocarids undergo a unique larval development. They hatch as antizoeae or pseudozoeae, pass through several pelagic stages, and metamorphose to a postlarva resembling the adult (Giesbrecht 1910). In all stages except the first propelagic stage, the second maxillipeds are well developed and subchelate. In the first propelagic stage the second maxillipeds have all segments well developed but the dactylus is not reflexed (Manning & Provenzano 1963; Pyne 1972). During the two propelagic larval stages no feeding occurs since the mandibles, maxillules and maxillae are not functional (Gurney 1937; Manning & Provenzano 1963; Pyne 1972). Feeding only occurs during the pelagic stages when the maxillipeds are subchelate. The feeding mechanism of the larva is similar to that of the adult. Food is grasped by the raptorial limbs and transferred to the other maxillipeds (Pyne 1972).

There are no morphological or behavioural features of any larval stage that indicate a feeding mechanism different from that of the adult. In no larval stage are the mouthparts morphologically adapted to filter feeding.

(iii) *Morphological evidence*

According to Manton (1977), raptatory feeding on large and/or hard food is often the end result of an evolutionary trend stemming from a simple raptatory habit. She further states that

'this habit has given place many times to filter feeding, an activity dependent on a higher order of limb differentiation and coordination between successive limbs than possessed by simple raptatory feeders'. Filter feeding cannot be regarded as an ancestral feeding mechanism, but must have arisen in parallel, during the evolution of filter-feeding taxa. It is probable, according to Manton (1977), that ancestral Malacostraca were bottom-living in habit and may have been detritus feeders or scavengers. The absence in adult and larval hoplocarids of any structures similar to those present in malacostracan filter feeders reinforces the idea that stomatopods descended from a simple raptatory ancestor. Features of the mouthparts and feeding mechanisms support this.

The mandibles of malacostracans with predaceous feeding habits usually bear strong distal cusps, with few or no grinding surfaces, good articulations with the head and powerful musculature. Stomatopod mandibles have well developed incisor and molar processes, which are also present in other, so-called, less advanced Malacostraca. Usually, a large, extensive molar process indicates a filter-feeding habit, in contrast to the reduction of that area which occurs in raptatory members of the same group. Rather than the large molar process bearing molar ridges, as in the filter-feeding *Hemimysis* and *Paranaspides* (Manton 1977), the stomatopod molar processes bear well developed cusps used in grinding ingested food inside the proventriculus (see § 6). The incisor processes are similar to those of other large-food-feeding Malacostraca in that they have strong distal cusps. The mandibles of early pelagic larval stomatopods are heavily serrated and lack the well developed molar processes of the adults (Manning & Provenzano 1963; Pyne 1972; Morgan & Provenzano 1979). The maxillules and maxillae of larval and adult stomatopods are small and lack the filter plates typical of *Nebalia*, *Euphausia*, mysids and *Paranaspides* (Cannon 1927; Mauchline 1967; Manton 1977). In stomatopods, the maxillules bear robust proximal and distal endites, used to push food between the mandibles. The maxillae comprise lobed endites bordered with simple setae. The median setose margins of the endites align along the ventral midline, preventing the escape of food material held between the mandibles and maxillules. Their role is passive during feeding; they do not function in food manipulation. The maxillae play an active role in regurgitation of indigestible fragments from the proventriculus (see § 6). During regurgitation, a ventrally directed current of water is produced by the lateromedial closure of the maxillae. It is difficult to envisage such a feeding strategy stemming from a filter-feeding form.

The maxillipeds of both adult and larval stomatopods are subchelate. The setation of the endopods forms a ventral screen to prevent the escape of food material from the more dorsal mouthparts. If one assumes that the ancestral hoplocarid did resemble Schram's aeschronectid, that is, lacked subchelae, there is still no evidence of endites or exopods analogous to those present in other filter-feeding Malacostraca.

Furthermore, there is no morphological or functional evidence that the stomatopod feeding mechanism could be derived from a filtratory mechanism without radical and probably non-functional intermediate changes in limb structure. A direct evolution from a leptostracan form is not supported by available evidence.

It is probable that the early phyllocarid radiation included both raptatory and filter-feeding forms. Present palaeontological evidence provides no information on the structure of the feeding appendages of ancestral hoplocarids. The morphological and ontogenetic evidence suggests that the hoplocarid ancestor was probably raptatory.

5. The anatomy of the proventriculus of *Alima laevis* (Hess)

In the Decapoda, raptorial feeding with little or no external treatment of food has been linked with the presence of an internal masticatory apparatus, or gastric mill (Patwardhan 1936; Reddy 1935), although Fryer (1977) has shown that in atyid carids this relationship does not exist. Reddy attempted to extrapolate the trend in gastric specialization in Decapoda to the Stomatopoda, concluding that the decapod gastric form could be derived directly from that of stomatopods. Siewing (1956) also attempted to derive the eucaridan and peracaridan gastric apparatuses from that of the Stomatopoda, with the inclusion of the syncaridan proventriculus as an intermediate form.

Stomatopods have a unique gastric structure and mechanism that is functionally linked with the specialized mandibular mechanism.

(*a*) *General anatomy*

The proventriculus of stomatopods occupies almost the entire cephalic region from the rostrum to the mandibles (figure 15). It is divided into an anterior cardiac stomach and a posterior pyloric stomach. At the junction of the cardiac and pyloric regions is a narrow channel through which all macerated food passes.

The cardiac stomach extends anteriorly from the oral opening as a cuticular sac (figure 16). Ventrally, the proventriculus extends from the anterodorsal folding of the labrum. There is no fusion of the anterior part of the foregut to the surrounding exoskeleton. The gastric cuticle is fused posteriorly to the mandibular pleurite. The dorsolateral extremity of this fusion is the posterior ventral tubercle of the mandibular endophragm (p v t, figure 2). The gastric cuticle then extends posteriorly, over the dorsal surface of the mandibular molar process, and ventrally, alongside the posterior surface of the incisor process to fuse with the paragnaths (figure 2). Dorsally, the cardiac stomach follows the contours of the carapace to the cervical groove, where it curves medially, beneath the dorsal process of the mandibular endophragm (d pr, figures 2, 15). The dorsal posterior section of the cardiac stomach is folded anteriorly such that the fold (herein termed the posterior dorsal cardiac fold, p d c f, figure 15) is appressed to the upper surface of the posterior cardiac plate. The posterior cardiac plate is an anteriorly convex plate (figures 15, 16, p c p) formed by a system of ossicles. Functionally, it represents a system of sieves and channels through which the movement of fluids and suspended solids occurs.

The narrow pyloric region of the proventriculus comprises the ampullae and the narrow flattened dorsal pyloris (figures 15, 17). Anteriorly, the pyloric stomach connects with a small chamber formed at the end of the posterior cardiac plate (the cardiopyloric channel). Posteriorly, the pyloric stomach connects with the post-ampullary chamber, from which the midgut and digestive glands arise.

(*b*) *The ossicles of the proventriculus*

Unlike the cardiac stomachs of other malacostracans that ingest large pieces of food, the cardiac stomach of stomatopods is virtually devoid of ossicles or setae. Apart from the posterior cardiac plate there are two pairs of ossicles, the anteroventral cardiac ossicles (a v c) and the posterolateral cardiac ossicles (p c) (figure 16).

The anteroventral cardiac ossicles are long and slender and lie along the anterior lateral

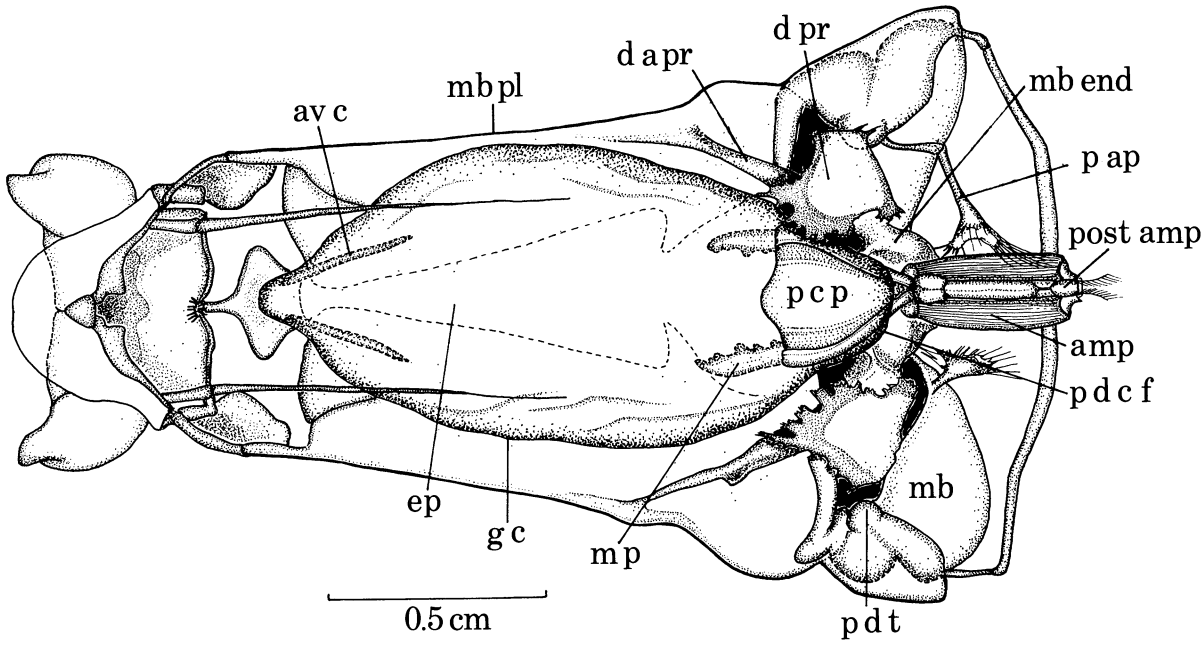


FIGURE 15. *A. laevis*: dorsal view of the proventriculus and surrounding skeleton after removal of the carapace.

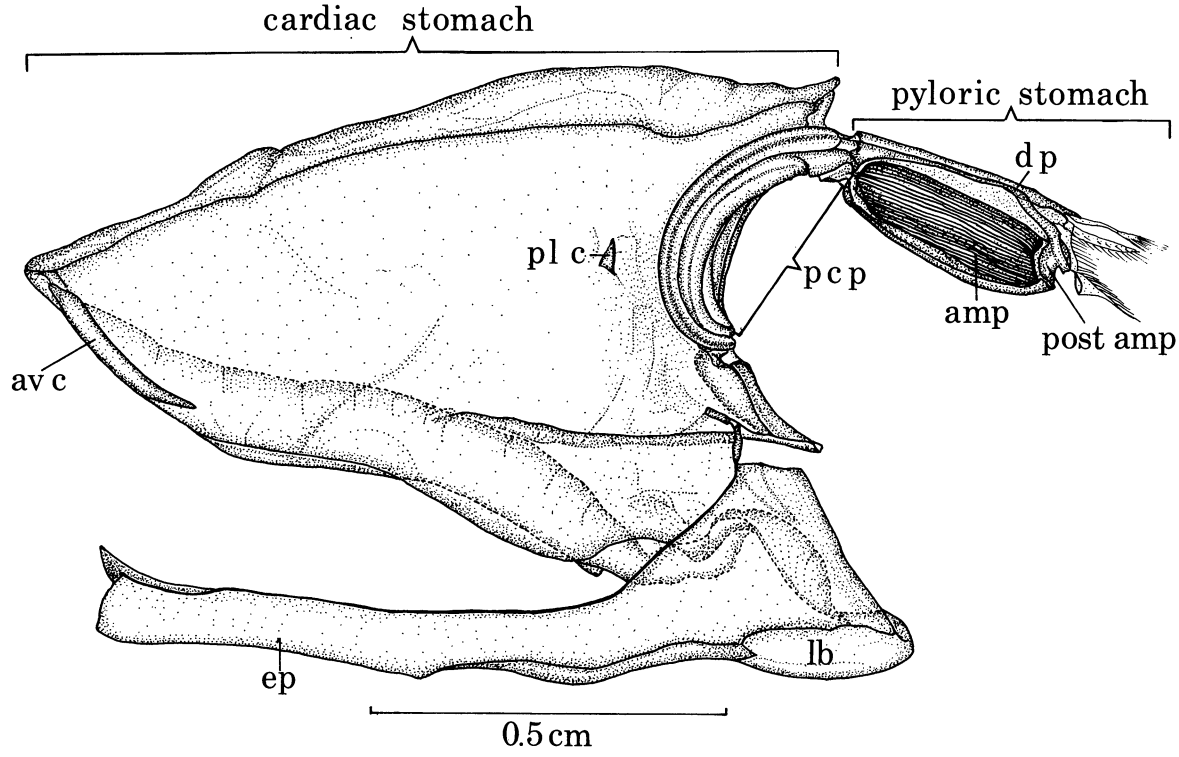


FIGURE 16. *A. laevis*: lateral view of the proventriculus after removal of the musculature and cephalothoracic skeleton.

margins of the ventral cardiac stomach (figure 16, a v c). They curve anterodorsally, terminating at the anterior extremity of the cardiac stomach. They support the anterior end and provide areas for muscle attachment.

The posterolateral cardiac ossicles are small, triangular structures lying on the posterior midlateral wall of the cardiac stomach, anterior to the posterior cardiac plate (figure 16, pl c). The apex of the triangle projects towards the lumen and supports a row of small, tooth-like cuticular processes along its posterior margin (see §5*d*).

Seven further ossicles comprise the posterior cardiac plate (figure 17): the unpaired median

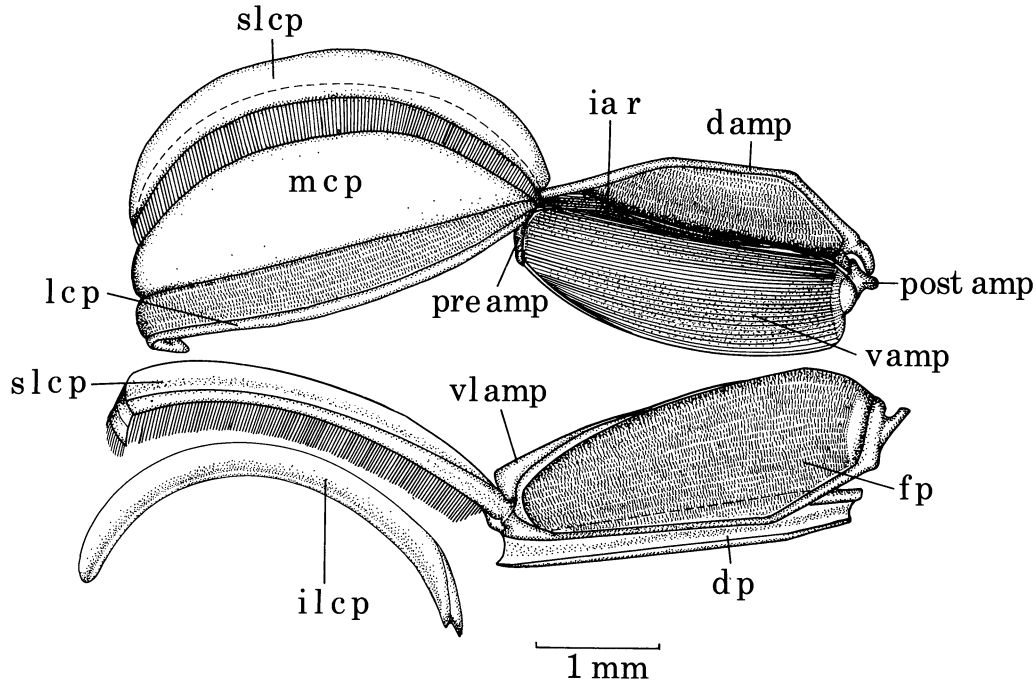


FIGURE 17. *A. laevis*: dorsal view of the posterior cardiac plate and ampullae. The ossicles of the left side have been separated to expose the ventral ossicles.

cardiac plate ossicle; the paired lateral cardiac plate ossicles; the paired inferior lateral cardiac plate ossicles; and the paired superior lateral cardiac plate ossicles.

The median cardiac plate ossicle forms the central, oval, convex dome of the posterior cardiac plate (m c p, figure 17). It is lightly calcified, flexible and has a textured surface (figure 19, plate 1). Laterally, the cuticle is slightly raised, less calcified and covered with a mat of fine velvety setae, which is appressed to an overlying row of setae born on the medial margin of each superior lateral cardiac plate ossicle (figures 19, 20, plate 1). Lateral to the mat of setae, the median cardiac plate ossicle fuses on each side with the lateral cardiac plate ossicle.

The lateral cardiac plate ossicles form the supportive framework of the median cardiac plate ossicle, following the anterior curvature of the latter (l c p, figure 17). Posteriorly, each bifurcates and the dorsal arms converge and fuse. The ventral arm of each expands to form a flange that fuses to the lateral margins of the anterior ventral pyloric ossicle (a v p, figure 18*b*, *c*). Along the posterior ventral margin, the fused lateral cardiac plate ossicles curve anteriorly to articulate with the posterior margin of the anterior ventral pyloric ossicle.

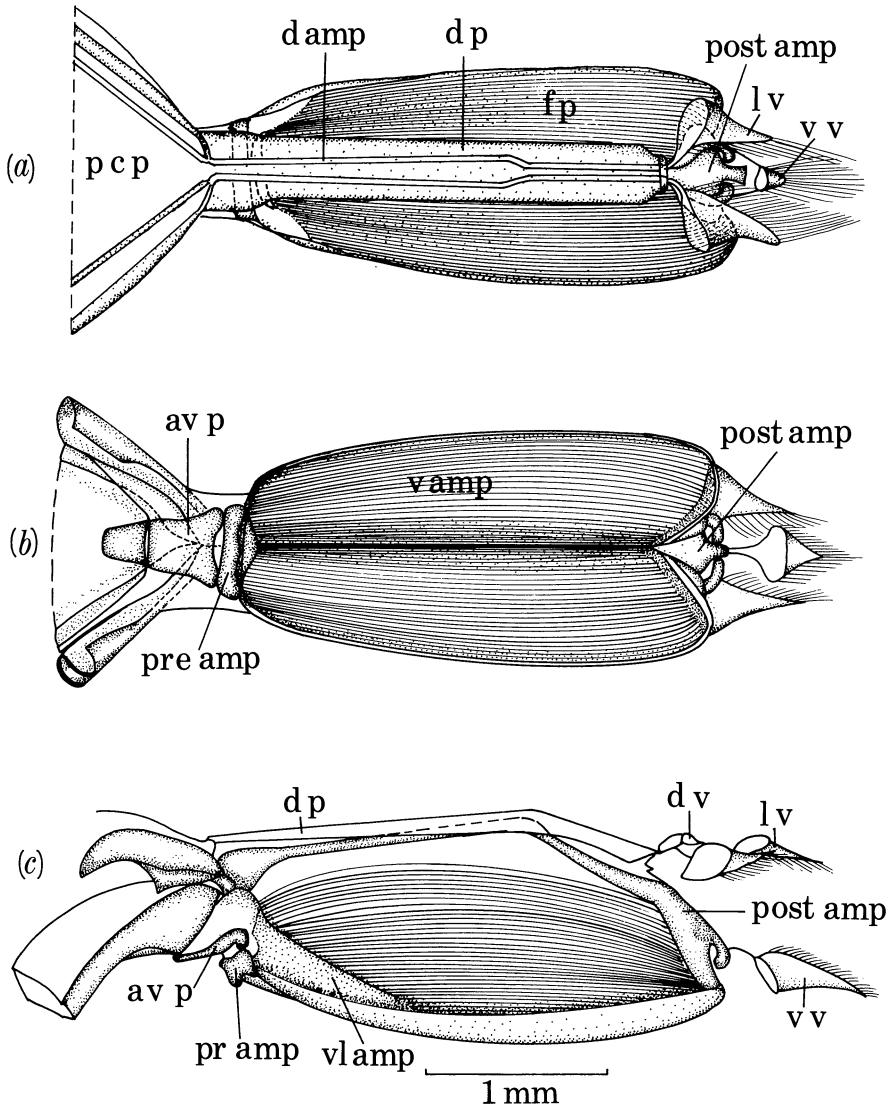


FIGURE 18. *A. laevis*. Ossicles of the ampullae: (*a*) dorsal view; (*b*) ventral view; (*c*) lateral view.

The inferior lateral cardiac plate ossicles are long curved rods that overlap the lateral cardiac plate ossicles. The ventral margin is recurved dorsally and connects with the ventrolateral margin of the lateral cardiac plate ossicle by a thin layer of cuticle (figure 17). The dorsomedial margin of the inferior lateral cardiac plate ossicle (i l c p, figure 17) connects with a fold of cuticle extending from the medioventral margin of the superior lateral cardiac plate ossicle (s l c p). Posteriorly, each inferior lateral cardiac plate ossicle tapers to a fine rod that articulates with the anterior tip of the lower margin of the ventrolateral ampullary ossicle.

The superior lateral cardiac plate ossicles are similar in shape and size to the inferior lateral cardiac plate ossicles. Each overlaps the collateral inferior cardiac plate ossicle to which it

is connected medioventrally (s l c p, figure 17). Posteriorly, each ossicle tapers to articulate with the anterior tip of the narrow dorsal ampullary ossicles. Along the medial margin of each superior lateral cardiac plate ossicle is a row of long setae that overlies the velvety setae of the lateral margins of the median cardiac plate ossicle (figures 19, 20, plate 1). Another row of short, strong setae overlies the long setae (figure 20, plate 1). A narrow channel is formed between the cuticular fold connecting the inferior and superior lateral cardiac plate ossicles and the cuticular connection of the inferior lateral cardiac plate ossicle with the median cardiac plate ossicle. This channel forms the major route of communication between the posterior cardiac plate and the ampullae.

There are 12 pyloric ossicles, namely: the unpaired anterior ventral pyloric ossicle; the unpaired preampullary ossicle; the unpaired dorsal pyloric ossicle; the paired dorsal ampullary ossicles; the paired filter presses; the paired ventrolateral ampullary ossicles; the paired ventral ampullary ossicles; and the unpaired posterior ampullary ossicle.

The anterior ventral pyloric ossicle is a small rectangular ossicle that extends along the posterior surface of the posterior cardiac plate (a v p, figure 18*b*, *c*). It is fused anteriorly to the ventral arms of the lateral cardiac plate ossicles. The anterior ventral pyloric ossicle articulates along its posterior margin with the preampullary ossicle. It forms the floor of the cardiopyloric channel connecting the lateral channels of the posterior cardiac plate with the ampullae.

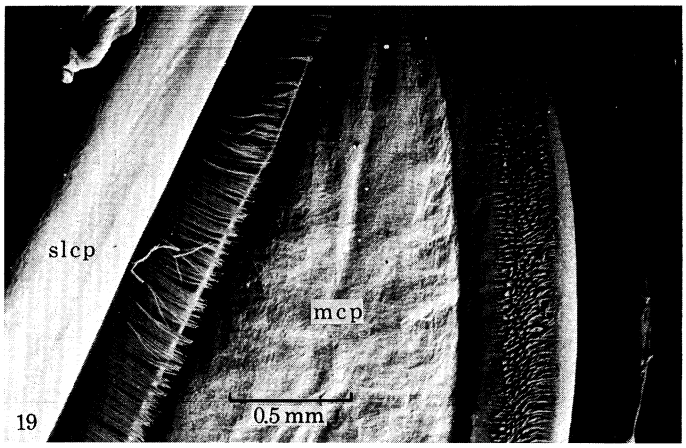
The preampullary ossicle (pr amp, figure 18*b*, *c*) is a small rectangular bar at the anterior ventral end of the ampullae. It extends from its dorsal articulation with the anterior ventral pyloric ossicles to a ventral fusion with the ventral ampullary ossicles. The preampullary and anterior ventral pyloric ossicles have muscle attachments that are involved in the pumping action of the posterior cardiac plate and ampullae.

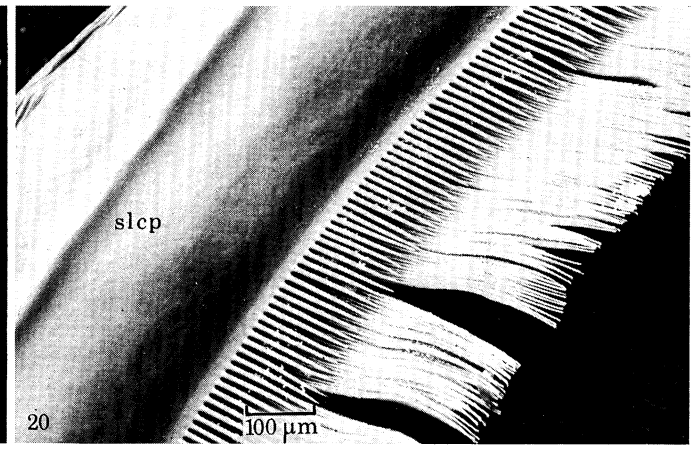
The dorsal pyloric ossicle (d p, figures 17, 18*a*, *c*) is a long, rectangular ossicle overlying the ampullae. It is not heavily calcified and forms a channel from the posterior margin of the posterior cardiac plate to the postampullary chamber. Anteriorly, it connects with the gastric cuticle of the cardiac stomach underlying the posterior dorsal cardiac fold. Its lateral margins curve around the dorsal ampullary ossicles, to which they are connected by a band of cuticle.

