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Functional Morphology of the Mouthparts and Gastric Mill in *Penaeus plebejus* Hess (Decapoda: Penaeidea)

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Abstract

P. plebejus is both a macrophage and a detritivore. Mouthpart structure of adult *P. plebejus* is similar to that of other macrophagous decapods, but the proventriculus is less calcified than in reptant decapods and the triturative surfaces of the gastric mill are small. These features have led previous authors to postulate that maceration of large food by penaeids occurs mainly at the mouthparts. In *P. plebejus*, the mouthparts function as in macrophagous reptant decapods, the food being torn between the mandibles and third maxillipeds and swallowed with little maceration. The proventriculus exhibits a rhythmic macerating action in which shell fragments and sand ingested with the diet play a part. The proventriculus of *P. plebejus* is functionally analogous to a gizzard.

Introduction

The relationship of diet with the functional morphology of the mouthparts and proventriculus has been established for many reptant decapods (Schaefer 1970; Caine 1975*b*; Hinton and Corey 1979; Kunze and Anderson 1979; Suthers and Anderson 1981). In general, macrophagy has been associated with both robust mouthparts and a well-calcified foregut, and reduced development of these structures has been established for detritivory (Caine 1975*a*; Coombs and Allen 1978; Kunze and Anderson 1979).

However, for some natant decapods this is not a consistent generality. Although the detritivorous diet of some penaeid shrimps has been well documented (e.g. Dall 1968; Moriarty 1977), only a few authors have acknowledged the predatory and macrophagous nature of penaeids (Racek 1959; Marte 1980). The ossicles of the proventriculus are not well calcified, in contrast to the more robust mouthparts, leading some workers to suggest that most of the mastication may occur at the mouthparts (Patwardhan 1935; Meiss and Norman 1977). Mouthpart function has not been included in their discussion, and has received only little attention (Alexander *et al.* 1980), and the function of the gastric mill has not been described in the living animal. In this account, the diet of the eastern king prawn, *Penaeus plebejus* Hess, 1865, is discussed and related to the structure of the proventriculus and the masticatory action of the mouthparts and gastric mill.

Materials and Methods

Live *P. plebejus* were purchased from the Sydney Fish Markets or caught with a drag net at Putney on the Parramatta River, N.S.W., and maintained in seawater aquaria at 21°C, salinity 34-37 (practical salinity scale) on a substrate of fine sand. The captured animals were fed on prawn and fish at intervals of 2-3 days.

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The feeding procedure was observed on approximately 12 individuals. Live specimens were starved for 48 h then held under the water with the ventral surface upwards. Movements were recorded on Ektachrome Super 8 Type G movie film with a Beaulieu camera. Observations were facilitated by vivisection of obscuring limbs. This did not appear to affect the function of the remaining limbs, as a general impression of the movements obtained before the operation was confirmed following the vivisection.