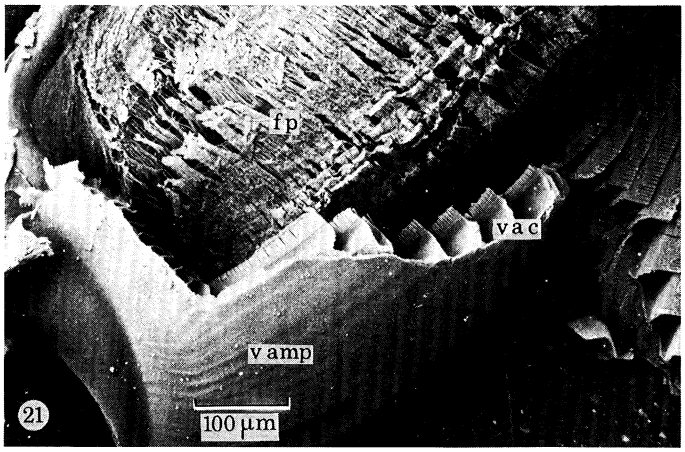
The dorsal ampullary ossicles are long, narrow rods which, together with the ventral ampullary ossicles, form the supporting framework for the filter press (d amp, figures 17, 18*a*). Anteriorly, they articulate with the superior lateral cardiac plate ossicle and fuse with the ventrolateral ampullary ossicles on the ventral anterior tip. The two dorsal ampullary ossicles are closely adpressed along their medial margins, thus separating the dorsal pyloric channel from the upper ampullary chamber. Posteriorly, each bifurcates into a large dorsoventral arm and a small lateromedial arm. The dorsoventral arm fits into a depression at the posterior end of the ventral ampullary ossicle and is also connected to that ossicle laterally. The lateromedial arm fuses with the posterior ampullary ossicle.

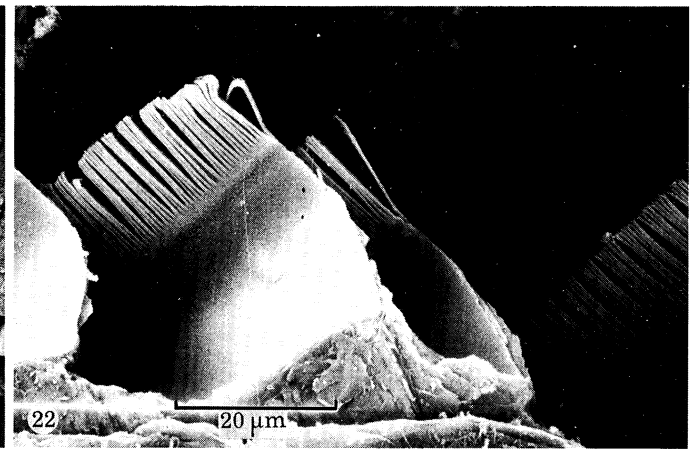
The filter presses (f p, figures 17, 18) are ovoid convex structures, each supported by the dorsal ampullary ossicle along its upper surface and by the ventrolateral ampullary ossicle on its lower surface. The inner curved surface is covered with a mat of fine setae of characteristic structure (figure 21, plate 1), which are appressed to the setae of the ventral ampullary ossicle. The posterior ventral margin connects with the ventral ampullary ossicle by a narrow band of cuticle.

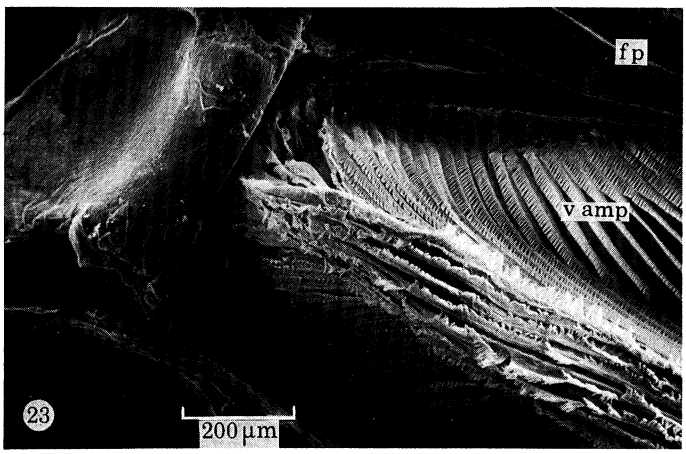
The ventrolateral ampullary ossicles are short rod-like ossicles fused anteriorly to the dorsal

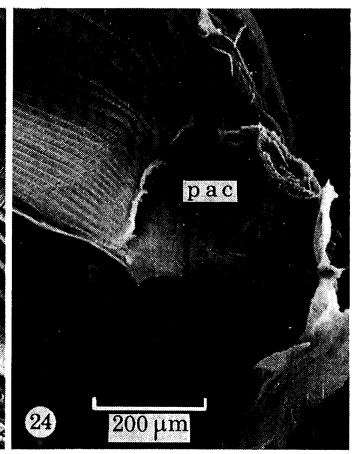












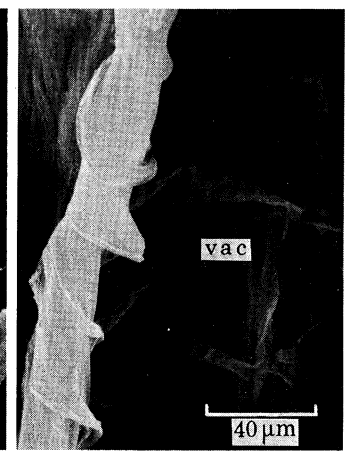


FIGURE 19. Scanning electron micrograph (s.e.m.) of the anterior surface of the posterior cardiac plate of *H. stephensoni* showing: the surface texture of the median cardiac plate ossicle (m c p), the mat of setae underlying the superior lateral cardiac plate ossicle (s l c p), and the setae of the superior lateral cardiac plate ossicle (left).

FIGURE 20. *O. nepa*: s.e.m. of the two setal layers extending from the superior lateral cardiac plate ossicle (s l c p) and overlying the lateral channels of the posterior cardiac plate.

FIGURE 21. *A. laevis*: lateral view of the posterior half of the ampullae, with part of the ventral ampullary ossicle (v amp) removed to expose the filter press (f p) and ventral ampullary channels (v a c).

FIGURE 22. The ventral ampullary channels of *A. laevis* under high magnification, showing the setae overlying the channels formed between the horizontal ridges of the ventral ampullary ossicle.

FIGURE 23. *G. graphurus*: dorsal view of the anterior region of the ampullae with the filter presses (f p) splayed to expose the channels of the ventral ampullary ossicle (v amp).

FIGURE 24. *G. graphurus*: dorsal view of the posterior region of the ampullae, showing the entrances to the ventral ampullary channels (v a c) from the post-ampullary chamber (pa c).

(*Facing p.* 294)

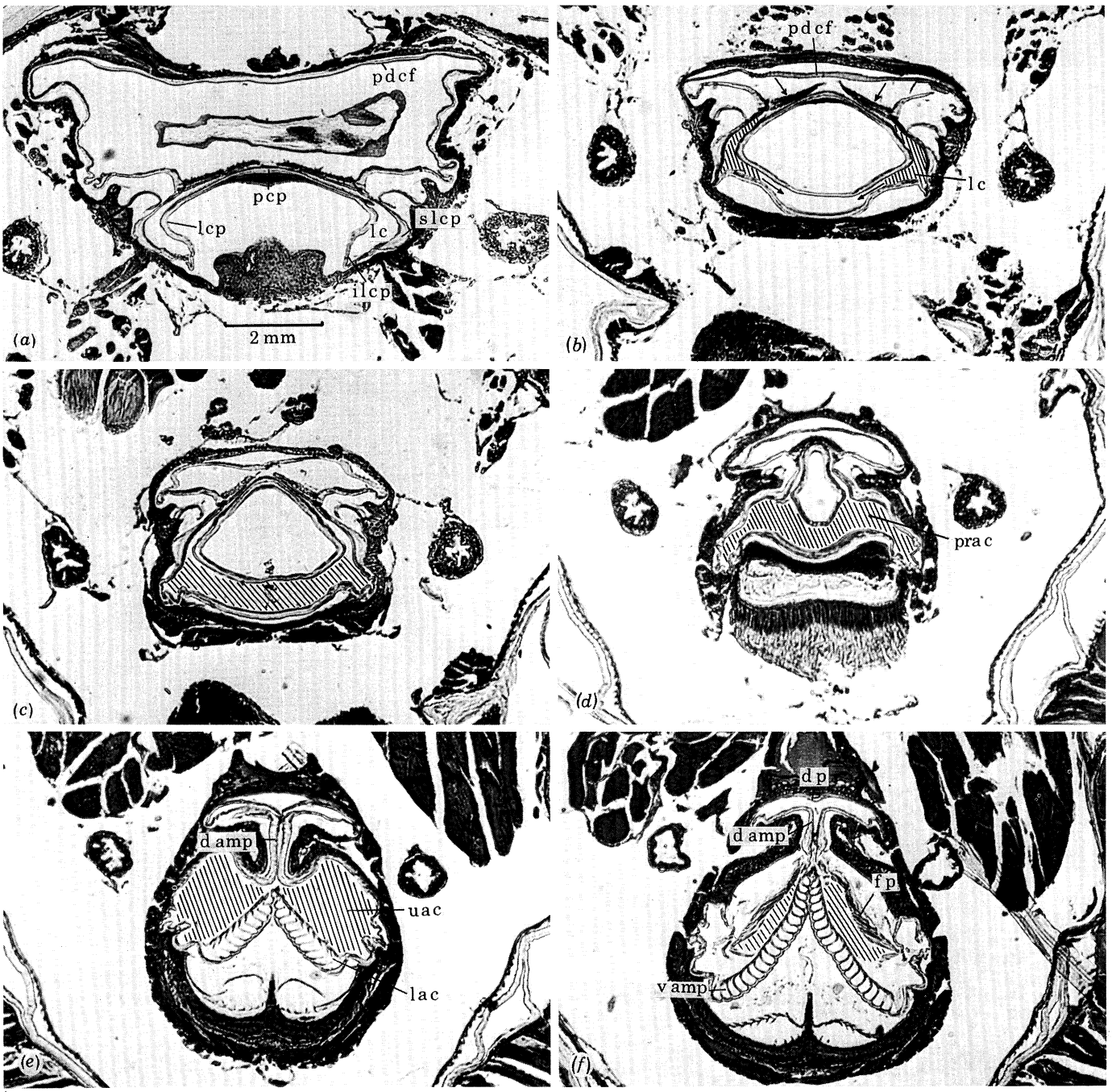


FIGURE 28. Transverse sections of the posterior cardiac plate and ampullae, showing the passage of macerated food material from the lateral channels of the posterior cardiac plate into the ampullae (macerated food is represented by cross hatching).

ampullary ossicles (vl amp, figures 17, 18*c*). The anterior flange of each abuts against the lateral margin of the preampullary ossicle and is connected to the anterior half of the lower margin of the filter press.

The ventral ampullary ossicles are the largest ampullary ossicles and constitute the filtratory mechanism of the ampullae (v amp, figures 17, 18*b*). Each is deeply concave and bears numerous longitudinal ridges from which the filtratory setae arise (figures 21, 22, plate 1). These two ossicles curve dorsally to fuse along the midline, forming the interampullary ridge (figure 23, plate 1), which curves anteroventrally to the preampullary ossicles, to which both ventral ampullary ossicles are fused. Posteriorly, the interampullary ridge terminates abruptly at the fusion with the posterior ampullary ossicle (figure 24, plate 1). The longitudinal ridges terminate, leaving a shallow transverse bar which receives the dorsoventral process of the dorsal ampullary ossicle.

The posterior ampullary ossicle is a small triangular ossicle fused along its anterior margin with the median posterior section of the fused ventral ampullary ossicles. Midway along the two sides of the posterior ampullary ossicle (post amp, figures 17, 18), it is fused to the latero-medial arms of the dorsal ampullary ossicles such that a channel is formed between the bifurcation of the dorsal ampullary ossicle, the interampullary ridge and the long axis of the posterior ampullary ossicle. The paired channels connect with the single postampullary chamber. The latter is endodermal in origin, thus marking the beginning of the midgut.

6. The function of the proventriculus

(*a*) *The movement of food into the proventriculus*

As soon as food material is pushed into the proventriculus by the actions of the maxillules, mandibular incisor processes and labrum, the molar processes of the mandibles are brought together and the food is held between them. Simultaneously, the lateral cardiac folds are brought medially by the combined contraction of the lateral cardiac floor muscles (l c fl m, figures 25, 26) and the lateral cardiac longitudinal muscles (l c l m, figure 25). The labrum is also moved posteriorly by the elasticity of the ventral gastric cuticle. This ingestive process is then repeated; the mandibles are moved laterally and the maxillules push food over the labrum, which then moves anterodorsally. During successive movements the food is pushed anteriorly inside the proventriculus until it is full.

Experiments aimed at detecting textural selectivity of food material showed that *A. laevis* does not show any preference for soft, fleshy food over exoskeletal elements. Animals (60–100 mm, total length) were offered a variety of foods such as prawn flesh, exoskeleton and squid (pieces varied from 1–5 mm). In all cases they ingested exoskeletal and fleshy material, with differences arising only in the degree of preingestive treatment of food. Gut contents and observations of animals in aquaria confirm this result. No external maceration of food occurred during feeding in any of the species investigated.

(*b*) *Mastication in the cardiac stomach*

The function of the cardiac stomach is to reduce large fragments of food to a fine suspension of particles which is transferred to the pyloric stomach through the setose screens of the posterior cardiac plate. Three processes are involved, grinding and cutting by the mandibular molar

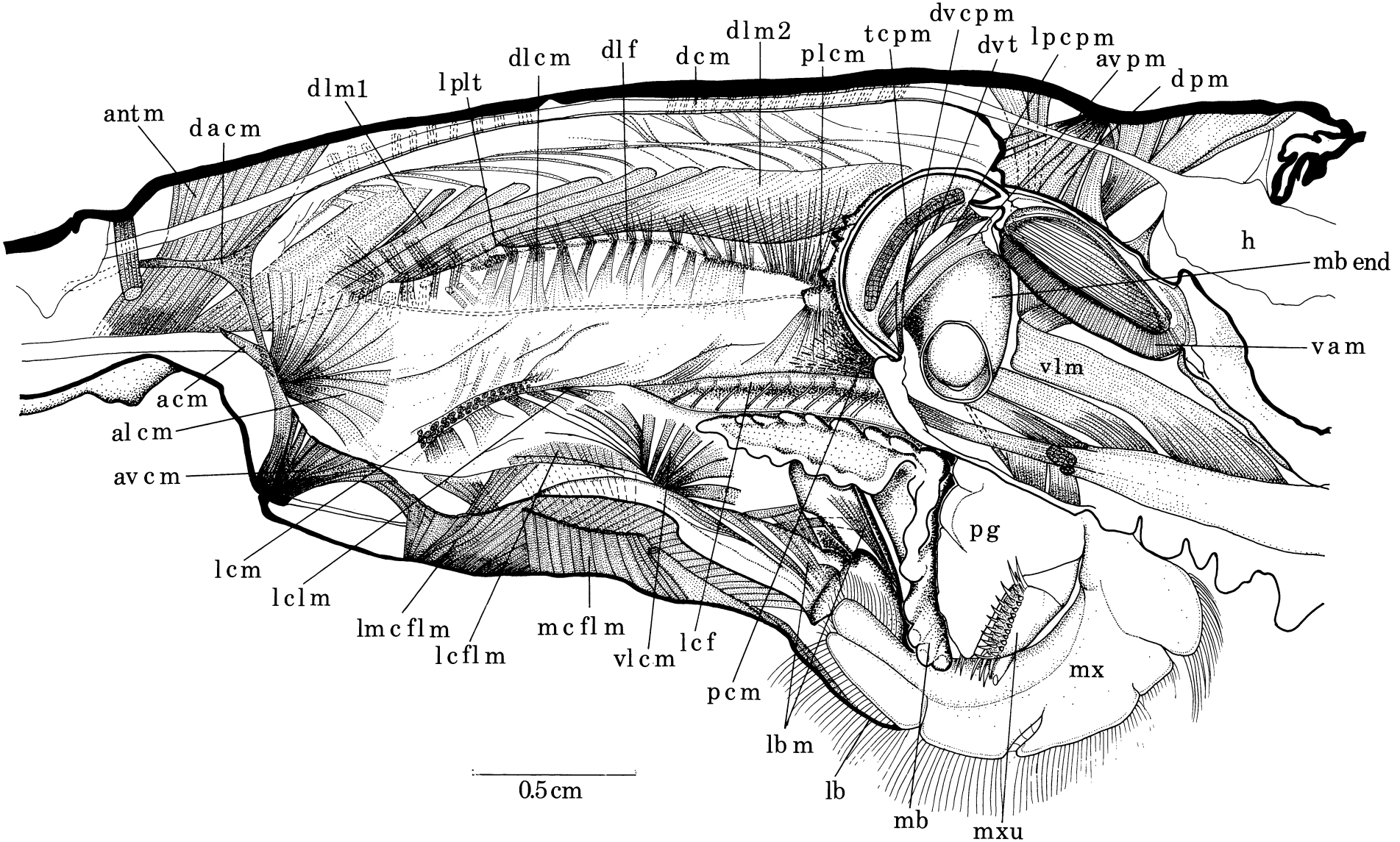


FIGURE 25. *A. laevis*: internal view of the musculature of the proventriculus exposed by median sagittal section.

processes, muscular contractions of the cardiac stomach, and the action of digestive juices poured into the cardiac stomach from the digestive gland. The last process is described in §6*e*.

Accompanying mandibular occlusion and separation, there are sequences of muscular contractions in three regions of the cardiac stomach: the posterior half of the lateral wall; the dorsal anterior gastric wall; and the median floor of the cardiac stomach, anterior and dorsal

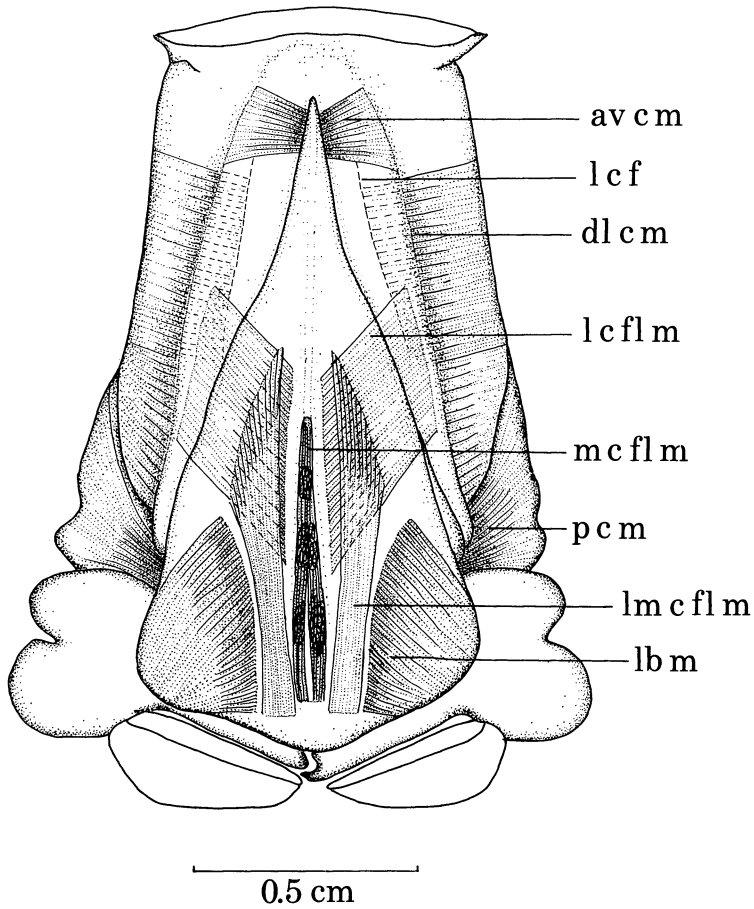


FIGURE 26. *A. laevis*: ventral view of the musculature of the proventriculus.

to the line of fusion of the labrum with the epistome. The muscles associated with medial movements of the posterior lateral wall are the lateral cardiac longitudinal muscles (l c l m), the posterior cardiac muscles (p c m) and the ventrolateral cardiac muscles (vl c m, figures 25, 26). The antagonists to these muscles are the posterior lateral cardiac muscles (p l c m) and the dorsolateral cardiac muscles (dl c m, figures 25, 26). The muscles associated with medial movements of the dorsal anterior gastric wall are the dorsolateral cardiac muscles (dl c m) and the anterolateral cardiac muscles (al c m, figures 25, 26). The antagonistic muscles are the dorsal cardiac muscles (d c m) and the dorsal anterior cardiac muscles (d a c m, figure 25). The median floor of the cardiac stomach is raised by the labral muscles (lb m), the latero-medial cardiac floor muscles (lm c fl m) and the lateral cardiac floor muscles (l c fl m, figures 25, 26). The floor is lowered by the actions of the anteroventral cardiac muscles (av c m), the

anterior bundles of the lateromedial cardiac floor muscles (lm c fl m) and the median cardiac floor muscles (m c fl m, figures 25, 26).

The expansions and contractions that macerate food material while circulating and maintaining digestive juices in the foregut can be divided into three phases corresponding to figure 27*a–c*.

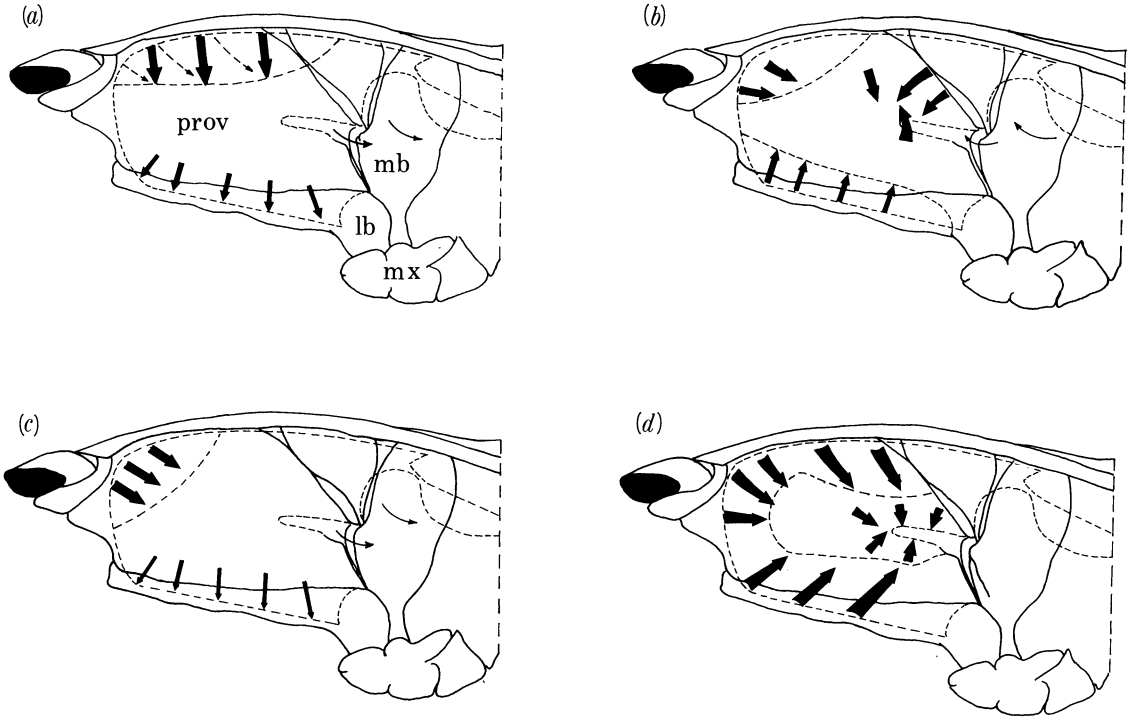


FIGURE 27. Lateral views of the proventriculus (dashed outline) drawn schematically to illustrate the movements of the proventriculus during, (*a*)–(*c*), the maceration of food and, (*d*), the pumping of macerated food into the pyloric stomach. (*a*) The dorsal cardiac gastric wall is moved ventrally and the ventral cardiac gastric floor expanded. (*b*) The floor of the cardiac stomach is raised; the lateral cardiac folds are brought medially; the rostral part of the proventriculus is moved posteriorly and the molar processes of the mandibles occluded. (*c*) The gastric floor is lowered and food is pressed ventrally by posteroventral movement of the rostral part of the proventriculus. The molar processes of the mandibles are swung laterally. (*d*) The floor of the cardiac stomach is raised; the rostral part of the proventriculus is moved posteriorly; the roof of the cardiac stomach is moved ventrally and the lateral cardiac folds are brought medially.

During the first phase (figure 27*a*), the dorsal gastric wall is moved ventrally by contraction of the dorsolateral cardiac muscles. Contraction of these muscles is sequential, commencing anteriorly and ending with contraction of the posterior bundle adjacent to the dorsal anterior process of the mandibular endophragm. During this movement, the ventral part of the proventriculus expands while the molar processes are held apart within the cardiac stomach.

During the second phase (figure 27*b*), the floor of the cardiac stomach is raised by an anteroposterior sequence of muscular contractions. Following this, contractions of the lateral cardiac longitudinal muscles and posterior cardiac muscles bring the lateral cardiac folds and posterolateral cardiac ossicles medially, in front of the posterior cardiac plate. Immediately after this movement, the mandibles are brought medially, during which action the anterodorsal part of the gut wall is moved posteroventrally by contraction of the dorsolateral cardiac

muscles and the anterolateral cardiac muscles (dl c m, al c m, figure 25). These movements consolidate fragments of food ventral to the lateral cardiac folds, between the mandibles. During these sequential muscular contractions there is no net inflow of material to or from the cardiac stomach. This contrasts with the simultaneous muscular contractions associated with the transfer of fluids into the pyloric stomach.

The third phase is a recovery and circulating phase, during which the floor of the cardiac stomach is lowered, the mandibles are rotated laterally and the lateral cardiac folds moved apart (figure 27*c*). Finally, contractions of the dorsolateral cardiac muscles cause a piston-like movement of the rostral part of the gut which pushes food material posteroventrally.

Each sequence of the masticatory cycle (figure 27*a–c*) occupies about 1 s and the sequence is rhythmically repeated every 1–2 s.

Approximately 5–15 min after ingestion, which is the time required to liquefy part of the food material, transfer from the cardiac stomach to the pyloric stomach commences. This action is produced by the simultaneous contractions of muscles that raise the gastric floor, lower the roof of the cardiac stomach, move the anterior wall posteriorly and occlude the lateral cardiac folds (figure 27*d*). The movement occurs between one and three times in succession and occurs sporadically during the masticatory process. This results in a 50–75 % reduction in foregut volume, causing the fluids to be passed from the cardiac stomach to the ampullae. The tight apposition of the labrum with the mandibles seals off the oral opening.

(*c*) *The movement of particles into the pyloric stomach*

The posterior cardiac plate is the only system of setal screening and channelling present in the cardiac stomach. All material that enters the pyloric stomach must flow along one of two routes: either through the screens overlying the lateral channels of the posterior cardiac plate, thence directly into the upper ampullary chamber; or directly over these screens into the dorsal pyloric stomach and into the upper ampullary chamber (figure 28, u a c).

Most food material is moved through the setal screens. Minute particles are collected on the setal mat between the lateral cardiac plate ossicles and the median cardiac plate ossicle. Contraction of the transverse cardiac plate muscle (t c p m, figures 4*a*, *b*, 25, 32) moves the lateral cardiac plate ossicles medially, pushing the setal mat against the overlying setal layers. Simultaneous contractions of the posterior cardiac plate muscles (p c p m, figures 4*a*, *b*, 31) move the superior lateral cardiac plate ossicles laterally, thus brushing material laterally, into the channels formed by the inferior lateral cardiac plate ossicles.

The flow across and through the setae of the posterior cardiac plate is mediated by the powerful contraction of the cardiac stomach, which creates sufficient pressure to force the liquefied food into and through the ampullae. Additional contractions of the ampullary muscles serve to further macerate the partially digested food (see §6*d*).

When fluids are moved along the lateral channels into the ampullae, the dorsal gastric wall is tightly pressed to the floor of the dorsal pyloric stomach and the dorsal cardio-pyloric channel is blocked by the posterior dorsal cardiac fold (p d c f, figure 28*b*, plate 2).

(*d*) *The movement of material through the ampullae*

The ampullae constitute both dorsal and ventral avenues of communication to the midgut and digestive gland. The dorsal pyloric stomach is vestigially represented by a fold of cuticle and is only functional at the posterior end, where it opens into the upper ampullary chamber.

This loss of function (if one assumes that ancestral hoplocarids possessed a functional dorsal pyloric stomach) has arisen from the specialization of the ampullae as a pump that feeds digestive fluids into the cardiac stomach. This contrasts with other Malacostraca, where the ampullae (if present) function as a filtratory device to separate solids from liquids (Jordan 1913; Agrawal 1963; Martin 1964; Schaefer 1970; Powell 1974; Scheloske 1976; Fryer 1977; Coombs & Allen 1978; Kunze & Anderson 1979).

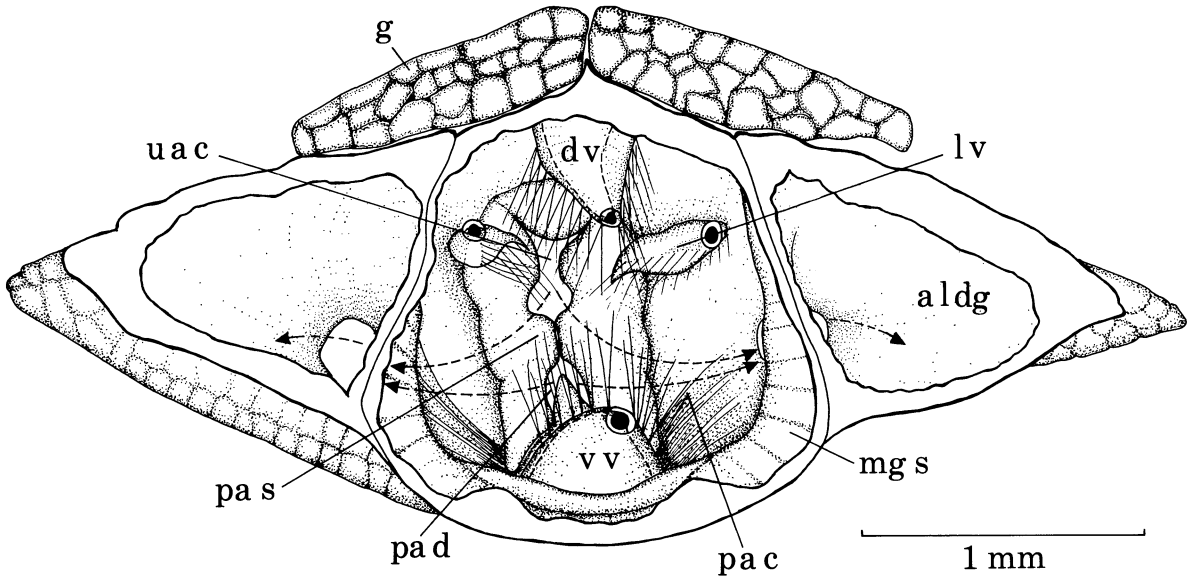


FIGURE 29. Posterior view, from the entrance to the midgut, of the post-ampullary chamber and anterior lobes of the digestive gland. Dashed arrows indicate the pathways of flow from the upper and lower ampullary chambers into the digestive gland.

Experiments were performed on both living and freshly killed specimens to determine whether the ampullae function in the separation or filtration of food material. Live animals were dissected to expose the ampullae and observe muscular activity. Freshly killed animals were also used to observe the passage of colour tracers through the ampullae. In the latter, the digestive tract was removed from the animal and transected anteriorly, midway along the ampullae, and posteriorly, 1 mm along the midgut. By means of a capillary tube of 0.2 mm inner diameter a 10 mg/ml solution of eosin or carmine suspension was injected into the upper ampullary chamber from the anterior end of the resulting portion of the gut. The filter press was gently pressed several times onto the setal mat overlying the lower ampullary channels to mimic the action observed in the living animal. Fluid was also injected into the ampullae to trace the pathway of flow in the absence of filter press action. In this case the ampullae were intact and fluid was injected through the posterior collecting ducts of the posterior cardiac plate. A longitudinal cut was made along the dorsal pyloric stomach and post-ampullary chamber and the tissues splayed to expose the paired ducts leading from the ventral ampullary channels (v a c) and emptying into the post-ampullary chamber (p a c) (figure 24, plate 1, and figure 29).

Particles larger than 0.5–1 μm do not pass through the ampullary setal sieves but pass out through the dorsal pyloric stomach into the post-ampullary chamber (figure 29, p a c).

Fine particles (less than 0.5 μm) pass through the setal layers into the ventral ampullary channels. The exits of both the dorsal pyloric stomach and the paired post-ampullary ducts are opened by relaxation of the post-ampullary sphincter (figure 29, pa s). The muscles of the sphincter insert on the posterior ampullary ossicles, thus separating the pyloric exit from the post-ampullary ducts. The ventral valve (figure 29, v v) also guards the exit of the post-ampullary ducts, preventing the entry of large particles into the lower ampullary channels. Subsequent flow of suspended particles from both upper and lower pyloric exits is directed to the lateral openings of the digestive gland.

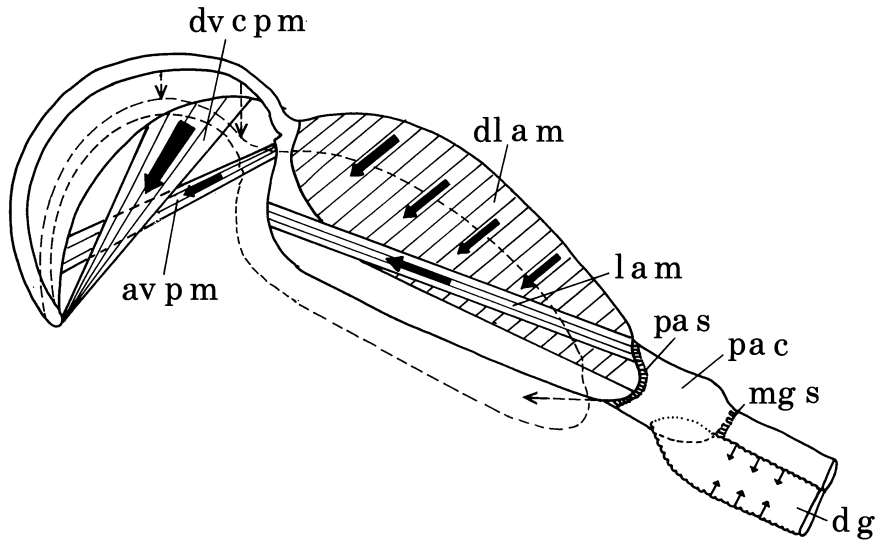


FIGURE 30. Lateral view of the posterior cardiac plate and ampullae (schematic representation), showing the principal muscular contractions (solid arrows) and the resultant movements of the ampullae (dashed lines and arrows) involved in dorsoventral ampullary pumping.

Further maceration of material occurs in the ampullae via the action of the filter press on the setae overlying the lower channels. Also, it is inferred that the filter press sweeps particles towards the dorsal pyloric exit.

Although separation of coarse and fine particles occurs during anteroposterior fluid flow through the pyloric stomach, the resultant fluids subsequently become mixed in the post-ampullary chamber and digestive gland. The major function performed by the ampullary filtration mechanism is related to the forward pumping of fluids into the cardiac stomach.

(*e*) *The flow of fluids to and from the digestive gland and into the midgut*

In stomatopods there is no intermediate channelling of large particles into the midgut or any system of channels and folds for fluid recirculation back to the cardiac stomach. Instead there is a temporal separation of actions resulting in a phasic digestive cycle, thus contrasting with the 'eumalacostracan' system based on the spatial separation of particles.

Details of these processes were ascertained by observations of anaesthetized dissected animals immersed in saline. Animals were starved for 24–48 h and then fed with pieces of prawn stained with congo red, which does not diffuse into the haemolymph or intercellular spaces, or through the peritrophic membrane. Following this, they were left undisturbed for different

time intervals (10 and 30 min, 1, 4, 8, 24 and 48 h, with at least two replicates for each). At each time an animal was placed in 7–10 °C saline (Powers (1973), for *Cancer magister*) and dissected to expose the ampullae and the path of the coloured tracer. A median section 5 mm wide and 10 mm long was removed from the dorsal exoskeleton, including part of the carapace posterior to the cervical groove and the median portions of the sixth and seventh thoracic somites. The associated dorsal longitudinal muscles were also removed. Observations were made for periods of between 10 min and 4 h, the latter being the maximum period before heart beat and muscular contractions became erratic. Satisfactory results were also obtained by anaesthetizing animals with 3% procaine hydrochloride (Oswald 1977) and dissecting in sea water.

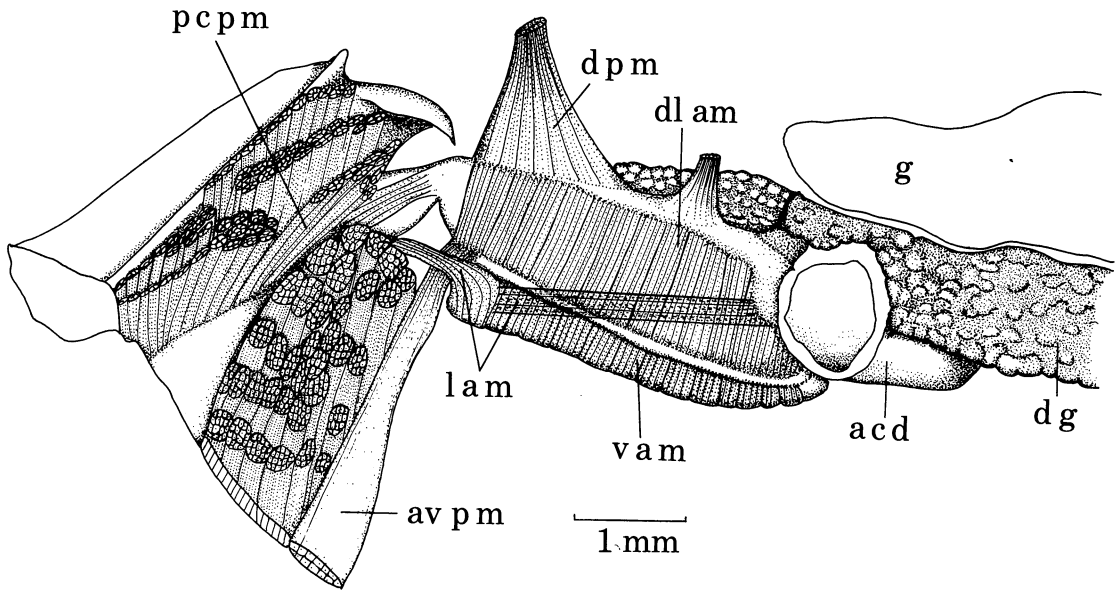


FIGURE 31. *A. laevis*: lateral view of the musculature of the pyloric stomach.

(i) *Ten minutes post-ingestion*

At this stage the foregut is full and its contents not macerated. The ampullae are undergoing two types of movements, rapid lateromedial pulsations (5–7 s^{-1}) of the ampullary walls and slower rhythmic dorsoventral movements (1–2 s^{-1}) of the ampullae themselves.

The rapid lateromedial pulsations are achieved by synchronous contractions of the dorsolateral ampullary muscles (dl a m, figure 31) and ventral ampullary muscles (v a m, figures 31, 32). The dorsolateral ampullary muscles undergo rapid contractions or slow tonic contractions corresponding to the rapid and slow ampullary movements respectively.

The dorsoventral movement is the principal pumping action during the initial digestive phase. During this movement, the ampullae and also the posterior cardiac plate are lowered. This opens the channels between the upper ampullary chamber and the posterior cardiac plate, while retaining the efficiency of the setal filters overlying the latter.

Digestive fluids are pumped into the ampullae by muscular peristalsis of the digestive gland. The relaxed post-ampullary sphincter allows secretions from the digestive gland to flow through the dorsal pyloric exit into the upper ampullary chamber. The ampullae move

dorsoventrally, pumping fluid into the cardiac stomach. The digestive fluids spurt through the setal layers of the posterior cardiac plate, in phase with the ampullary contractions. The specific muscular movements are illustrated in figure 34.

(ii) *Thirty minutes post-ingestion*

At this stage the proventriculus is full and fluid is flowing into the digestive glands. No rhythmic dorsoventral ampullary movements occur but there are posteroanterior movements resulting from contractions of the transverse cardiac plate muscles (t c p m), dorsoventral cardiac plate muscles (dv c p m) and lateral posterior cardiac plate muscles (l p c p m) (figures 4*a*, *b*, 25, 32).

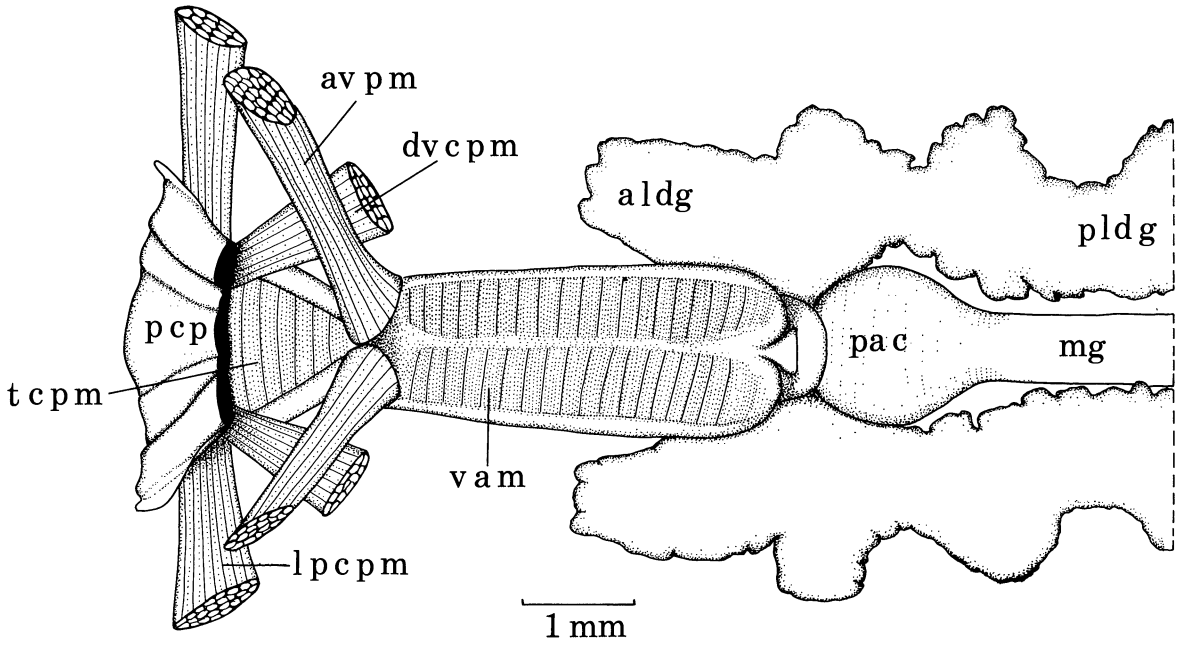


FIGURE 32. *A. laevis*: ventral view of the musculature of the posterior cardiac plate and ampullae.

Once posterior flow into the digestive gland has commenced, the principal mechanism for pumping digestive fluids anteriorly is by lateromedial ampullary pulsations, not dorsoventral pumping. This is because fluid flow in the latter case is along the upper ampullary chamber. Although dorsoventral pumping is more efficient in terms of the volume of liquid that can be transported per movement, it is an unsuitable mechanism once food material has entered the digestive gland. At this stage the digestive fluids must be filtered through the ampullary setae to prevent backflow of particles to the cardiac stomach.

Initial flow of fluids from the ampullae is always into the digestive gland and not the midgut. There are three mechanisms that prevent the latter. First, contraction of a sphincter muscle (mg s, figures 29, 39) at the entrance to the midgut reduces the size of the midgut opening. Consequently, the path of least resistance is that which leads to the digestive gland. Secondly, the post-ampullary valves offer some resistance to fluid flow. Liquids flow in a path ventral to the lateral valves and must be rechannelled to flow upwards and posteriorly if they are to reach the midgut. Thirdly, compacted material in the midgut acts as a block to fluid movement.

(iii) *One hour post-ingestion*

At this stage the digestive gland contains partially digested flocculent material, which can be observed moving backwards and forwards and circulating from right to left branch and vice versa. The peristaltic rhythm of the digestive gland is one contraction every 2 s. Postero-anterior movements of the posterior cardiac plate and ampullae occur very infrequently in comparison with activity levels 10–30 min after ingestion. Lateromedial ampullary pulsations

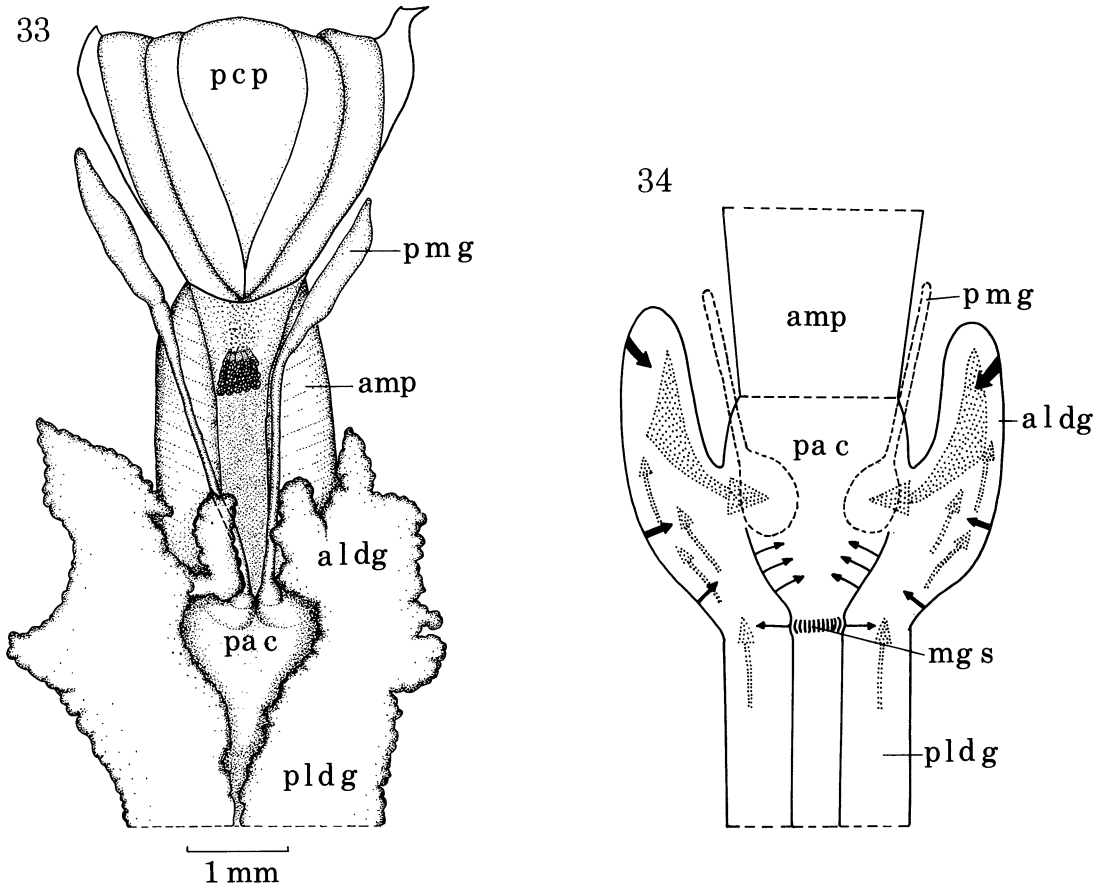


FIGURE 33. *A. laevis*: dorsal view of the posterior cardiac plate and ampullae, showing the peritrophic membrane glands.

FIGURE 34. Schematic diagram of the post-ampullary chamber and anterior part of the digestive gland, showing the directions of muscular contractions (solid arrows) and movements of particles (stippled arrows) during the compaction of material prior to its movement into the midgut.

occur at a lower frequency (short bursts of activity every 5 min). The flow of digestive juices into the cardiac stomach is reduced.

The midgut contains some compacted material that is invested by a peritrophic membrane secreted by tubular glands (p m g) arising from the roof of the post-ampullary chamber near the entrance to the midgut (figures 33, 34). These glands, previously designated as the dorsal caecum (Petricevic 1915; Siewing 1956), do not appear to function in digestion. No stained particles were observed to flow into them. The glandular tissue is cytologically similar to the

midgut epithelium. The glands exude a gelatinous matrix that is applied to the compacted food by the post-ampullary valves. Peritrophic membranes have been reported in many crustaceans, including branchiopods, cirripedes, copepods, and most malacostracans, including syncarids (personal observation; Forster 1953; Gauld 1956; Martin 1964; Georgi 1969; Rainbow & Walker 1977; Schlecht 1979). The source of the membrane in branchiopods, cirripedes carideans and gammarid amphipods appears to be the anterior midgut epithelium (Rainbow & Walker 1977; Forster 1953; Martin 1964). Martin also cited the works of Malloy (1958) on mysids and Beecher-Moore (1959) on the isopod *Idotea*, in which both workers stated that the membrane was secreted by the anterior dorsal caecum, a midgut derivative.

The compaction of material from the digestive gland, its investment in a peritrophic membrane and subsequent movement down the midgut is achieved in *A. laevis* by a combination of movements.

Material is accumulated into a dense mass in the anterior lobe of the digestive gland by synchronous, bilateral contractions of the anterior parts of the digestive gland. Excess fluids are taken up in the posterior lobe while the anterior lobe contracts, pushing the mass medially and posteriorly through the channel at the lateral margin of the post-ampullary chamber (figure 34). The compacted mass is moved posteriorly, towards the midgut, underneath and medial to the post-ampullary valves and ventral to the peritrophic membrane glands. Contraction of muscles investing the post-ampullary chamber and relaxation of the midgut sphincter allow material to be forced into the midgut (figure 34). Entry of material into the ampullae is prevented by closure of the post-ampullary sphincter.

(iv) *Four hours post-ingestion*

At this stage the cardiac stomach contains mainly skeletal elements and hard parts of food. The digestive gland is full and the midgut is more than half full. The hindgut also contains compacted waste.

(v) *Eight hours post-ingestion*

At this stage the cardiac stomach is almost empty. The digestive gland contains pale viscous fluids (mainly posteriorly) and congo red particles may also be observed in the cells. The midgut is half filled, with the posterior section empty; the hindgut is full, and faeces are present. Sporadic ampullary movements occur, but there is no peristalsis of the digestive gland and no accumulated material in the anterior lobe.

During this part of the cycle there is a change in fullness of the midgut. This is because there is a switchover in function from the movement of material into the midgut to the circulation of fluids within the digestive gland, and pyloric pumping occurs.

(vi) *One to two days post-ingestion*

At this stage the cardiac stomach is empty and the digestive gland contains little particulate matter. The midgut is mostly filled, the hindgut less than a third full and faeces are present. There is no pyloric pumping but the slow rhythmic peristalsis of the digestive gland continues (1 contraction per 5 s) and there is compaction of material anterior to the midgut.

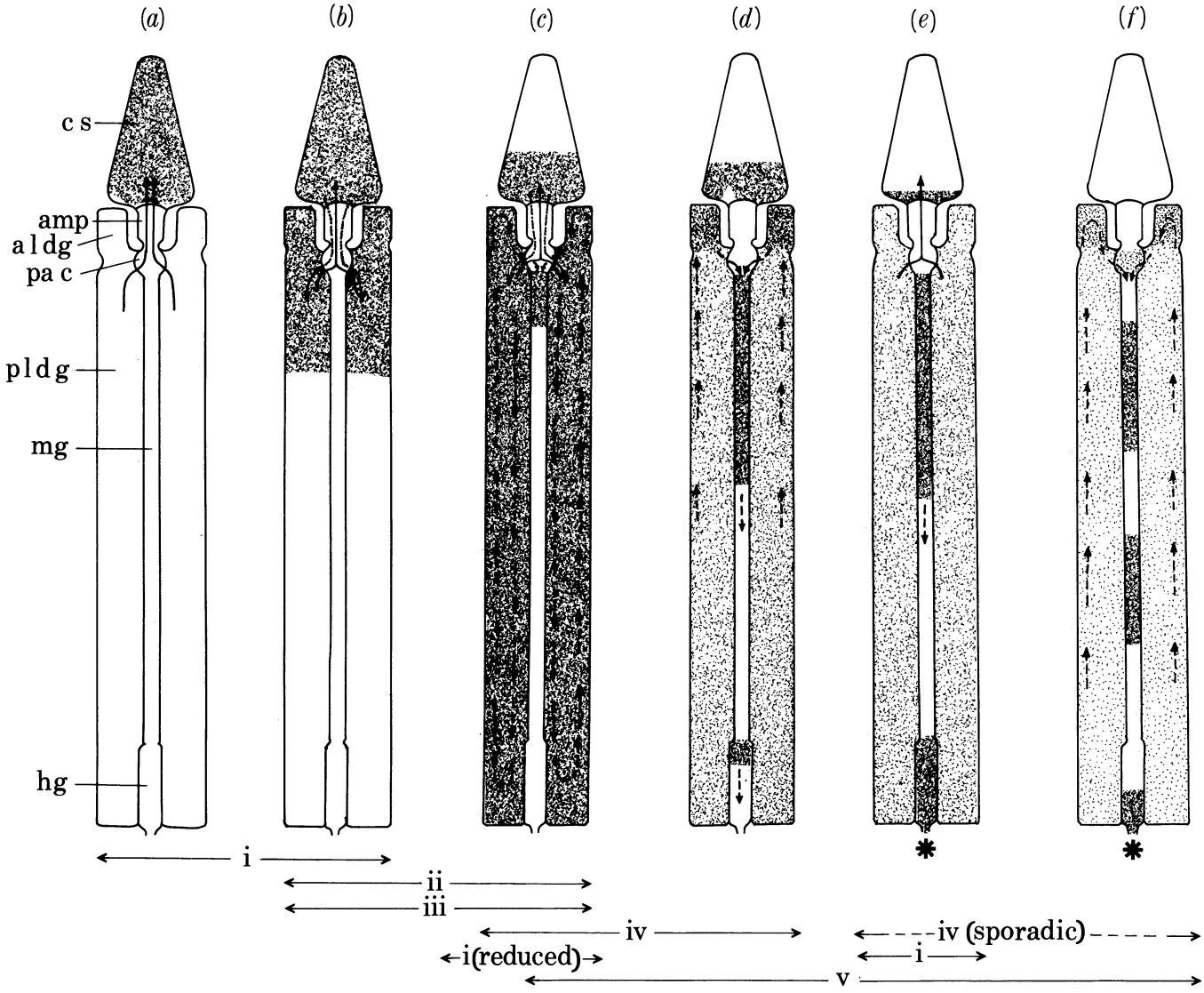


FIGURE 35. Schematic dorsal views of the alimentary tract, summarizing the major features of the digestive cycle: (*a*) 0–15 min post-ingestion; (*b*) 30–60 min post-ingestion; (*c*) 1–2 h post-ingestion; (*d*) 4 h post-ingestion; (*e*) 8 h post-ingestion; (*f*) one to two days post-ingestion. Solid arrows indicate movements of digestive fluids; dashed arrows indicate movements of food particles; stippling indicates the distribution and proportion of food particles in the different regions of the alimentary tract; and asterisks indicate that defaecation has occurred. Phases of the digestive cycle are: (i) secretion and circulation of digestive juices into the cardiac stomach; (ii) maceration of food in the cardiac stomach; (iii) passage of food particles to the digestive gland; (iv) circulation of particles in the digestive gland; (v) circulation of non-absorbed particles into the midgut, including compaction in the anterior lobe of the digestive gland and secretion of the peritrophic membrane.

(*f*) *Summary of digestive cycle*

Once ingestion of food into the cardiac stomach has commenced, the various events of food maceration, transport, digestion and passage to the midgut follow a phased sequence, as follows (figure 35).

Phase 1. Digestive juices are pumped into the cardiac stomach by slow, rhythmic dorso-ventral pumping and rapid lateromedial pulsations of the ampullae (figure 35*a*).

Phase 2. Food is macerated in the cardiac stomach by the mandibles and by contraction of the gastric wall. Lateromedial pulsations of the ampullae continue into phase 3, supplying digestive juices to the cardiac stomach (figure 35*b*).

Phase 3. Macerated food is circulated into the digestive gland, which begins peristalsis. Pyloric pumping is less frequent (figure 35*b*, *c*).

Phase 4. Non-assimilated food is cycled from the digestive gland into the midgut and is invested in a peritrophic membrane. Material is first accumulated in the anterior lobe and then the post-ampullary chamber, and, finally, is passed through the midgut sphincter (figure 35*c*, *d*).

Phase 5. The midgut sphincter is closed and another cycle of pyloric pumping of digestive juices into the cardiac stomach commences (figure 35*e*).

Phase 6. There is another cycle of passage of macerated material from the cardiac stomach into the digestive gland. Material is further compacted and moved along the midgut (figure 35*f*).

Phase 7. Another cycle of accumulation in the anterior lobe occurs with the subsequent passage of material into the midgut.

These cycles continue until the cardiac stomach is empty.

(*g*) *The regurgitation of material from the cardiac stomach*

Although most of the food ingested is macerated and emulsified and can pass through the setae of the posterior cardiac plate, indigestible fragments of sand, shell and heavily calcified or sclerotized material must be retained in the cardiac stomach. The only mechanism by which they can be evacuated is regurgitation. The action is similar to that associated with the pumping of fluids into the ampullae (figure 27*d*) except that there is no contraction of the muscles of the ventral floor or labrum. Consequently, the oral opening is not sealed against the incisor processes and material is ejected through the mouth.

Rhythmic contractions of the dorsal and lateral cardiac wall expel accumulated waste towards the mandibles. Finer sand grains are expelled with a current of water, whereas larger fragments are pushed between the mandibles, which are then retracted posteriorly in a rocking motion. This moves material from the molar to the incisor processes. Lateromedial and ventral movements of the maxillules move material distally. This is followed by ventrolateral and dorsomedial movements of the maxillae. Occlusion of the mandibles holds material in a space between the maxillae, whose medial closure then expels the contents with a jet of water.

Regurgitation does not occur until all assimilable material has been passed to the digestive gland and secretion of digestive juices into the cardiac stomach has ceased. It is, therefore, not energetically costly to the animal, since no food or digestive juices are lost during the process.

(*h*) *Proventricular structure in other squillid and gonodactylid stomatopods*

The foreguts of *A. fasciata*, *O. nepa*, *H. stephensoni*, *O. cultrifer* and *G. graphurus* were examined to investigate whether differences existed within and between the Squillidae and Gonodactylidae.

Variations were found in the relative proportions of the cardiac and pyloric regions in relation to body size. Differences were also found in the morphology of the anteroventral cardiac ossicles, the posterolateral cardiac ossicles, the cuticular processes adjacent to the posterolateral cardiac ossicles and the setation of the posterior cardiac plate. There were no

differences in the structure of the posterior cardiac plate or ampullae. The musculature was also constant among species, with similarly disposed groups of muscles associated with the various folds and ossicles. There are differences, however, in the relative sizes of particular groups of muscles, especially those associated with the anteroventral cardiac ossicles, the posterolateral cardiac ossicles and the lateral cardiac folds.

(i) *Relative proportions of the cardiac and pyloric regions*

The index of relative size used herein was the ratio of x to y indicated in figure 36*a*. In adults the ratio is approximately 1.4 for *A. laevis* and *H. stephensoni*, 1.7 for *A. fasciata* and *O. nepa*, 1.3 for *G. graphurus* and 1.1 for *O. cultrifer*. The squillids examined characteristically have a capacious foregut. There appears to be no tendency for an increase in size of the cardiac stomach in relation to the size of the pyloric stomach with increasing animal size. The two gonodactylids have relatively smaller cardiac stomachs than the squillids, with respect to both the dimensions of the pyloric stomach and the size of the animal. In *O. cultrifer* (figure 36*d*) the cardiac stomach is short, with the dorsal portion expanded. The lateral cardiac folds completely occlude the dorsal cardiac region from the ventral cardiac region. The ventral cardiac stomach forms a smaller masticatory region in comparison with those of the squillids and the molar processes of the mandibles penetrate almost half its length. The posterior cardiac plate in *O. cultrifer* is shielded from the ventral cardiac region by well developed folds. The cuticular processes (see (iv), below) overlap the posterior cardiac plate, forming paired, rigid dorsoventral folds that extend medially to the median cardiac plate ossicle. *G. graphurus* (figure 36*e*) is similar to *O. cultrifer*, although the reduction and separation of regions of the cardiac stomach are not as extreme.

Reduction of the cardiac stomach in gonodactylids, coupled with an increased ossification of parts of the gastric cuticle (see (ii) and (iii), below), facilitates mastication. This may be an adaptation to a diet consisting of a large amount of heavily calcified material, which must be regurgitated more frequently. Indigestible material is retained in the dorsal and ventral folds until the digestible material is evacuated to the pyloric stomach.

(ii) *The anteroventral cardiac ossicles*

The anteroventral cardiac ossicles of *O. nepa* (figure 36*b*) and *A. laevis* are similar. Those of *A. fasciata* (figure 36*a*) are longer in comparison with the length of the cardiac stomach and those of *H. stephensoni* (figure 36*c*) shorter.

In contrast, the anteroventral cardiac ossicles of gonodactylids are greatly enlarged. The dorsal part of each is expanded into a plate-like structure occupying the entire dorsolateral corner of the anterior foregut. These ossicles are larger in *O. cultrifer* (figure 36*e*) than in *G. graphurus* (figure 36*f*).

In addition to the anteroventral cardiac ossicles, each of the gonodactylids has another pair medial to the posterior half of the anteroventral cardiac ossicles. These are the ventral cardiac ossicles (v c, figures 36*d*, *e*). In *O. cultrifer* (figure 36*d*) these are more laterally placed than in *G. graphurus* (figure 36*e*).

(iii) *The posterolateral cardiac ossicles*

The posterolateral cardiac ossicles of the squillids examined (p l c, figure 36*a–c*) are similar in size and shape in all species. Those of the larger species, *O. nepa* and *H. stephensoni*, are more

heavily calcified. In the two gonodactylids, they are more dorsally located (p l c, figure 36*d*, *e*). They are large and rectangular, extending anterodorsally. In addition to these ossicles, the gonodactylids have another pair, the posterior cardiac ossicles (p c, figure 36*d*, *e*), narrow and rod-like, lying dorsoventrally between each collateral posterolateral cardiac ossicle and the anterior margin of the superior lateral cardiac plate ossicle. The posterior cardiac ossicles of *G. graphurus* are shorter than those of *O. cultrifer*, which extend along the posterior margin of the row of cuticular processes.

TABLE 2. THE LENGTH, WIDTH AND SPACING OF SETAE ON THE POSTERIOR CARDIAC PLATE

	long setae			short setae		
species	l./mm.	w./μm	sp./μm	l./mm	w./μm	sp./μm
A. laevis	0.3–0.32	2.7–3.3	2.7–3.3	0.9–0.11	4.2–4.8	5.7–6.3
A. fasciata	0.3–0.32	2.7–3.3	1.2–1.8	0.1–0.12	4.2–4.8	2.7–3.3
O. nepa	0.37–0.39	2.7–3.3	1.2–1.8	0.15–0.17	4.2–4.8	5.7–6.3
H. stephensoni	0.48–0.5	3.6–4.2	2.7–3.3	0.14–0.16	7.2–7.8	17.7–18.3
O. cultrifer	0.3–0.32	2.7–3.3	1.2–1.8	0.037–0.056	8.7–9.3	8.7–9.3
G. graphurus	0.17–0.19	2.1–2.7	0.9–1.5	0.023–0.042	8.7–9.3	8.7–9.3

Abbreviations: l., length; w., width; sp., spacing.

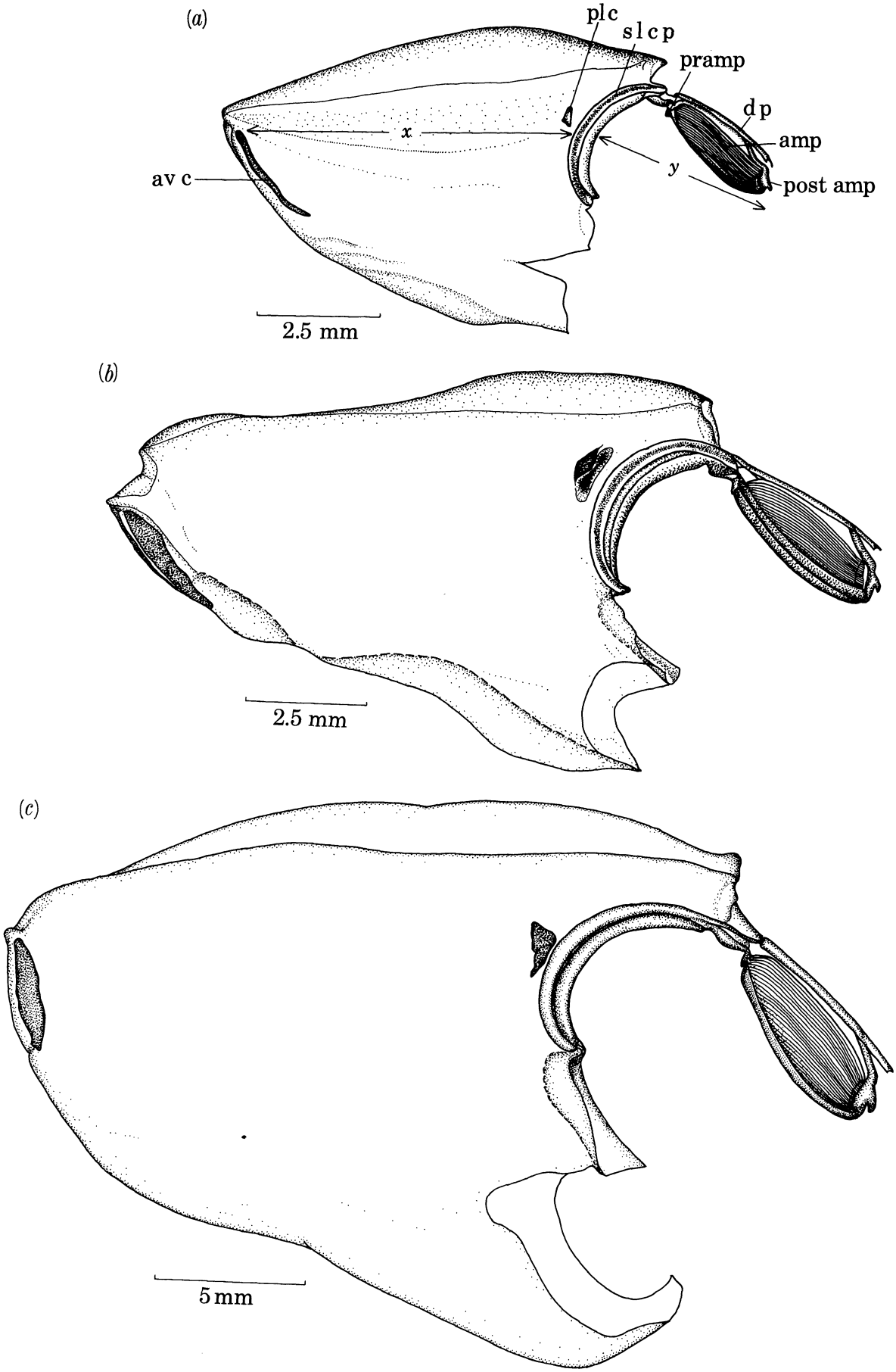
(iv) *The cuticular processes*

These lie along the apices of two folds on either side of the posterior cardiac plate (figure 37*a–f*). Their role appears to be to exclude large pieces of food from the posterior cardiac plate. They are not masticatory structures like the lateral teeth of the decapod gastric mill. Their associated muscles (i.e. the posterior bundles of the dorsolateral cardiac muscle) move the processes anteriorly, while contractions of the posterolateral cardiac muscles and related musculature of the lateral cardiac folds move the cuticular processes medially.

The cuticular processes of *A. laevis*, *A. fasciata* and *O. nepa* are similar (figure 37*a–c*), while those of *H. stephensoni* (figure 37*d*) are numerous and tooth-like. Those of *O. cultrifer* (figure 37*e*) are more numerous than those of squillids, extending almost to the roof of the cardiac stomach. They are rounded, not tooth-like, and are less robust than the corresponding structures in squillids. In *G. graphurus* (figure 37*f*) the cuticular processes are virtually absent, represented by a row of fine, denticulate protrusions. The role of the processes is replaced by the posterolateral cardiac ossicles, acting as ossified ridges that are more rigid than the cuticular processes. Each of the smaller posterior cardiac ossicles surmounts another ridge between the posterolateral cardiac ossicle and the superior lateral cardiac plate ossicle.

(v) *Setation of the posterior cardiac plate*

There are two rows of setae on the medial margin of each superior lateral cardiac plate ossicle, a row of short setae overlying a second row of long setae. The size and spacing of these setae in adults are shown in table 2. The squillids are generally similar although in *H. stephensoni* the short setae are more widely spaced and have serrated margins. In gonodactylids these setae are shorter, stouter and more widely spaced, and there is an additional row of small denticles dorsomedial to the two setal rows.


(a)
plc
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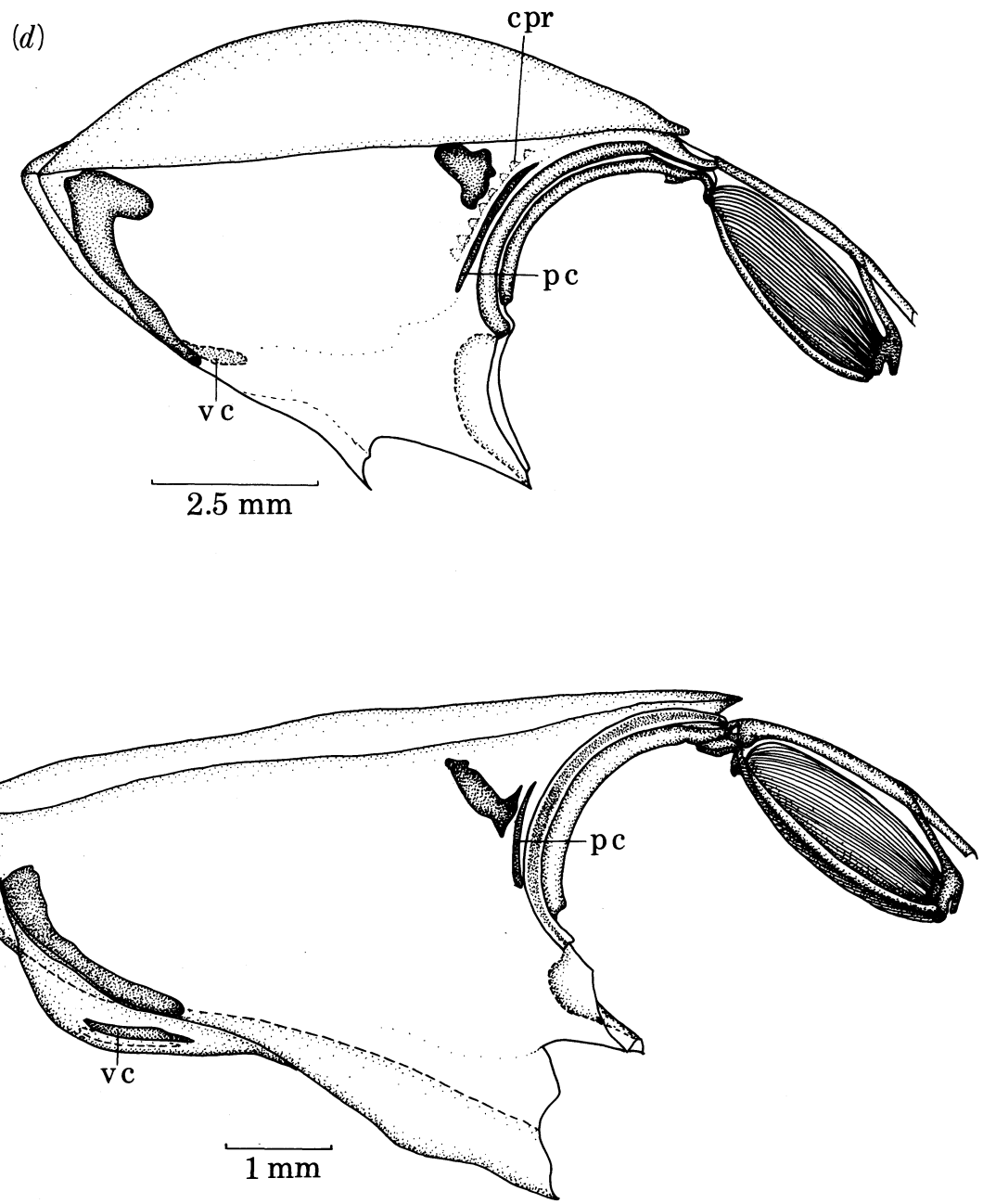


FIGURE 36. Lateral views of the proventriculus in: (*a*) *A. fasciata*; (*b*) *O. nepa*; (*c*) *H. stephensoni*; (*d*) *O. cultrifer*; (*e*) *G. graphurus*. The distance between the anteroventral cardiac ossicle and the posterior cardiac plate is *x*; *y* is the distance between the posterior cardiac plate and the end of the ampullae (see text for details).

(vi) *Trends within the* Squillidae

A. laevis, *A. fasciata* and *O. nepa* are similar in proventricular structure. The anteroventral cardiac ossicles show a progressive reduction in length in relation to an increase in animal size. Those of *H. stephensoni* are very short, supporting only the anterior parts of the cardiac stomach. The posterolateral cardiac ossicles are similar in relative size and shape in all four species. Those of the larger species, *O. nepa* and *H. stephensoni* are more heavily calcified.

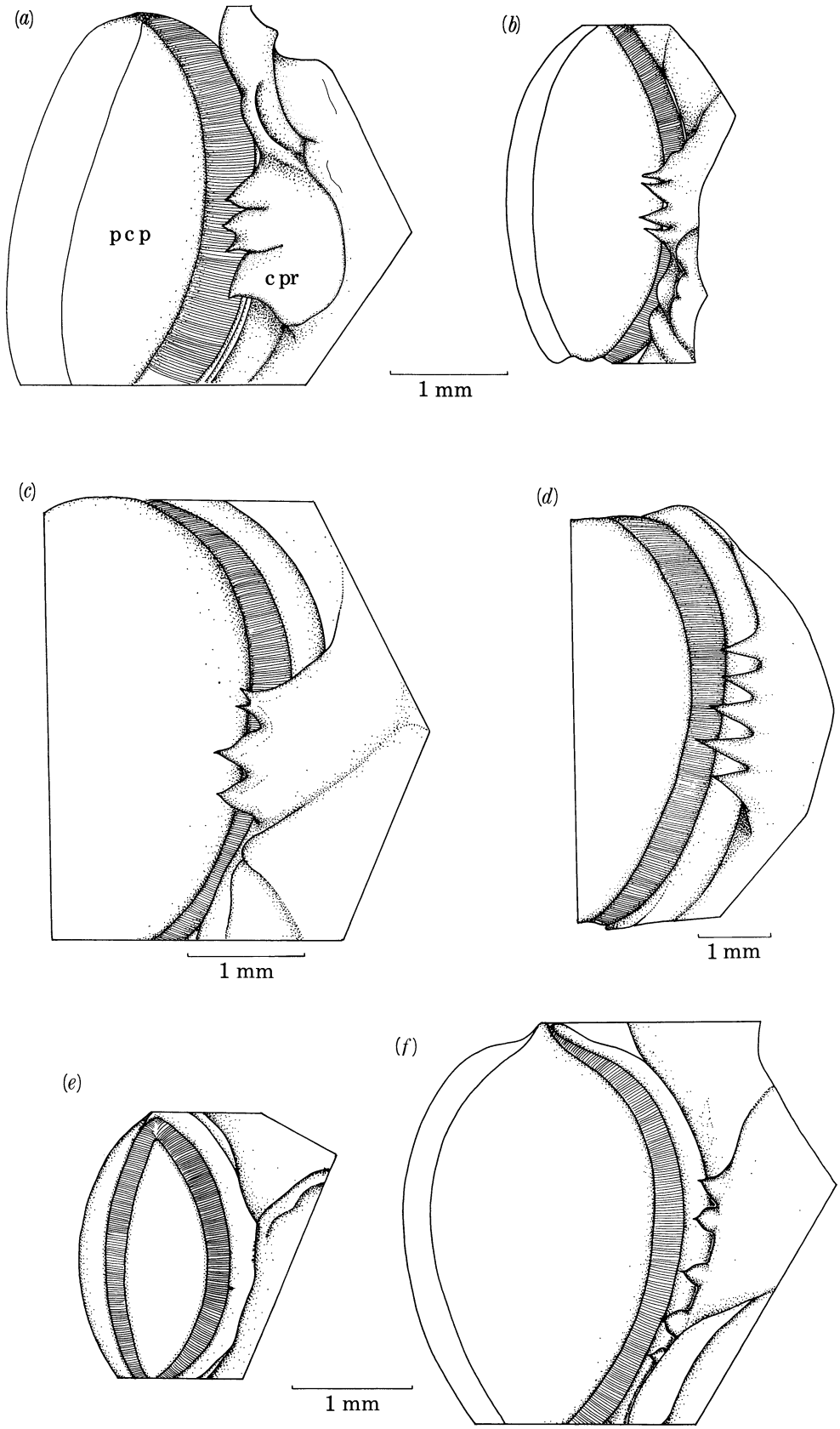


FIGURE 37. Anterior view of the cuticular processes (c p) which partially overlap the posterior cardiac plate (p c p) in the six species of stomatopods: (*a*) *A. laevis*; (*b*) *A. fasciata*; (*c*) *O. nepa*; (*d*) *H. stephensoni*; (*e*) *G. graphurus*; (*f*) *O. cultrifer*.

The cuticular processes are similar in *A. laevis*, *A. fasciata* and *O. nepa*; those of *H. stephensoni* more numerous and tooth-like. Associated with this difference, broad, widely spaced serrate setae overlie the long setae of the posterior cardiac plate. It is suggested that the lateromedial movement of the folds bearing the cuticular processes abrades material against the short setae of the posterior cardiac plate. The presence of broad, widely spaced, serrate setae may act as a means of increasing the masticatory efficiency of this action.

(vii) *Trends within the* Gonodactylidae

Certain features can be recognized as adaptations to dietary differences. The two gonodactylids share a suite of morphological modifications related to a diet of heavily calcified food material. The cardiac stomach is small relative to animal size. The gastric cuticle is more deeply folded to separate the smaller ventral region of the cardiac stomach from the enlarged dorsal region. Associated with this is the development of additional paired ossicles and the increased ossification of the anteroventral cardiac ossicles. The mandibles extend further within the ventral region of the cardiac stomach, allowing for more efficient mastication of food. The posterior cardiac plate is more effectively protected from abrasion by the greater ossification of the folded cuticle anterior to it.

The cuticular processes are reduced in *G. graphurus*. Their role in protecting the posterior cardiac plate from abrasion has been taken over by the enlarged posterior lateral cardiac ossicle, supported by the posterior cardiac ossicles.

The short setae of the posterior cardiac plate are shorter and more robust in gonodactylids. The functional significance of this modification is not clear. Perhaps it is associated with diet or with a modification to deflect coarse material from the lower setal layer. Short stout setae may also be more abrasive when the folds supported by the posterolateral cardiac ossicles are moved across their surfaces.

The differences between squillids and gonodactylids are more marked in *O. cultrifer* than in *G. graphurus*. In *O. cultrifer* there is a pronounced reduction of the cardiac stomach and expansion of the dorsal region. The anteroventral cardiac ossicles are larger and the ventral cardiac ossicles more widely spaced than those of *G. graphurus*. The posterolateral cardiac ossicles are shorter. The greater ossification and reduction in size of the cardiac stomach in *O. cultrifer* compared with *G. graphurus* is probably related to its larger size rather than representing a more specialized condition.

7. The digestive gland and midgut of *Alima laevis* (Hess)

The digestive gland of malacostracans has been studied by many workers (for reviews see Mansour-Bek (1954), Vonk (1960), Van Weel (1970), Barker & Gibson (1977, 1978) and Gibson & Barker (1979)). Most studies concern the histology and physiology of the digestive gland in decapods and, to a lesser extent, isopods and amphipods. Transmission electron microscopy has been applied to the study of the ultrastructure of the cells (Bunt 1968; Stanier *et al.* 1968; Jones *et al.* 1969; Clifford & Witkus 1971; Loizzi 1971; Moritz *et al.* 1973; Vernon *et al.* 1974; Schultz 1976). Investigations have been concerned with the identification and classification of the major cell types of the digestive gland, the processes of secretion, restitution and absorption with reference to cell types, and the identification and localization of storage products and enzymes.

Petricevic (1915) categorized the cells of the digestive gland in *Squilla mantis* using the system of Frenzel (1884) and Apathy & Farkas (1906). He recognized three types of cells, 'Fibrillenzellen' or F-cells, 'Alveolenzellen' or R-cells, and 'Blasenzellen' or B-cells. He further stated that the categorization of cell types in the stomatopod digestive gland was of little value in a functional interpretation. Unfortunately, Petricevic gave no illustration of the cells that he briefly described and it is difficult to make any comparisons with *A. laevis* or other malacostracans on the basis of his verbal description.

Most descriptions of the decapod digestive gland have adopted the classification proposed by Hirsch & Jacobs (1928), which defines four types of cells: E-cells, undifferentiated embryonic cells; F-cells, fibrillar or transitional cells; R-cells, 'Restzellen' or resorptive cells; and B-cells, secretory cells. There is, however, no general agreement on the characteristics of these cells.

The present study adopts the classification of Hirsch & Jacobs for comparative purposes, without implying the recognition of those cell types as functionally distinct entities.

(*a*) *The morphology of the digestive glands*

The digestive glands extend along the midgut, encircle the hindgut and fan out as finger-like caecal extensions at the posterior extremities of the telson (figure 38). Each gland consists of two lobes, an anterior, extending two-thirds of the length of the posterior lateral surface of the pyloric stomach, and a posterior, which extends along the remaining length of the alimentary canal. Petricevic (1915) described two anterior pairs of caeca, the 'Coeca anteriora dorsalia' or dorsal caecum, and the 'Coeca anteriora lateralia' or lateral lobe. The dorsal caecum was shown previously (§6*e*) to be separate from the digestive gland and to secrete the peritrophic membrane. The two major ducts of the digestive glands open from the post-ampullary chamber and carry a number of ramifying, blind-ending caecal extensions. Each duct is 0.52 mm in diameter in *A. laevis*, in contrast to the narrow midgut, 0.3–1 mm in internal diameter (figure 38).

The digestive gland is lined by a specialized epithelium comprising three types of cells. Surrounding this is a thick, PAS-positive basal lamina. Each major duct then has a layer of striated circular muscle fibres, approximately 6 μm thick, invested by an outer layer of connective tissue. The secondary ducts have a fine investment of circular muscle fibres (up to 2 μm thick) surrounded by connective tissue. In the intercaecal spaces are blood sinuses and squamous interstitial cells or 'wandering cells'. This matrix of connective tissue, interstitial cells and blood sinuses is cemented together by a PAS-positive ground substance. The entire gland is enclosed by a thin, PAS-positive membrane and a layer of connective tissue.

(*b*) *The cell types in the digestive gland*

(i) *Embryonic or E-cells*

The E-cells of *A. laevis* are similar to those described for Astacidae (Jacobs 1928; Hirsch & Jacobs 1928, 1930; Miyawaki *et al.* 1961; Davis & Burnett 1964; Bunt 1968; Loizzi 1971), Nephropidae (Barker & Gibson 1977), Brachyura (Van Weel 1955; Stanier *et al.* 1968; Monin & Rangneker 1974; Barker & Gibson 1978) and amphipods (Martin 1964; Moritz *et al.* 1973; Schultz 1976). They are the only cells in which mitotic activity is seen. Functionally, they represent a reservoir of unspecialized cells that subsequently differentiate into the more specialized absorptive and secretory cells. As in decapods and amphipods, the E-cells are the major cell type in the lining epithelium of the distal regions of the secondary ducts. They are

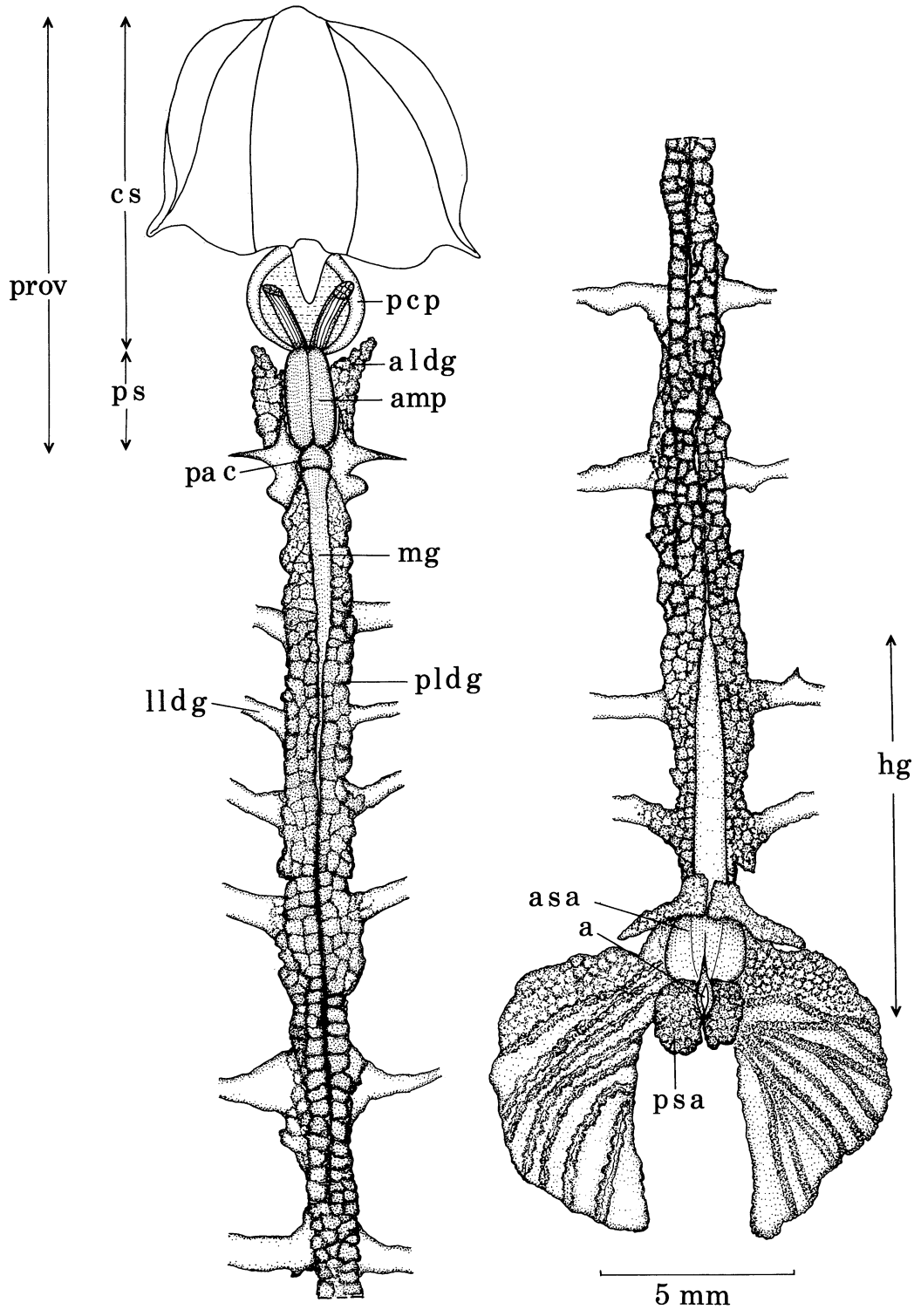


FIGURE 38. *A. laevis*: ventral view of the alimentary tract (bisected with anterior half on left). The cardiac stomach has been slit longitudinally.

commonly found at the blind-ending regions, where they may form a layer one to three cells thick. In *A. laevis* E-cells may also be found among the more differentiated cells in the larger, more proximal ducts, thus contrasting with *Homarus gammarus* (L.) and *Scylla serrata* (Forskål) (Barker & Gibson 1977, 1978), in which E-cells are confined to the terminal, blind-ending regions of the tubules.

Each E-cell is 15–20 μm tall and 9–15 μm wide, with a distal to centrally placed nucleus 4–8 μm in diameter (figure 39, plate 3). A brush border is usually present on the luminal surface, except where the cells form a syncytial layer, in which case only those cells facing the lumen of the tubule bear microvilli. The cytoplasm is typically devoid of inclusions. As the E-cells mature, they resemble absorptive cells and often contain one or two small lipid droplets in the cytoplasm.

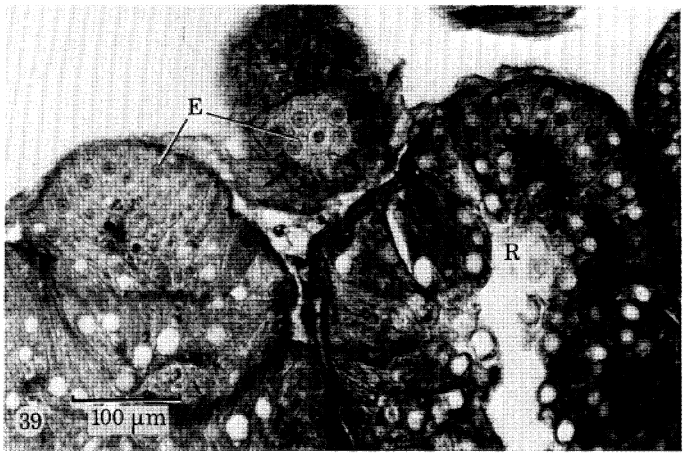
(ii) *Resorptive or R-cells*

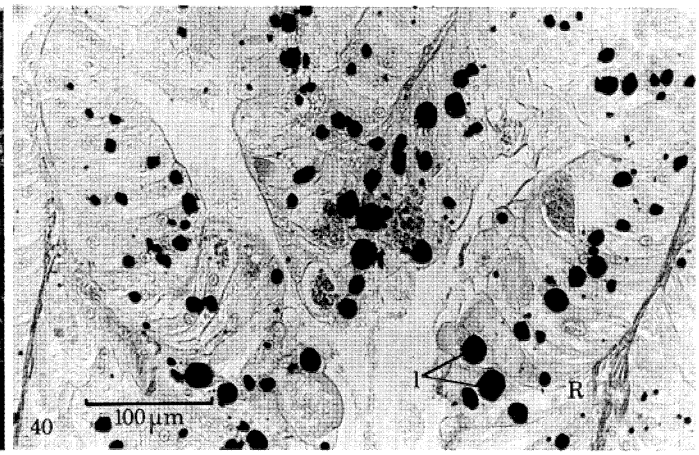
These, the most abundant cells in the epithelium of the digestive gland, are columnar, 25–65 μm tall and 8–15 μm wide, with basally located, round to oval nuclei, 6–8 μm in diameter and vesicular in appearance. Characteristic of R-cells is the presence of one or more large lipid droplets (figure 40, plate 3) and many glycogen granules (PAS-diastase) in the distal cytoplasm. Bordering the proximal surface of the R-cells is a brush border of regular thickness (*ca.* 1 μm) which is positive for both PAS and alcian blue. Figure 41 (plate 3) shows the presence of a thin (0.1–0.2 μm) mucopolysaccharide layer on the surface of the microvilli, the surface enteric coat, which consists of short filaments. Numerous, irregularly shaped mitochondria are present in the proximal cytoplasm, immediately below a prominent apical zone that is devoid of cytoplasmic organelles. The apical zone is 0.2–0.6 μm thick and appears striated in electron micrographs, due to the extension into the cytoplasm of the microvillar core filaments (figure 42, plate 3). The apical borders between cells are marked by tight junctional complexes. Numerous ovoid inclusions up to 1 μm in diameter occur in the distal cytoplasm. These contain storage products, calcium spherules and myelin-like figures similar to those in the R-cells of *Procambarus clarkii* (Girard) (Bunt 1968).

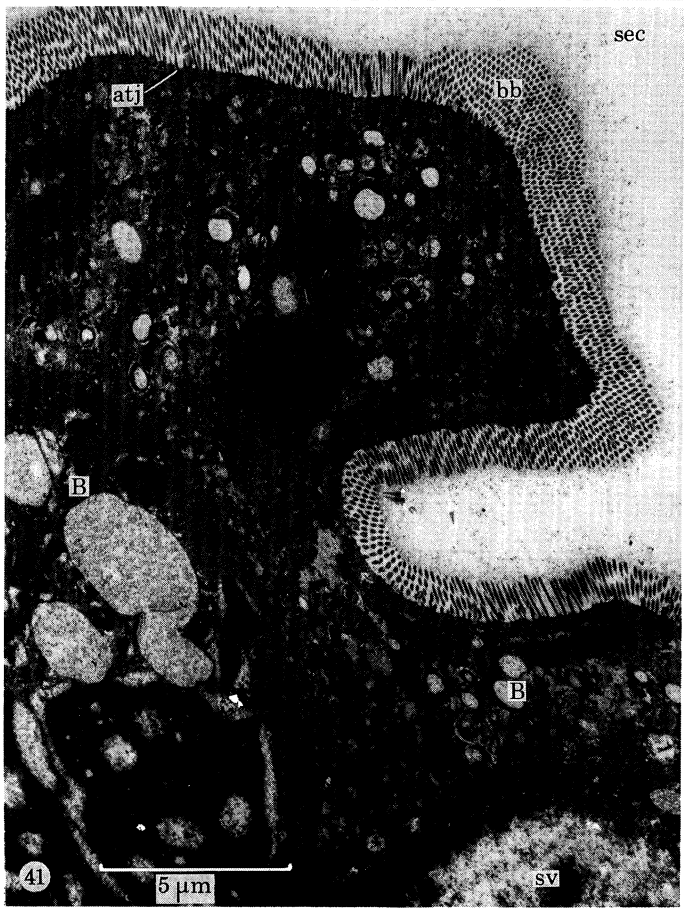
(iii) *Secretory or B-cells*

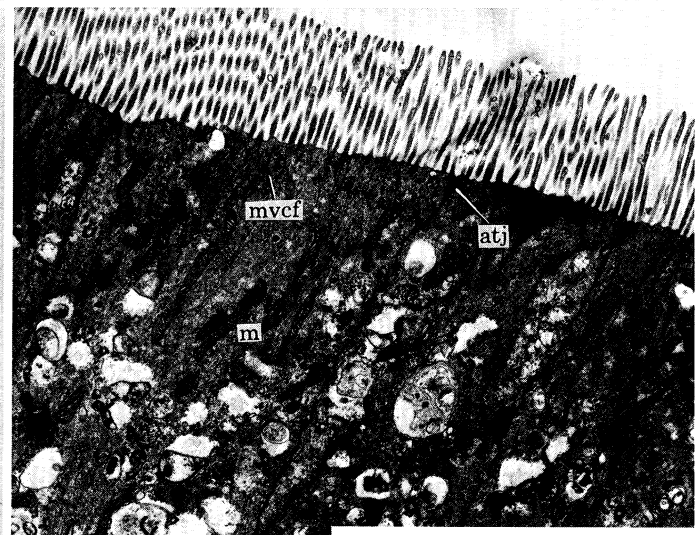
B-cells range from columnar, 48 μm tall and dilated proximally, to almost spherical, 35–40 μm in diameter, accommodating large secretory vacuoles (figure 43, plate 3). The secretory vacuole gives a strong positive reaction to PAS, alcian blue and mercuric bromophenol blue. A brush border is present similar to that of R-cells.

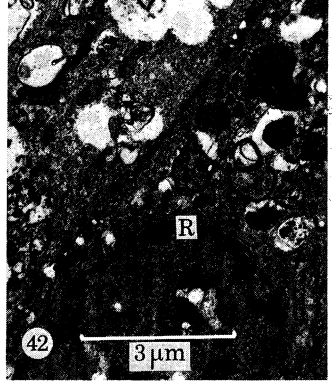
B-cells tend to be confined to the proximal regions of the digestive gland, although a few may be found in the secondary tubules. The nuclei of mature B-cells are compressed below the secretory vacuole and are devoid of nuclear inclusions. No evidence was found for the presence of the 'apical complex' described by Loizzi (1971) for *Orconectes virilis* Hagen and *Procambarus clarkii* and also by Barker & Gibson (1977, 1978) for *Homarus gammarus* and *Scylla serrata*. In ripening B-cells there is an aggregation of vacuoles distal to the secretory vacuole. The vacuoles are typical of cells in the final stages of maturation, during which the vacuolar inclusions coalesce to form a single large vacuole. The apical regions of B-cells show a specialization different from that described by Loizzi; there is a dense basophilic region proximal to the secretory vacuole. This region is proteinaceous and is present only in ripe B-cells before secretion (figure 43, plate 3).











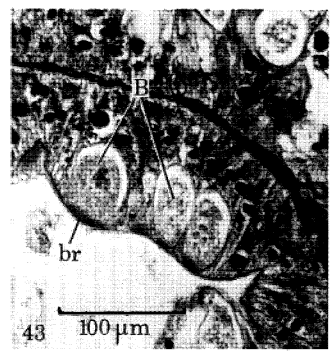


FIGURE 39. Transverse section of the digestive gland of *A. laevis* (azan-stained), showing aggregations of E-cells in the distal parts of the gland and also adjacent to R-cells.

FIGURE 40. Transverse section of the digestive gland of *A. laevis* (unstained, Flemmings-fixed), showing the localization of osmiophilic lipids (l) in the R-cells.

FIGURE 41. *A. laevis*: transmission electron micrograph of a transverse section of the digestive gland, showing developing R- and B-cells. On the surfaces of the brush borders (b b) of both cell-types is a prominent surface enteric coat (s e c). Apical tight junctions (a t j) and an absence of organelles in the apical zone are characteristic of resorptive cells. The secretory vacuoles (s v) of the B-cells are in different stages of maturation; the secretory vacuole on the lower right containing fine granular and densely clumped material is almost ripe.

FIGURE 42. *A. laevis*: transmission electron micrograph of a transverse section of the digestive gland, showing developing R-cells. Immediately below the brush border is the apical zone, devoid of organelles and striated in appearance due to the extension into the cells of microvillar core filaments (m v c f). Apical tight junctions (a t j) are prominent and also the numerous mitochondria (m) lying below the apical zone, oriented with their long axis towards the lumen. Numerous membrane-bound granules and small lipid droplets fill the supranuclear cytoplasm.

FIGURE 43. Transverse section of the digestive gland of *A. laevis* (Flemmings-fixed, azan-stained), showing mature B-cells. Note the basophilic region (b r) that borders the luminal surfaces of the ripe secretory vacuoles.

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The contents of the secretory vacuoles vary in appearance according to their developmental state, with mature cells containing highly granular, deeply staining secretory products. Immature B-cells often contain small lipid droplets in the distal cytoplasm. Extrusion of the secretory vacuole usually results in cellular degeneration. Entire cells, including nuclei, are often found in the lumen of the tubule. Holocrine secretion appears to be the predominant secretory mechanism in *A. laevis*. There is also evidence of merocrine secretion during periods of starvation and waning digestive cycles. In these cases small secretory vacuoles are pinched off from the cell, the apical membrane is reconstituted and the nucleus remains intact. During periods of starvation, large R-cells are frequently sloughed into the major ducts, liberating stored lipid droplets. Merocine secretion may predominate during such physiological conditions to facilitate extracellular digestion of storage products.

Fibrillar or F-cells, similar to those described for decapods and amphipods (Van Weel 1955; Davis & Burnett 1964; Bunt 1968; Stanier *et al.* 1968; Loizzi 1971; Moritz *et al.* 1973; Schultz 1976; Barker & Gibson 1977, 1978) appear to be absent in *A. laevis*. A few cells show some of the features of F-cells, but none conform in all characteristics. The similarities shared with the F-cells of decapods and amphipods are: strongly basophilic with large (12–15 μm) basal nuclei and prominent nucleoli; columnar (45–60 μm tall, 12–15 μm wide) and usually compressed proximally by the adjacent cells; having one or more cytoplasmic inclusions in the supranuclear cytoplasm that react with mercuric bromophenol blue, indicating proteins; brush border present. Several features of these cells, however, prove they are not true F-cells. There are no striations in the cytoplasm indicative of extensive development of rough endoplasmic reticulum in parallel profiles. They are scarce in comparison with B-cells. A supranuclear vacuole is absent in some and small lipid droplets may be present. The overall size is greater than that of F-cells described by previous authors. The brush border is of similar thickness to that of R-cells (1 μm). In true F-cells it is less than 1 μm thick (Loizzi 1971; Barker & Gibson 1977).

(*c*) *The cells of the midgut*

The midgut comprises two-thirds of the length of the alimentary canal. It is composed of an inner convoluted layer of epithelial cells, invested by a thin basal lamina and surrounded by a layer of circular muscle (3–5 μm thick). Outside the circular muscle is a 30–40 μm layer of connective tissue containing blocks of longitudinal muscle fibres, blood sinuses and interstitial cells embedded in an acidophilic, PAS-positive ground substance. The surrounding 'tunica propria' differs from that of the digestive gland in two respects, the presence of longitudinal muscle fibres and the higher proportion of mucopolysaccharide ground substance.

The cells of the midgut are monotypic. All are tall (30–90 μm, usually 60 μm) columnar cells with central oval nuclei that contain prominent acidophilic nucleoli. Bordering the proximal surface of the cells is a brush border, 1–3 μm thick. In the cytoplasm proximal to the nucleus are a number of vacuolar inclusions similar to those found in R-cells. Midgut cells closely resemble R-cells, except that they lack glycogen or lipid storage products and have longer microvilli (1–3 μm as compared with 1 μm in R-cells).

(*d*) *Sites of absorption in the digestive gland and midgut*

Certain ultrastructural features common to R-cells and midgut epithelial cells are specializations for absorption. There is extensive microvillar development; each microvillus has a

filament extending along its length and into the apical cytoplasm of the cells for about 1 μm (figure 42, plate 3). There are small, electron-lucent vacuoles which increase in size distally and appear to be incorporated into lysosome-like structures concentrated in the supranuclear cytoplasm. Between the filamentous extensions of the microvilli are numerous mitochondria, typical of absorptive cells. There is extensive development of rough endoplasmic reticulum in the distal half of the cytoplasm, and infolding of the basement membrane associated with a ramifying network of endoplasmic reticulum. These features are analogous to similar characteristics in vertebrate absorptive cells (Fawcett 1966; Bunt 1968; Loizzi 1971). Between the borders of the epithelial cells, apical tight junctions preclude the absorption of material into the intercellular space (also mentioned by Loizzi for crayfish).

(*e*) *Digestive enzymes*

It is generally held that the digestive gland is the sole source of digestive enzymes. A wide variety of enzymes and their role in digestion have been investigated by two approaches. The first is by direct assay of digestive gland extracts or digestive juices canulated from the proventriculus (for reviews see Mansour-Bek (1954), Arvy (1969), Brockerhoff *et al.* (1970), Van Weel (1970) and Gibson & Barker (1979)). The second is the histochemical localization of specific enzymes, which gives an indication of cellular specialization and the sequence of digestive processes, especially in relation to phasic changes in cell types. Most studies of this type have been carried out on decapods (Gibson & Barker 1979).

In the present investigation only acid and alkaline phosphatases were examined histochemically, in an attempt to assess the relative importance of the digestive gland and midgut in the absorption of digested products. The role of acid and alkaline phosphatases in the transport of nutrients across membranes has been investigated by a number of authors (Monin & Rangneker (1974) cite the major recent studies). Acid and alkaline phosphatases have been localized in the R-cell cytoplasm and the brush borders of R- and B-cells of *Scylla serrata* (Monin & Rangneker 1974; Barker & Gibson 1978). Barker & Gibson (1977, 1978) also found acid phosphatases in the midgut epithelia of *Homarus gammarus* and *Scylla serrata*, but alkaline phosphatase was found only in the midgut epithelia of *Scylla*. This, they stated, was possibly related to the shorter midgut length of *Scylla*, thus invoking active uptake as compared with passive uptake in the long midgut of *Homarus*.

In *A. laevis* both acid and alkaline phosphatases were found on the brush borders of all cells facing the major ducts (R- and B-cells). Intense positive reactions were also found in the cytoplasmic granules of developing secretory cells, and in the granular extrusion bodies present in the lumen of the digestive gland. The epithelial cells of the midgut showed only slight acid phosphatase activity but no evidence was found for alkaline phosphatase activity.

Animals fed with saccharated iron(II)carbonate were tested for sites of iron absorption by means of the Prussian blue reaction. Only the R-cells gave a positive result, with the most intense reaction occurring in R-cells bordering the major secretion ducts. Less intense reactions were present in the proximal cytoplasm of immature R-cells of the secondary secretion ducts. No evidence of iron uptake into the cells of the midgut were found.

(*f*) *Conclusions concerning cellular differentiation and secretory mechanisms in* Stomatopoda

In *A. laevis* there are several morphological and histological characteristics of the digestive gland that resemble those of isopods, amphipods and decapods. The cells are differentiated into secretory B-cells and absorptive R-cells. The embryonic E-cells are present in the distal tubules and, to a lesser extent, on the inner surfaces of the secondary secretory ducts. Secretion is asynchronous and holocrine, although merocrine secretion may occur. When the gut is empty and all waste material has been cycled from the digestive gland to the midgut, the digestive gland undergoes a phase of restitution. Storage products are lipids and glycogen, which vary according to the nutritional status of the animal.

Other characters appear unique to stomatopods. The digestive gland, essentially a pair of hollow tubes, has few ramifying caecal extensions. F-cells appear to be absent, suggesting that the sequence of cell proliferation differs from that in decapods (Gibson & Barker 1979). From the histological evidence, cell proliferation is non-cyclical; E-cells give rise to R- and B-cells. The possibility of R-cells transforming to secretory cells in a manner similar to that described by Hassal & Jennings (1975) cannot be excluded.

The functioning of the digestive gland is not dependent on particle size since the diet consists of animal protein previously macerated in the proventriculus. The large diameter of the lumen of the digestive gland probably reflects a specialization toward rapid, monophasic secretion coupled with transport of digestive juices into the proventriculus and subsequent rapid absorption and storage of assimilated products, rather than a specialization to accommodate larger-sized food. Although feeding in stomatopods is intermittent and large quantities are ingested over a small time period, digestion and movement of material into the digestive gland are also rapid (see §6*e*). Unlike herbivorous and omnivorous crustaceans, which feed frequently and often hold material in the foregut for a relatively long period, *A. laevis* shows little intermixture of gut contents from different feeding sessions. Adaptations for rapid secretory, absorptive and restitutional phases are likely to arise in such feeding strategies. Holocrine secretion may be regarded as an adaptation to rapid intermittent feeding and digestive cycles, especially following periods of starvation. A similar explanation for the occurrence of holocrine secretion in decapods has been proposed by various workers (for review see Gibson & Barker (1979)).

8. Discussion

(*a*) *The* Eumalacostraca *and hoplocaridan affinities*

Moore (1969) defined the Eumalacostraca on the basis of their differences from the Phyllocarida, including the absence of a bivalved or hinged carapace, articulated caudal furca and seventh abdominal somite. The presence of a bivalved carapace does not imply any affinities on a class basis. Siewing (1956, 1963) regarded the leptostracan bivalved carapace, together with its carapace adductor muscles, as a specialization, but the functional and phylogenetic significance of the bivalved arrangement is still not clear. Some phylogenetic significance may attach, however, to the fact that the phyllocarid carapace is not fused to any of the post-cephalic somites. This feature is shared by the extinct Eocarida, a group regarded by Brooks (1969*a*) to be ancestral to the Eucarida and Peracarida. The Eocarida were distinguished from other

eumalacostracans by the presence of a unisegmental protopod and furca, archaic features, which Brooks proposed as distant links with the Cephalocarida.

A furca is also present in bathynellacean and stygocaridacean syncarids, but not universally in phyllocarids. Briggs (1978) showed that a furca was absent in the Canadaspididae but present in the Perspicarididae, both members of the order Canadaspidida.

A third feature, which again does not provide a clear distinction between the Phyllocarida and the Eumalacostraca, is the presence or absence of a seventh abdominal segment. Within the lophogastrid Mysidacea there are indications of a seventh pretelsonic segment. It is present as a distinct transverse groove between the sixth and seventh segments in embryonic forms. A pair of seventh abdominal somites is also present in embryos of some Mysidacea (Manton 1928). The embryology of *Nebalia* was shown by Manton (1934) to be malacostracan but little phylogenetic information can be gained beyond this. The lack of palaeontological evidence for either a phyllocarid with six abdominal segments or a hoplocarid with seven abdominal segments is of neutral phylogenetic significance. Schram (1973) has indicated the existence of 'an extensive and diverse early Palaeozoic phyllocarid radiation' comprising groups such as the sairocaridid hoplostracans, which, according to Schram, shared features in common with hoplocarids. It is reasonable to suggest that the presence of six pretelsonic abdominal segments in the Hoplocarida and Eumalacostraca is a result of convergence from separate phyllocarid-like ancestors.

The abdominal musculature of stomatopods was regarded by Hessler (1964) as being precaridoid and intermediate between the leptostracan and caridoid conditions. He suggested that the absence in the hoplocaridan skeletomusculature of transverse muscles, which are characteristic of the Eumalacostraca, was of no significance. He proposed that transverse muscles are actually 'enlarged dorsoventral muscles whose ventral insertions sank into the ventral longitudinal muscles and eventually fused medially with the ventral end of the other member of the pair'. This proposal, however, requires substantiation. The simplicity of the abdominal musculature in stomatopods closely resembles the phyllocarid form. Certain specializations of the skeletomusculature are uniquely hoplocaridan. The basic pattern of coiling of the muscles, which Hessler describes as a link between the caridoids and the hoplocarids, may also be regarded as the only functionally possible solution to the locomotory requirements of the two groups. It is possible that this pattern may have arisen independently in the Hoplocarida and Eumalacostraca.

Burnett & Hessler (1973) regarded the Phyllocarida as ancestral to all Eumalacostraca; however, the Leptostraca are the only group for which some of the biology is known and this group probably branched off from the early phyllocarid stock earlier than the remaining phyllocarid groups (Sanders 1955, 1957, 1959). Palaeontological evidence provides no information on the patterns of adaptive radiation within the Phyllocarida. Briggs (1978) modified the classification of the Phyllocarida to include the five orders Leptostraca, Canadaspidida, Hymenostraca, Hoplostraca and Archaeostraca, emphasizing that the last three must only be considered tentative. The alternative, Briggs suggested, would be to elevate the Leptostraca and Canadaspidida to subclass status, which 'would imply differences between these three divisions of equal rank to those separating them from the Eumalacostraca'.

Bergström (1979) held the known archaeostracans to be unacceptable as eumalacostracan ancestors and postulated an unknown separate evolution of the Eumalacostraca as a monophyletic group, independent from the Phyllocarida, from Cambrian common ancestors, the

unity of the Hoplocarida and Eumalacostraca being defined by the constant number of abdominal segments. Bergström gave no consideration to the shared features of the phyllocarids and hoplocarids. There is no evidence for the existence of his hypothetical eumalacostracan ancestor or for the subsequent hypothetical caridoid form from which he proposed the Hoplocarida and other 'Eumalacostraca' diverged. Bergström failed to discuss which characters are convergent similarities and which are not and reverted to the opinion of neontologists in his conclusions regarding polyphyly versus monophyly.

The evidence for a monophyletic origin of the Eumalacostraca is weak. However, there is some evidence for the possibility of an eocarid ancestry for Eucarida and Peracarida (Brooks 1969*a*). An evolution of the Hoplocarida as a group separate from the eocaridan–eucaridan–peracaridan assemblage follows from this. The eocarid characteristics and proposed phylogeny (Brooks 1969*a*) are at variance with a hoplocarid affinity. The retention in the Hoplocarida of many phyllocarid-like characters cannot be the result of secondary specialization from an eocarid stock.

Similarly, if phyllocarid evolution has progressed from an ancestry different from that of the Eumalacostraca (Bergström 1979), then the close morphological alliance of the Hoplocarida with a phyllocarid-like form and their characteristic differences from other Eumalacostraca may be used as an argument for the independent evolution of the Hoplocarida. This further implies that the Eumalacostraca, as previously defined, is not a monophyletic group.

The characters linking the Hoplocarida with the Phyllocarida have been outlined by Siewing (1963). These require re-examination. The possession of a heart with segmental vessels and ostia was regarded by Siewing as indicating that the abdominal gills of stomatopods were original. The supposed existence of a seventh pair of abdominal arteries (Komai & Tung 1931) has been refuted by Burnett (1972). The circulatory system in Leptostraca is primitive with the heart having seven pairs of ostia (three cephalic and four thoracic) and 12 pairs of lateral arteries which supply internal organs (Kaestner 1970). In stomatopods there are 12 or 13 pairs of ostia and 14 pairs of lateral arteries (Burnett 1972). If the ostia were original, as Siewing stated, then presumably their phyllocarid ancestor also had a similar arrangement of ostia and arteries. There is, however, no evidence for this.

The major features of stomatopods that provide good evidence for phyllocarid-like ancestry are: cephalic kinesis, the similarity in cephalic musculature (Siewing 1963); the extension of the viscera, especially the gonads, throughout the body; and the skeletomusculature (Hessler 1964).

Confounding these similarities are a number of peculiar specializations of stomatopods, such as the subneural artery with a great number of rami communicantes (Siewing 1963), the movable segment bearing the eyes (Grobben 1919), the triflagellate first antenna, the three-segmented protopod of the pereiopods and the presence of four segments instead of five in the hoplocaridan endopod. These have been overlooked in favour of a monophyletic derivation of the Hoplocarida as part of the Eumalacostraca. It is now clear that there are other major differences in internal morphology that contradict Siewing's (1956) conclusions regarding the proventriculus in stomatopods. The evidence obtained in the present work does not support the existence of homologies in proventricular structure between stomatopods and other eumalacostracans.

(*b*) *Functional morphology of stomatopods and conclusions concerning the evolution of the* Hoplocarida

The present analysis of the comparative functional morphology of the mouthparts and the proventriculus in stomatopods necessitates a reinterpretation of the evolutionary relationships of the Hoplocarida.

Manton's (1964) investigation of mandibular mechanisms in arthropods has paved the way for comparative studies of these mechanisms within the major arthropod phyla. Stomatopods are large-food feeders, but, unlike trophically similar eumalacostracans, they have retained the 'primitive' mandibular musculature found in branchiopods, leptostracans and syncarids. Superimposed on this 'primitive' template are specializations related to the external and internal treatment of food by the mandibles. The dual-purpose mandible is capable both of transverse biting by the incisor processes and of rolling promotor–remotor movements of the molar processes. Strong transverse biting is achieved by the replacement of the transverse mandibular tendon by an extensive endophragmal skeleton, which supports the well developed transverse mandibular muscles 5c and adductor muscles 4. Muscles 5b and 6 are enlarged and serve as powerful promotors of the molar processes. The axis of swing is almost vertical, as in *Chirocephalus* and *Nebalia*, and there is a strong dorsal articulation. The latter features are usually associated with grinding and squeezing actions of the incisor processes (Manton 1964). Stomatopods use their incisor processes to grip or grind the food while it is torn apart by the maxillipeds. The absence of an oesophagus allows large pieces of food to be pushed directly into the proventriculus for mastication by the molar processes.

The mandibular mechanism of stomatopods is uniquely different from that employed by other eumalacostracans. The similarities in musculature are general similarities which are also shared by non-malacostracan crustaceans such as anostracan branchiopods.

The structure of the other mouthparts and their function during feeding support the proposition of a raptatory hoplocarid ancestor. Although the raptorial appendages and elaborate feeding mechanism represent extremes in hoplocaridan specialization, the maxillules and maxillae are simple in both adults and larvae. No structures comparable to those of filter-feeding malacostracans are found on any of the feeding appendages. The actions of the third, fourth and fifth maxillipeds are simple raptatory movements, during which the subchelae tear apart prey. The maxillae function as a passive screen which holds food in the pre-oral cavity. During regurgitation of indigestible material from the proventriculus, they help to expel the material with a ventrally directed current of water.

The stomatopod proventriculus is highly specialized and functionally complex. The cardiac stomach lacks the masticatory ossicles or setose channels typical of Eucarida and Peracarida. It is probable that during the evolution of carnivorous hoplocaridans, several specializations of the proventriculus arose, including the loss of the oesophagus, the development of supporting ossicles for muscle attachment and the development of the posterior cardiac plate and ampullae. The posterior cardiac plate, a complex filtratory device formed by overlapping ossicles and setae, is the only avenue of communication between the cardiac and pyloric regions. Food is reduced to a fine suspension by the combined actions of the mandibular molar processes, muscular movements of the cardiac stomach and digestive juices pumped forwards into the cardiac stomach by the ampullae. The digest is pumped in a posterior direction through the setae of the posterior cardiac plate, through the ampullae and into the

digestive gland by simultaneous contractions of the cardiac gastric muscles. A dorsal pyloric stomach, communicating directly with the midgut, is absent. The pyloric stomach comprises the ampullae, a complex filtratory structure connecting anteriorly with the posterior cardiac plate and, posteriorly, with the post-ampullary chamber. The ampullae function primarily in pumping digestive juices into the cardiac stomach. The elaborate setal filters prevent the forward return flow of suspended material from the digestive gland into the cardiac stomach. Although filtration also occurs during posterior flow, the materials from the upper and lower ampullary chambers are admixed in the post-ampullary chamber before their passage into the digestive gland. The forward and backward movements of fluids occur in a cyclical pattern which is coupled with the phasic transportation of material into the digestive gland and from the digestive gland into the midgut. The digestive gland, unlike that of decapods, comprises E-, R- and B-cells. F-cells are absent. Secretion appears to be holocrine, correlating with the carnivorous, sporadic feeding strategy of stomatopods. The structure of the digestive gland is specialized for rapid secretion and transport of digestive juices and for rapid assimilation.

The similarity in ampullary structure between decapods and stomatopods is a result of independent evolution related to different functions. The ampullary mechanism in decapods functions as a filter during posterior movement of liquids, and the dorsal pyloric stomach conveys larger particles and wastes directly to the midgut. In stomatopods, the ampullae function in pumping digestive fluids anteriorly. The repeated occurrence of lateral folds (variously modified) in the pyloric stomach among representatives of most malacostracan groups indicates a common adaptive theme in proventricular structure that is not unique to the Eumalacostraca, and not indicative of a common eumalacostracan ancestor. The hoplocarid proventriculus is a specialized structure evolved in association with a carnivorous feeding habit and probably derived from that of a raptatory phyllocarid-like ancestor.

These results, therefore, indicate an independent evolution of the Hoplocarida from the early malacostracan ancestral stock. The evidence suggests there have been three major radiations from this ancestral stock, the Phyllocarida, the Hoplocarida and the other Eumalacostraca.

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List of symbols used on figures

a	anus
a c m	anterior cardiac muscle
al c m	anterolateral cardiac muscle
a l d	duct from anterior lobe of digestive gland
a l d g	anterior lobe of digestive gland
a mb ap	anterior mandibular apodeme
amp	ampullae
ant	antenna
ant m	antennal muscle
antu	antennule
a s a	anterior anal sac
a s p	posterior anal sac
av c	anteroventral cardiac ossicle
av c m	anteroventral cardiac muscle
av p	anteroventral pyloric ossicle
av p m	anteroventral pyloric muscle
b	basis
B	B-cell
c	carapace
c g	cervical groove
cor	cornea
cp	carpus
c pr	cuticular processes
c s	cardiac stomach
cx	coxa
d	dactylus
d a c m	dorsal anterior cardiac muscle
d amp	dorsal ampullary ossicle
d a pr	dorsal anterior process of the mandibular endophragm
d c m	dorsal cardiac muscle
d e	distal endite
d g	digestive gland
dl a m	dorsolateral ampullary muscle
dl c m	dorsolateral cardiac muscle
dl f	dorsolateral fold
d l m	dorsal longitudinal muscle
d l m1, d l m2	anterior and posterior dorsal longitudinal muscles
dm ap	dorsomedian apodeme of the mandibular endophragm
d p	dorsal pyloric ossicle
d p m	dorsal pyloric muscle
d pr	dorsal process of the mandibular endophragm
d v	dorsal valve
dv c p m	dorsoventral cardiac plate muscle
dv t	dorsoventral tendon
e	endite
e1, e2	first and second endites of the second maxillary segment
E	E-cell
end br	endophragmal bridge
ep	epistome
epp	epipod
f p	filter press
g	gonad
g c	gastric cuticle
h	heart
hg	hindgut
ia r	inter-ampullary ridge
i l c p	inferior lateral cardiac plate ossicle
i p	incisor process of mandible
l a c	lower ampullary channels
l a m	lateral ampullary muscles
lb	labrum
lb m	labral muscles
l c	lateral channels of the posterior cardiac plate
l c f	lateral cardiac fold
l c fl m	lateral cardiac floor muscles
l c l m	lateral cardiac longitudinal muscles
l c m	lateral cardiac muscle
l c p	lateral cardiac plate ossicle
l l d g	lateral lobe of the digestive gland
lm c fl m	lateromedial cardiac floor muscle
l p c p m	lateral posterior cardiac plate muscles
l pl t	longitudinal pleural tendon
l v	lateral valve
m	merus
mb	mandible
mb b	mandible body
mb c	articulation of mandibular condyle
mb end	mandibular endophragm
mb p	posterior margin of mandible
mb pl	mandibular pleurite
m c fl m	median cardiac floor muscle
m c p	median cardiac plate ossicle
mg	midgut
mg s	midgut sphincter
m p	molar process of mandible
mx	maxilla
mxp1	first maxilliped
mxp2	second maxilliped
mxp3	third maxilliped
mxp4	fourth maxilliped
mxp5	fifth maxilliped
mxu	maxillule
mxu ad m	adductor muscle of the maxillule
p	propodus
pa c	post-ampullary chamber
pa d	entrance to the post-ampullary ducts from the post-ampullary chamber
palp	maxillulary palp
p ap	posterior apodeme of the mandibular endophragm
pa s	post-ampullary sphincter
p c	posterior cardiac ossicle
p c m	posterior cardiac muscles
p c p	posterior cardiac plate
p c p m	posterior cardiac plate muscles
p d c f	posterior dorsal cardiac fold
p d t	posterior dorsal tubercle
p e	proximal endite
pg	paragnath
pl c	posterolateral cardiac ossicle
p l c m	posterior lateral cardiac muscle
p l d g	posterior lobe of the digestive gland
p mb ap	posterior mandibular apodeme
p m g	peritrophic membrane gland

post amp	posterior ampullary ossicle
pra c	preampullary chamber
pramp	preampullary ossicle
prov	proventriculus
p s	pyloric stomach
p v t	posterior ventral tubercle
R	R-cell
s l c p	superior lateral cardiac plate ossicle
t c p m	transverse cardiac plate muscle
u a c	upper ampullary chamber
v a m	ventral ampullary muscle
v amp	ventral ampullary ossicle
v c	ventral cardiac ossicle
vl amp	ventrolateral ampullary ossicle
vl c m	ventrolateral cardiac muscles
v l m	ventral longitudinal muscle
v pr	ventral process of the mandibular endophragm
v v	ventral valve
x	axis of swing
I, II, III, IV	first, second, third and fourth maxillary segments, respectively
2	anterior mandibular remotor 2
3	mandibular promotor 3
4	posterior mandibular remotor 4
5a	mandibular remotor 5a
5b	mandibular promotor 5b
5c	transverse remotor 5c
6	mandibular promotor 6

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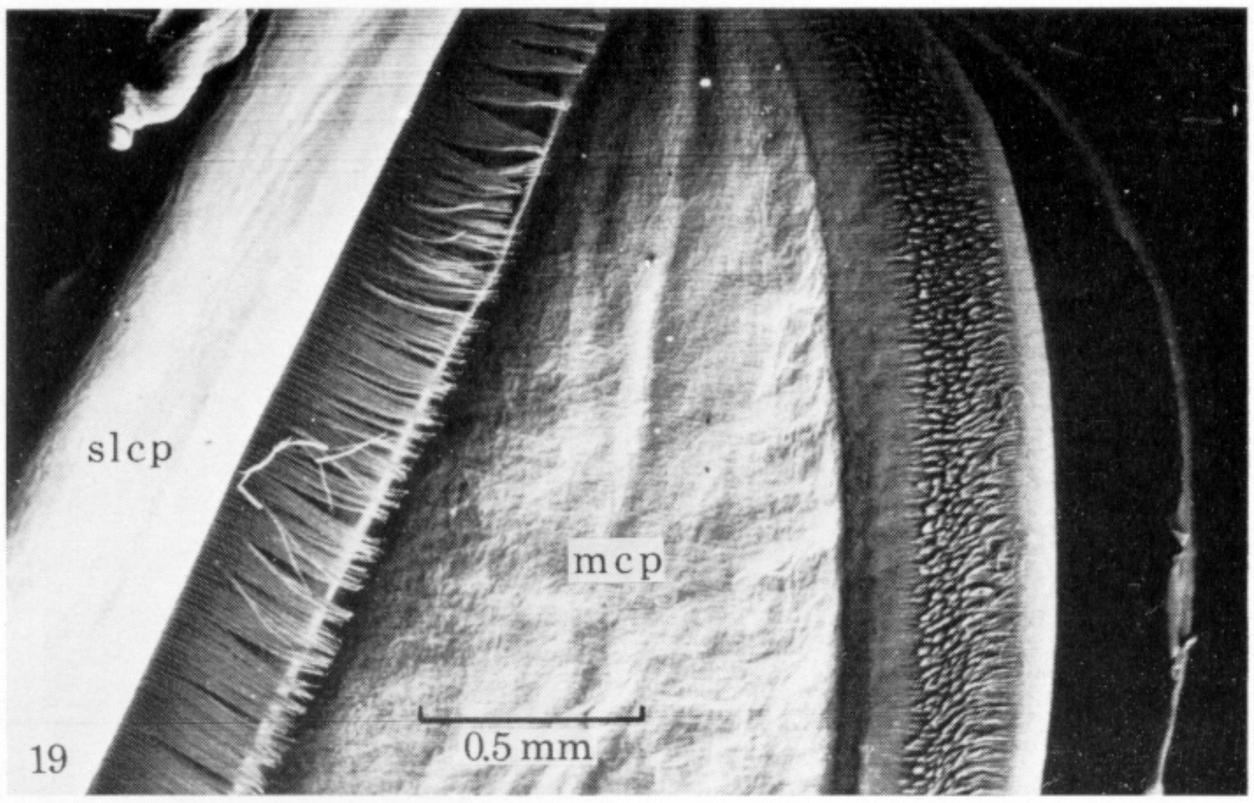
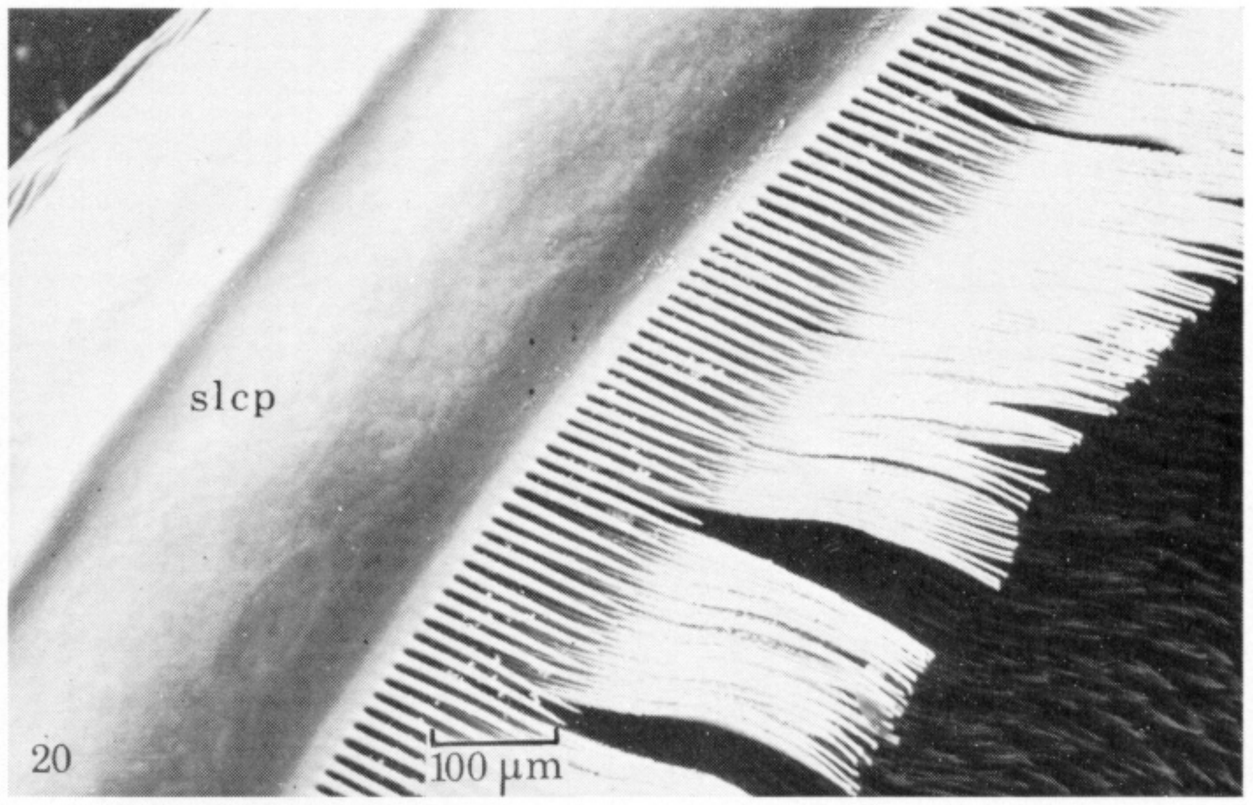
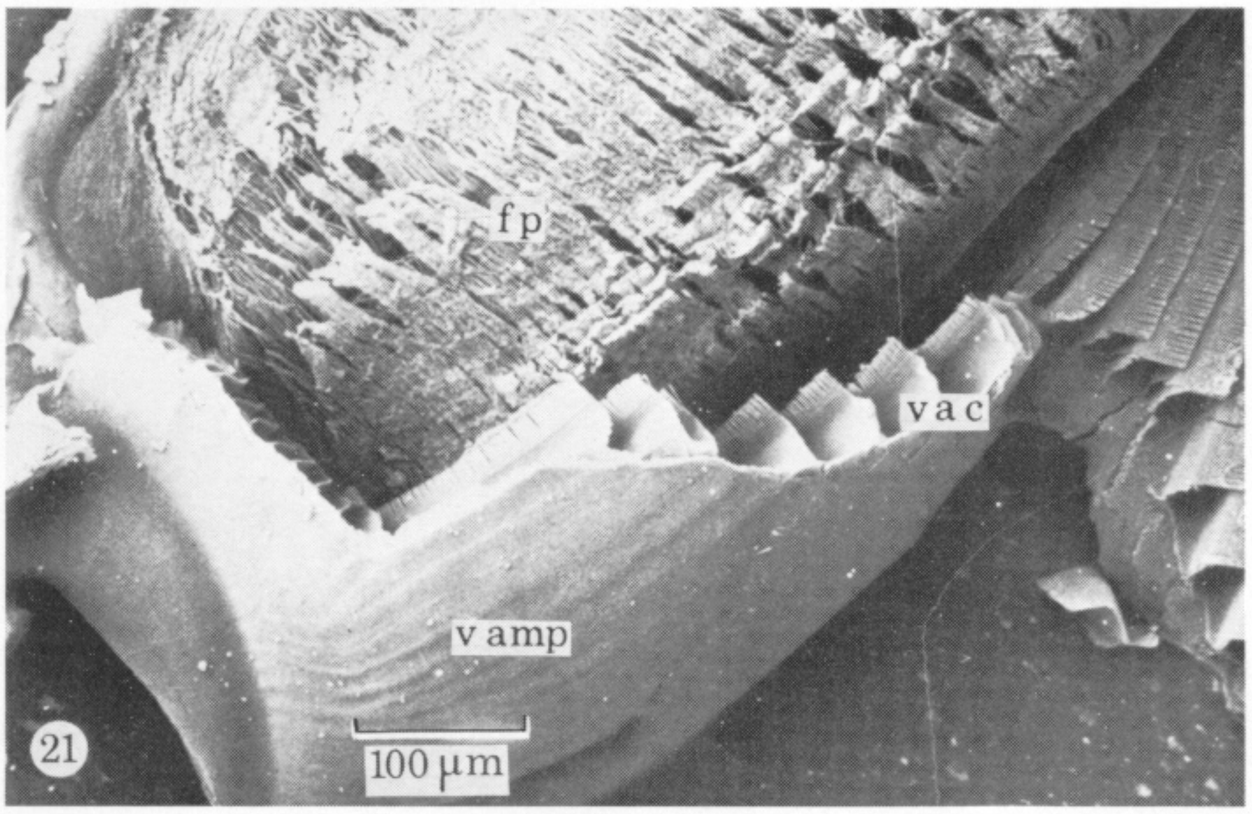
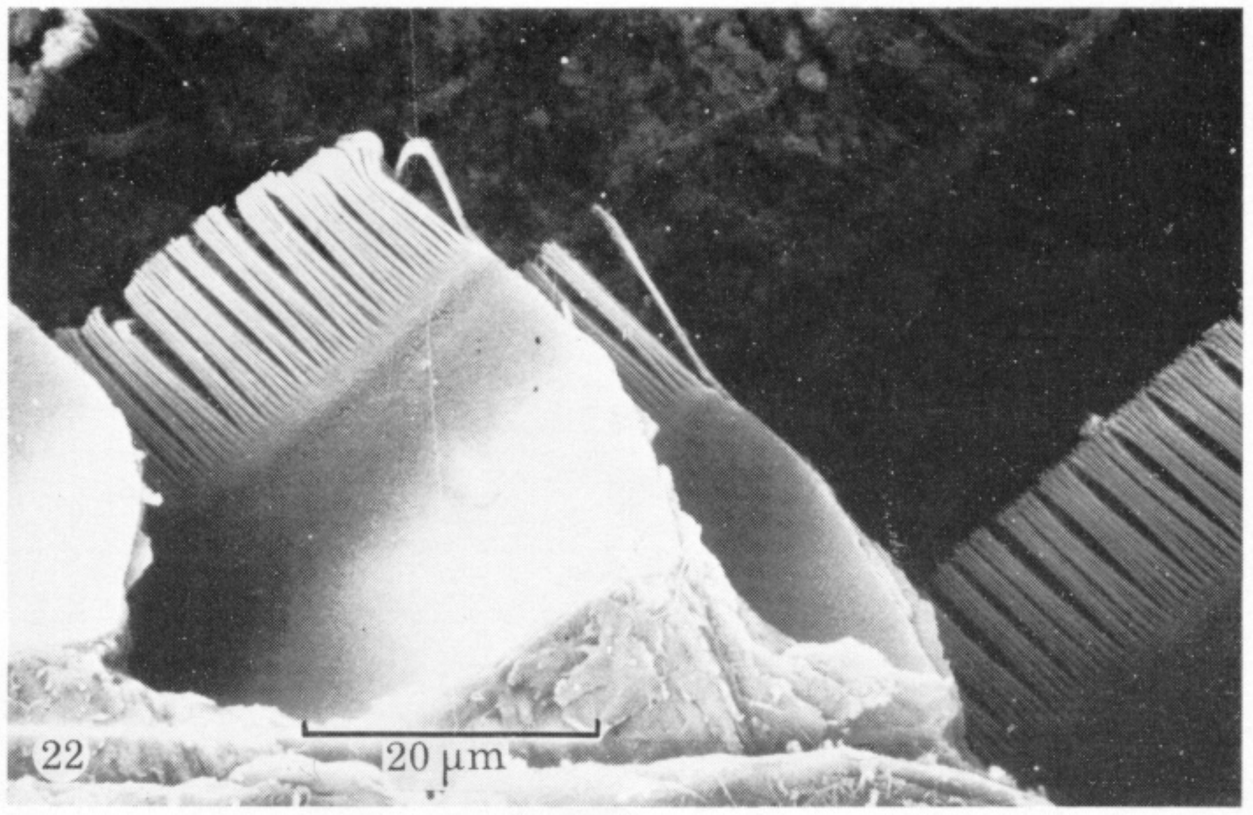
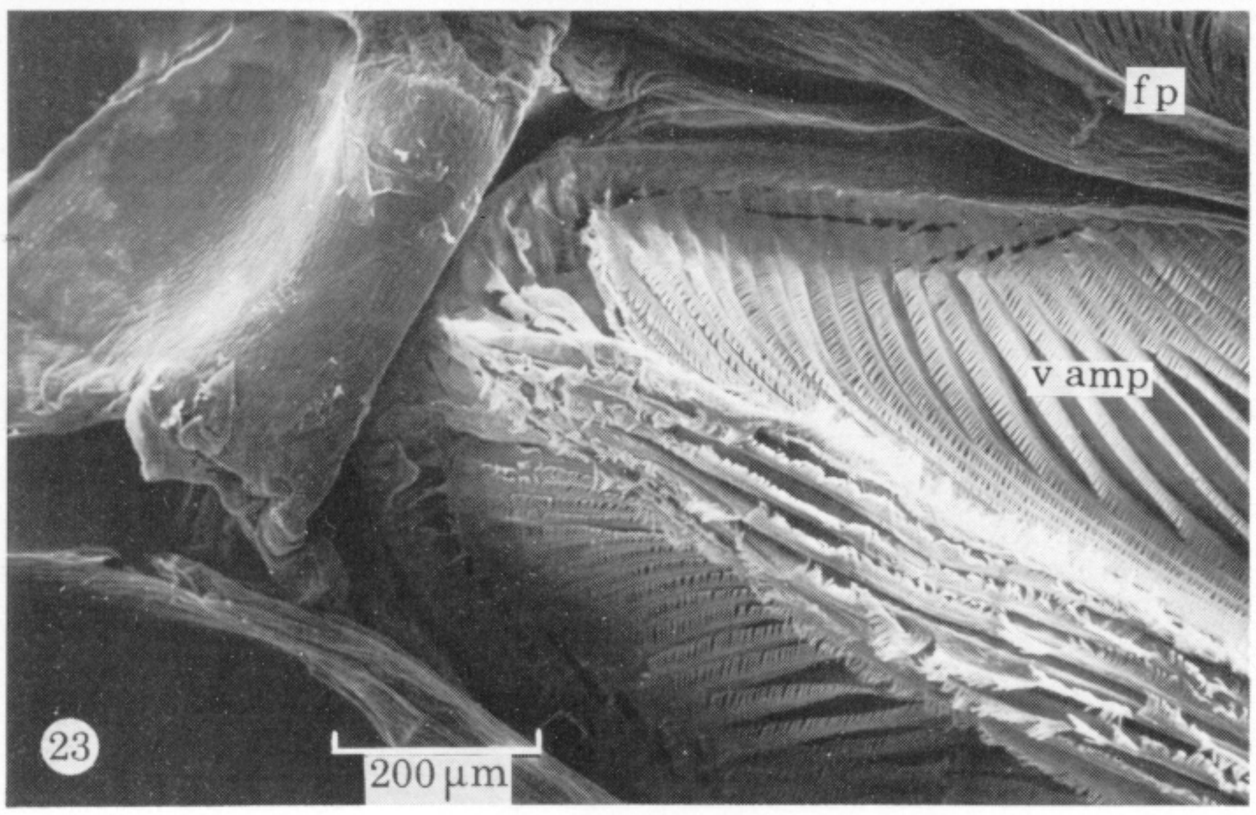
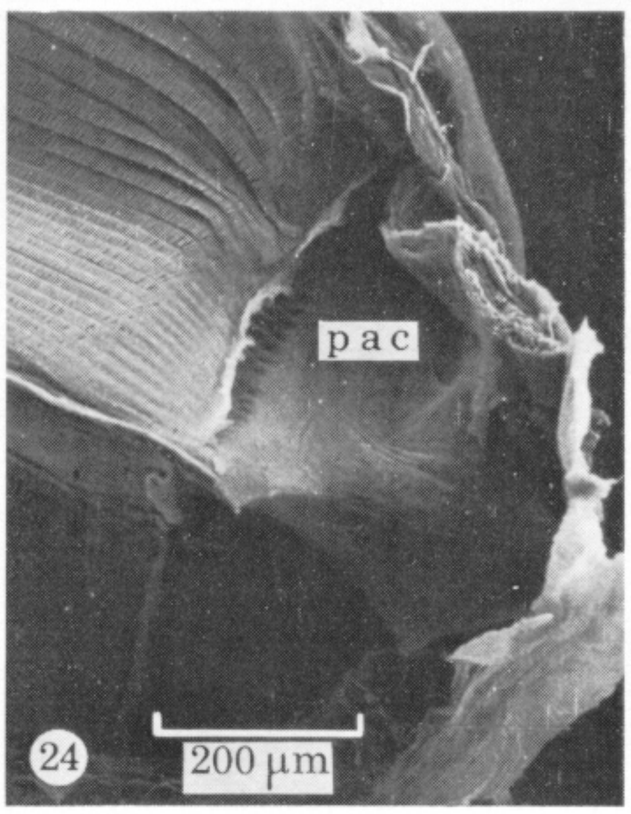












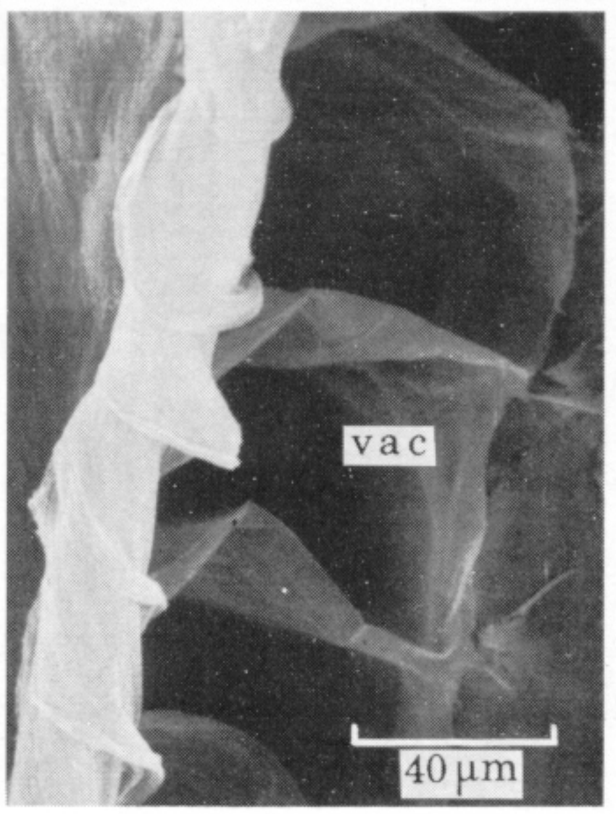


FIGURE 19. Scanning electron micrograph (s.e.m.) of the anterior surface of the posterior cardiac plate of *H. stephensoni* showing: the surface texture of the median cardiac plate ossicle (m c p), the mat of setae underlying the superior lateral cardiac plate ossicle (s l c p), and the setae of the superior lateral cardiac plate ossicle (left).

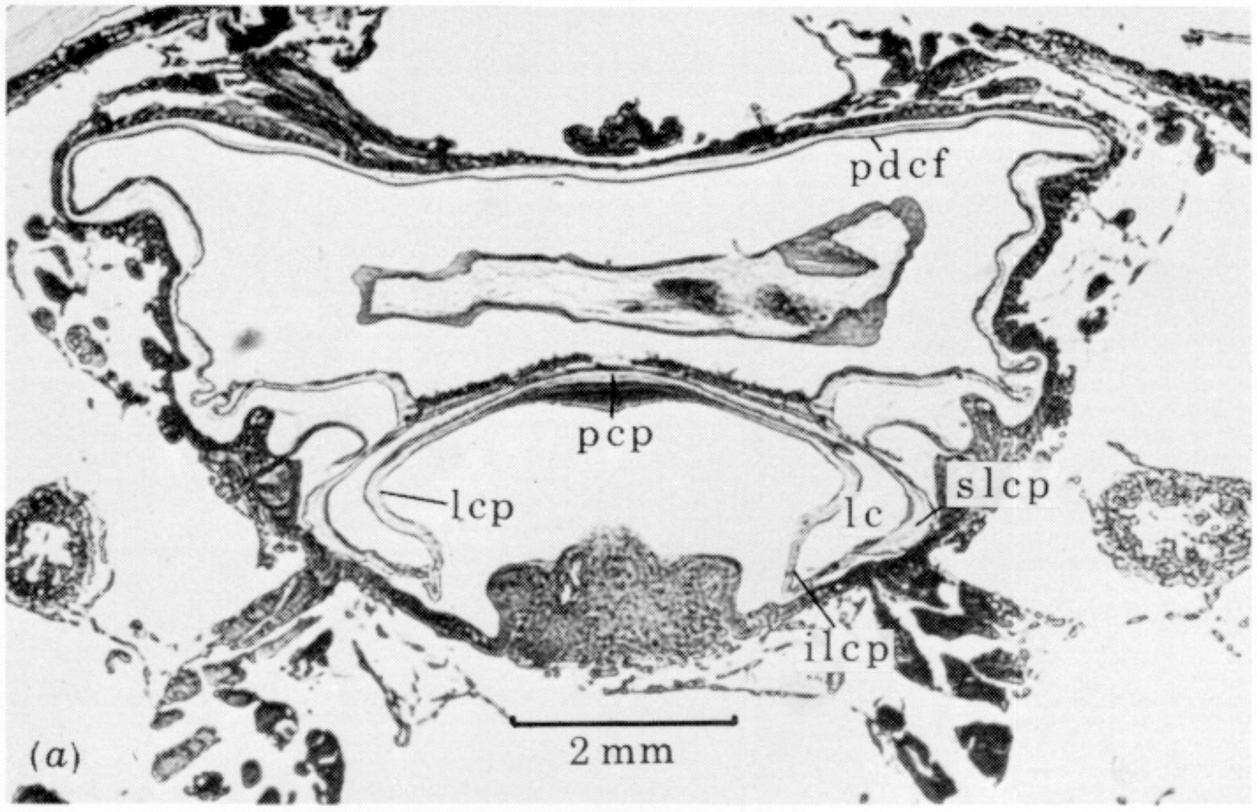
FIGURE 20. *O. nepa*: s.e.m. of the two setal layers extending from the superior lateral cardiac plate ossicle (s l c p) and overlying the lateral channels of the posterior cardiac plate.

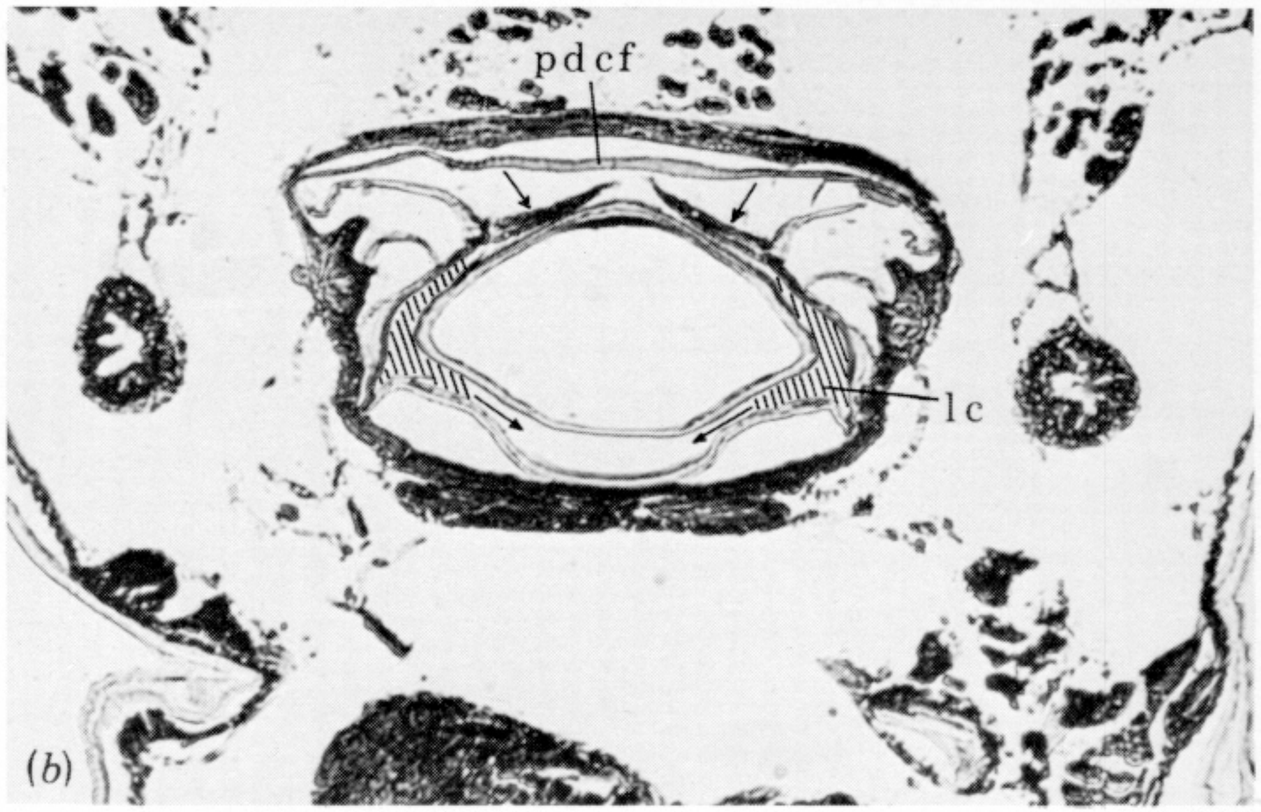
FIGURE 21. *A. laevis*: lateral view of the posterior half of the ampullae, with part of the ventral ampullary ossicle (v amp) removed to expose the filter press (f p) and ventral ampullary channels (v a c).

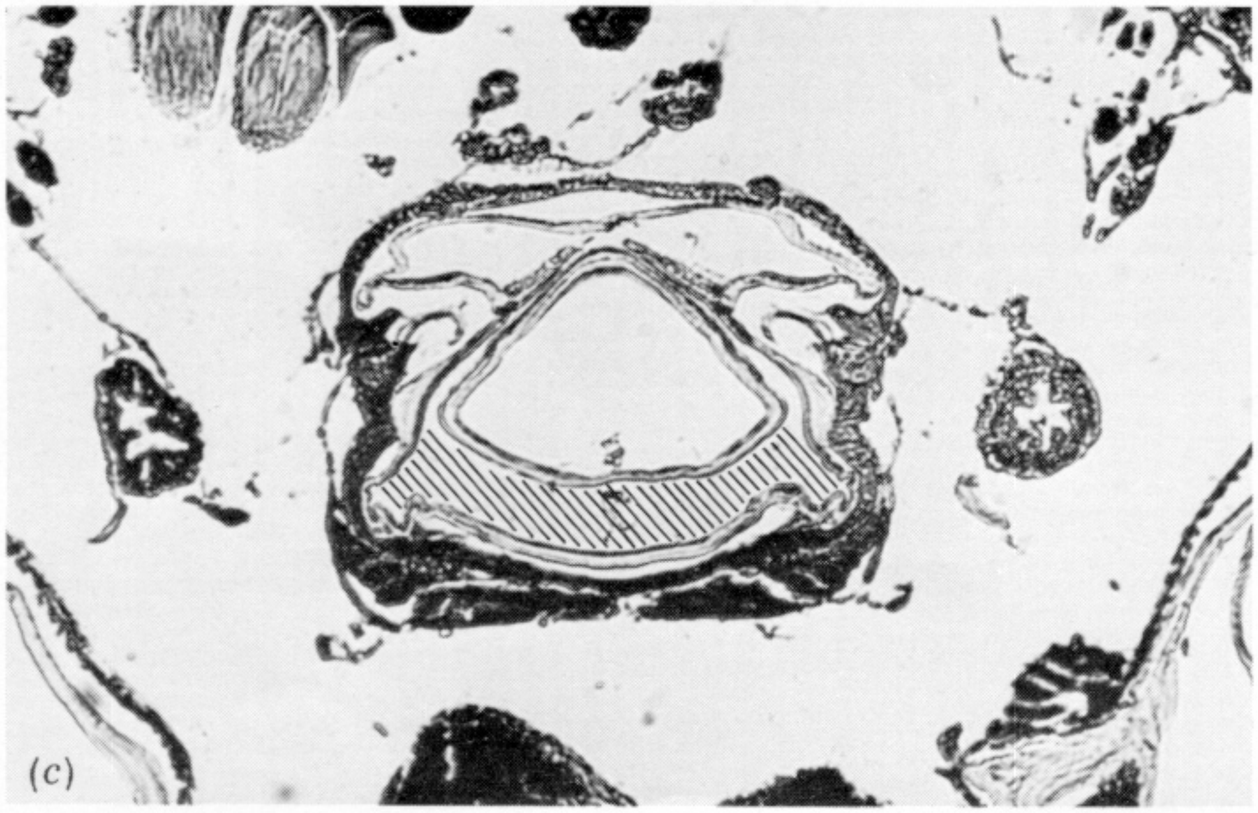
FIGURE 22. The ventral ampullary channels of *A. laevis* under high magnification, showing the setae overlying the channels formed between the horizontal ridges of the ventral ampullary ossicle.

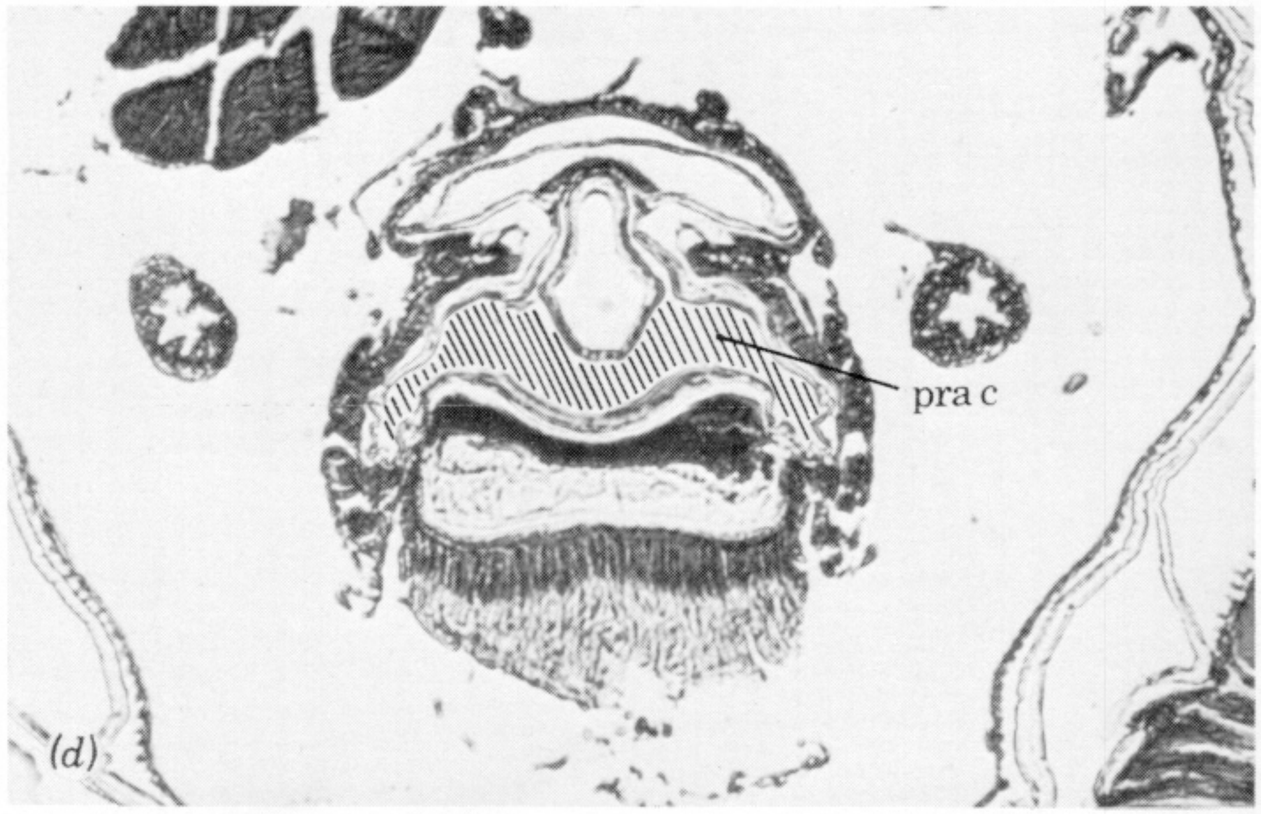
FIGURE 23. *G. graphurus*: dorsal view of the anterior region of the ampullae with the filter presses (f p) splayed to expose the channels of the ventral ampullary ossicle (v amp).

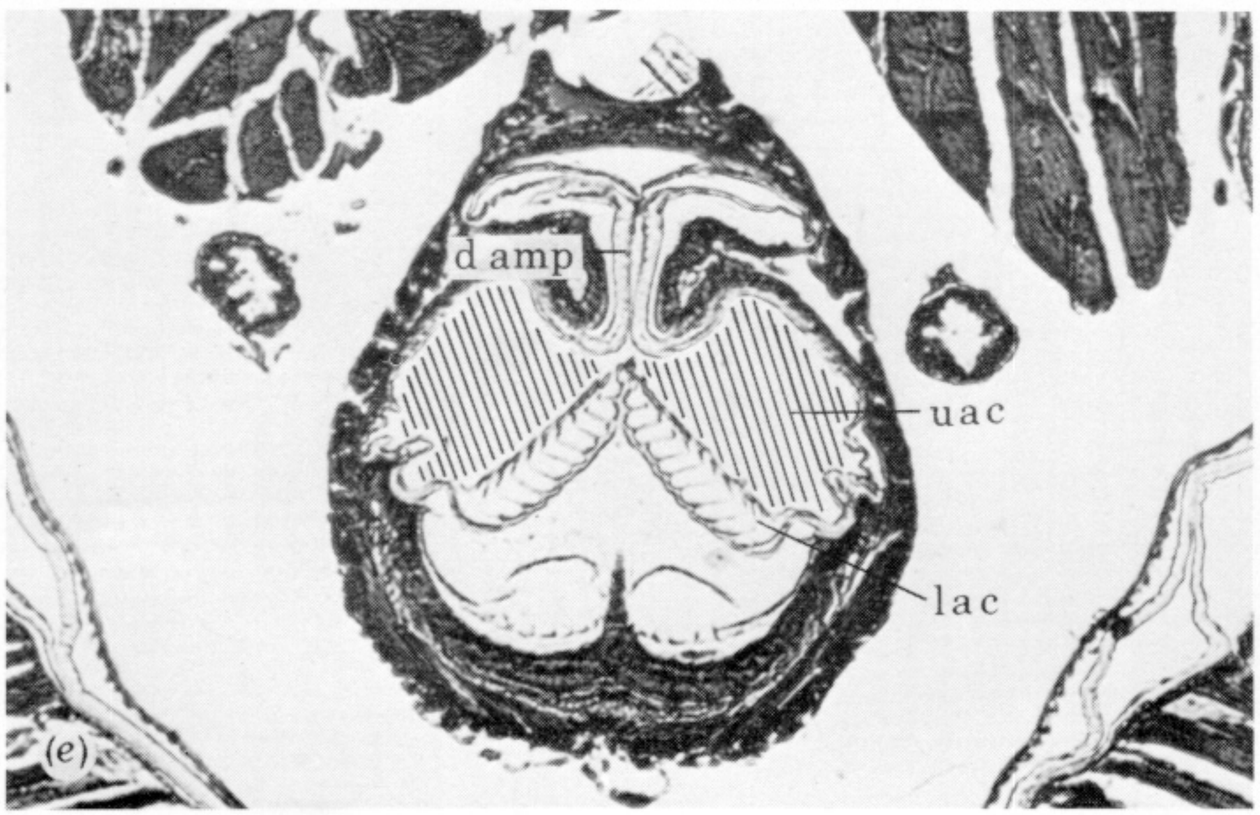
FIGURE 24. *G. graphurus*: dorsal view of the posterior region of the ampullae, showing the entrances to the ventral ampullary channels (v a c) from the post-ampullary chamber (pa c).











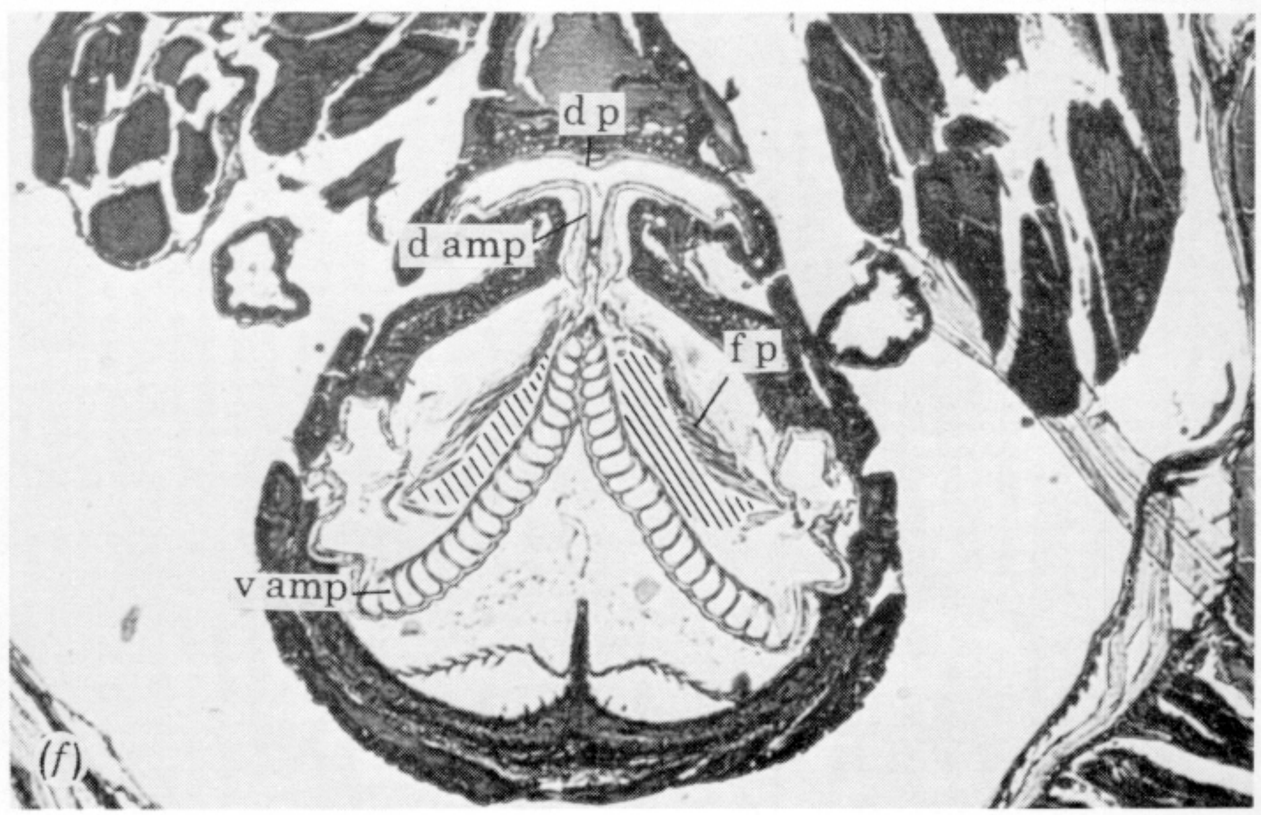
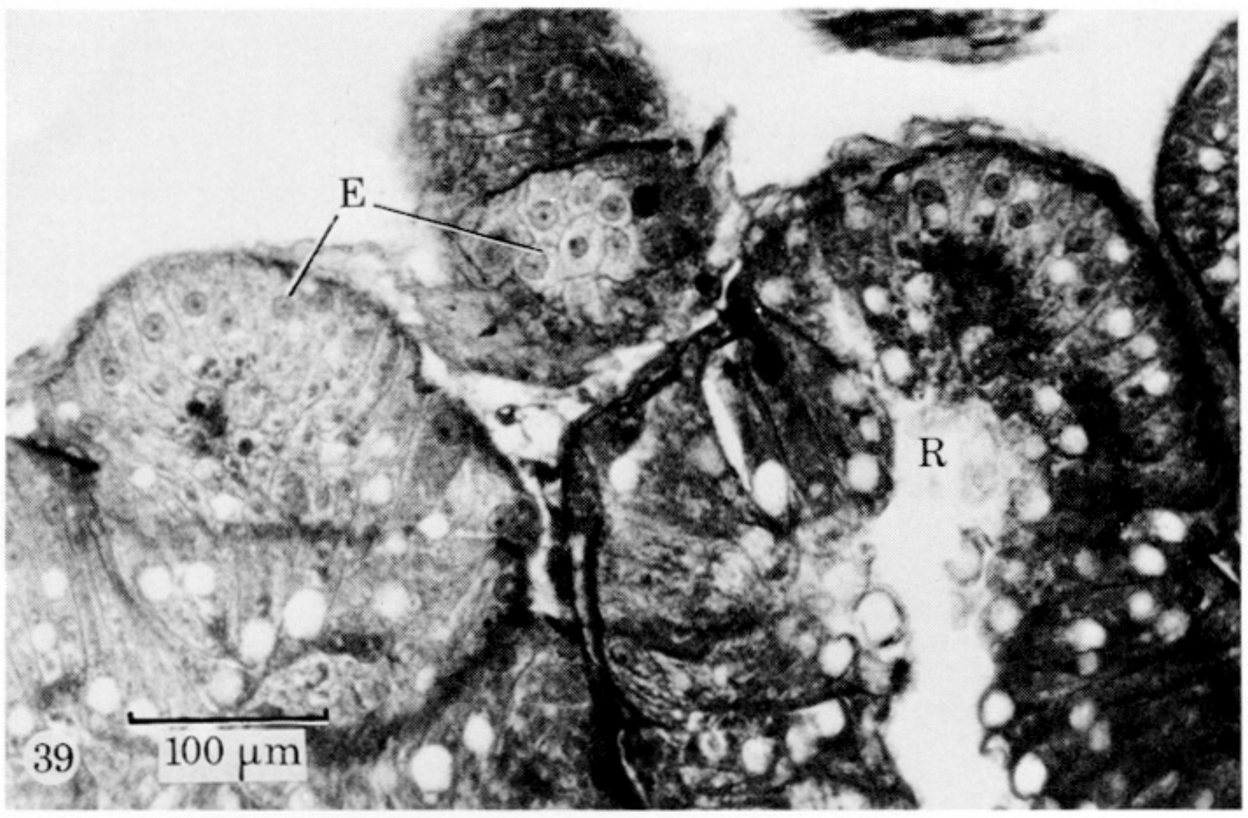
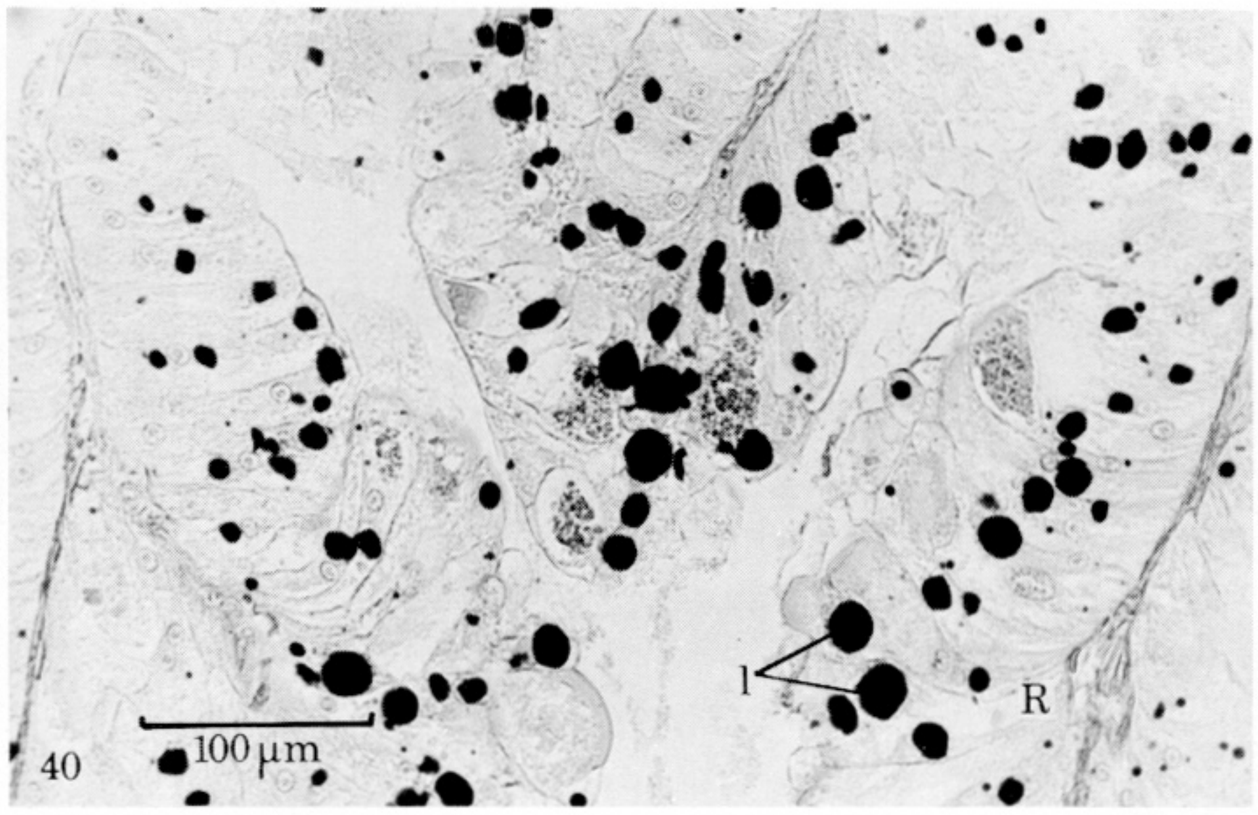
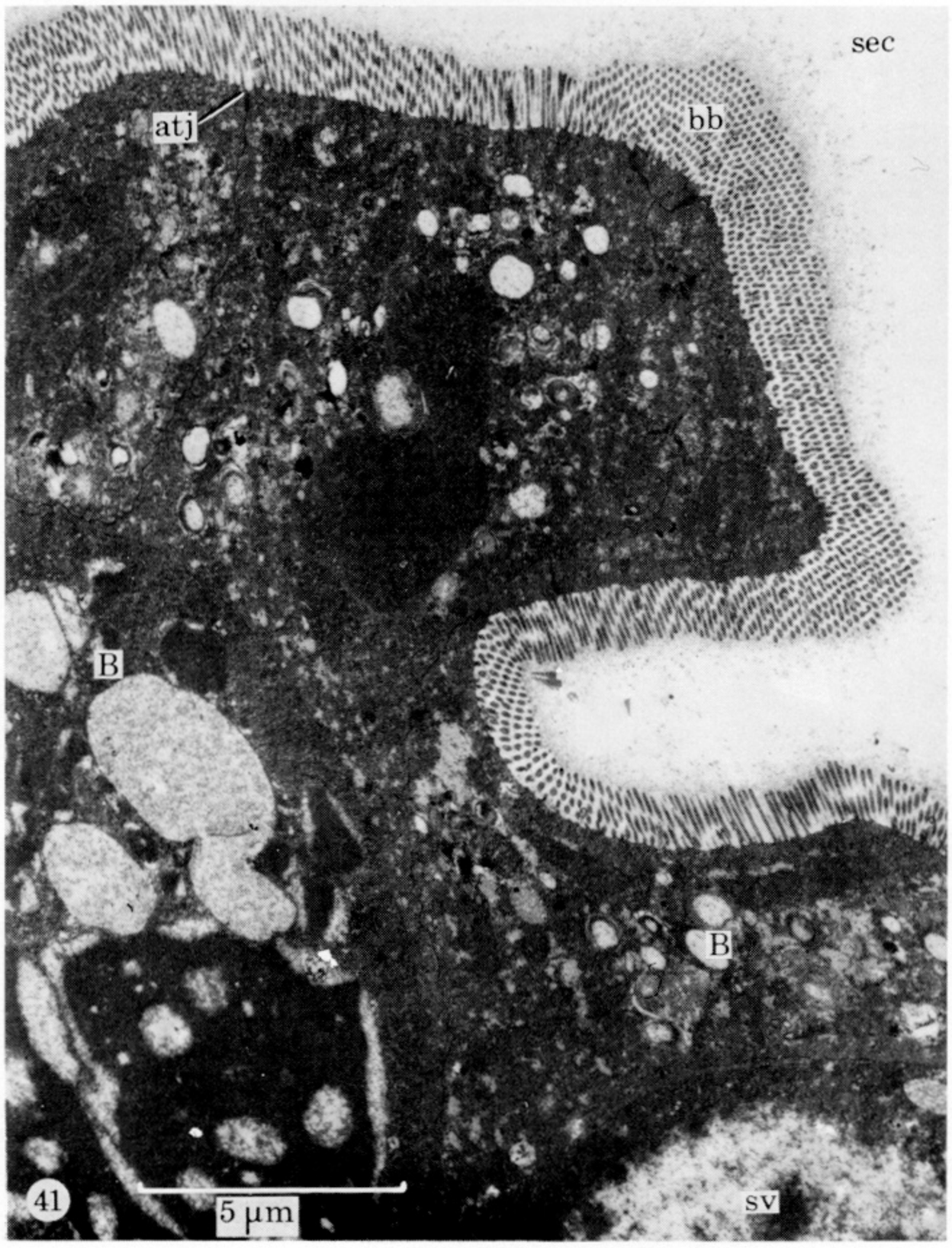


FIGURE 28. Transverse sections of the posterior cardiac plate and ampullae, showing the passage of macerated food material from the lateral channels of the posterior cardiac plate into the ampullae (macerated food is represented by cross hatching).







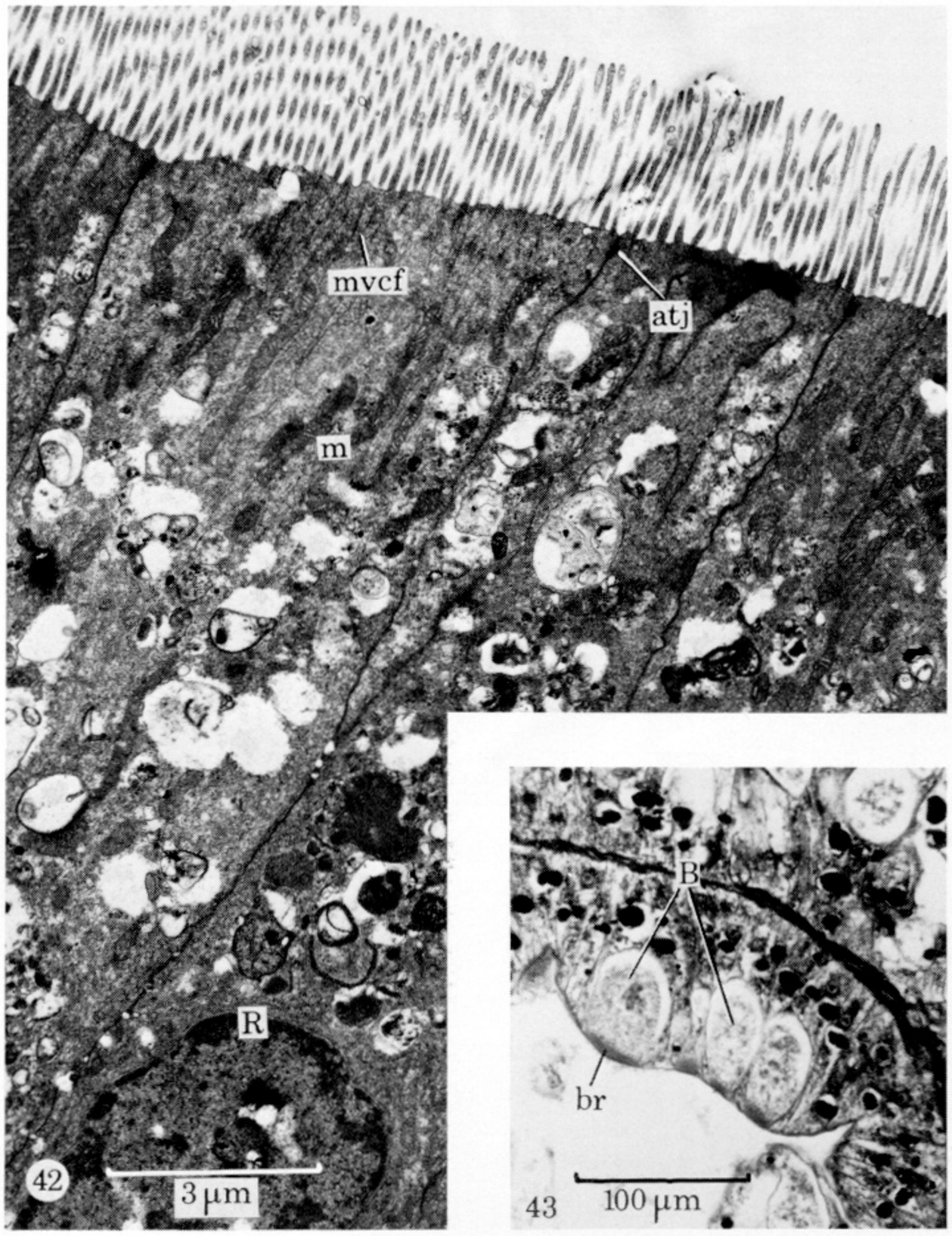


FIGURE 39. Transverse section of the digestive gland of *A. laevis* (azan-stained), showing aggregations of E-cells in the distal parts of the gland and also adjacent to R-cells.

FIGURE 40. Transverse section of the digestive gland of *A. laevis* (unstained, Flemmings-fixed), showing the localization of osmiophilic lipids (l) in the R-cells.

FIGURE 41. *A. laevis*: transmission electron micrograph of a transverse section of the digestive gland, showing developing R- and B-cells. On the surfaces of the brush borders (b b) of both cell-types is a prominent surface enteric coat (s e c). Apical tight junctions (a t j) and an absence of organelles in the apical zone are characteristic of resorptive cells. The secretory vacuoles (s v) of the B-cells are in different stages of maturation; the secretory vacuole on the lower right containing fine granular and densely clumped material is almost ripe.

FIGURE 42. *A. laevis*: transmission electron micrograph of a transverse section of the digestive gland, showing developing R-cells. Immediately below the brush border is the apical zone, devoid of organelles and striated in appearance due to the extension into the cells of microvillar core filaments (m v c f). Apical tight junctions (a t j) are prominent and also the numerous mitochondria (m) lying below the apical zone, oriented with their long axis towards the lumen. Numerous membrane-bound granules and small lipid droplets fill the supranuclear cytoplasm.

FIGURE 43. Transverse section of the digestive gland of *A. laevis* (Flemmings-fixed, azan-stained), showing mature B-cells. Note the basophilic region (b r) that borders the luminal surfaces of the ripe secretory vacuoles.