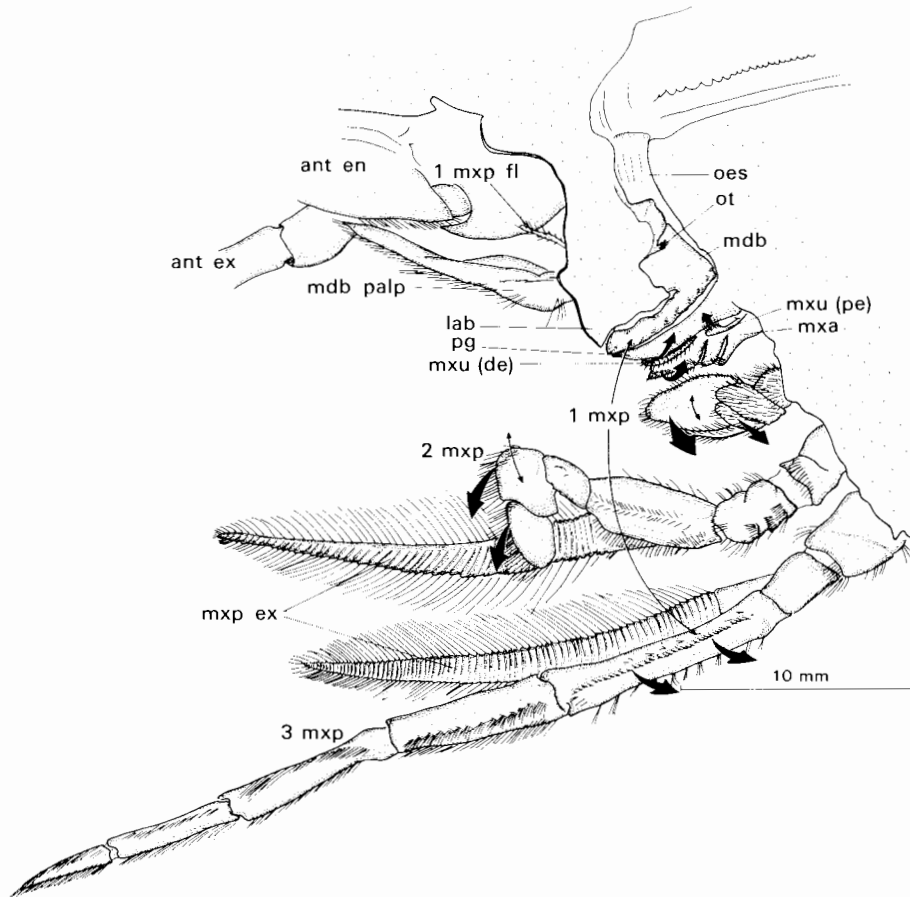


Fig. 1. *P. plebejus*: mouthparts *in situ* of the right-hand side, shown in medial section. Arrows indicate movements of mouthparts during mastication. *ant en*, antennal endopod; *ant ex*, antennal exopod; *lab*, labrum; *mdb*, mandible; *mdb palp*, mandibular palp; *mxu (pe)*, proximal endite of maxillule; *mxu (de)*, distal endite of maxillule; *oes*, oesophagus; *ot*, oesophageal tooth; *pg*, paragnath.

To describe the structure of the proventriculus, foreguts were excised from six fresh specimens of *P. plebejus* (30–50 mm carapace length), digested in 4% (w/v) KOH for 3–6 h at 55°C and stained by the Alizarin Red S method (Humason 1972), cleared in glycerine, then drawn with the aid of a camera lucida.

Dorsal views of the functioning gut through the transparent carapace of three specimens (30–40 mm carapace length) were recorded with a Sony UTU video-recorder for up to 0.5 h each, using unrestrained animals fed on prawn flesh stained with a vegetable dye. With this technique, the dorsal ossicles of the gastric mill could be clearly seen, moving in the living animal. Two samples from Sydney Harbour ($n = 10$) and one from Tweed Heads ($n = 10$), N.S.W. were also obtained for an examination of gut contents.

Results

Mouthpart Structure and Function

Penaeid mouthpart structure was described by Young (1959) and Tirmizi and Khan (1970), and the setal types of the maxillipeds have been discussed by Alexander *et al.* (1980). Structurally, the mouthparts of *P. plebejus* are generally similar to those of other decapods except for the maxilliped exopods and mandibular palps (Fig. 1).

The coordinated functioning of the mouthparts was observed as follows. When feeding on large food items, the three anterior pairs of pereopods wrap around the food item in a basket fashion, pushing it up against the mandibles. These limbs are chelate and play a part in cutting, sorting and manipulating the food ventrally, while it is held by the three maxillipeds. The crista dentata of the third maxillipeds grip the food, while more distally the carpus angles ventrally, with the dactyl and propodus being folded laterally across the food. With the proximal portion of the food clamped between the mandibles, the food is torn apart by the third maxillipeds pushing out anteroventrally (Fig. 1). The feeding pereopods do not assist with this action and starved prawns with the third maxillipeds removed appear incapable of masticating and ingesting large food items. The second maxillipeds, often by alternate strokes, lacerate the food and are also involved in either pulling it to the mandibles or bracing the food against the third maxillipeds. The first maxilliped endites crush and lacerate the food string as it passes to the maxillae.

The maxillae assist in manipulating the food, drawing it towards the mandibles between cutting strokes in a characteristic, vigorous threshing motion by alternate brushing strokes. The proximal endite of the maxillule extends between the paragnaths (Fig. 1) and presumably helps to push food anteriorly and dorsally. The paragnaths probably function as lips in preventing food from escaping from between the mandibles. Behind the incisor blades of the mandibles, the food is crushed and softened by the broad molar processes. The oesophageal tooth, supported by the labrum, intrudes between the molar processes. This tooth presumably helps push food up into the oesophagus by the dorsoventral movements of the labrum.

Despite the pronounced tearing action between the mandibles and third maxillipeds, prawn flesh is usually ingested as a continuous 'string' up to 3 cm long that can be pulled away intact from the mouthparts and out of the oesophagus. The gut contents of animals obtained in the field also included these strips of flesh and thus the food that enters the gut is often not particularly well masticated. The exopods of the third and second maxillipeds extend out laterally and are situated away from the feeding and respiratory area. During feeding, they are almost stationary, twitching occasionally with the motion of the endopods. The function of these structures is unclear.

Structure and Function of the Proventriculus

The structure of the proventriculus (Fig. 2) is consistent with the description by Meiss and Norman (1977) for *Penaeus duorarum* and *P. aztecus*, with some deviations in interpretation. According to the classification of Maynard and Dando (1974), there are 33 proventricular ossicles in most of the Reptantia. Meiss and Norman (1977) state that there are only 14 ossicles in the genus *Penaeus*, but actually describe 16. Delineation of the ossicles is difficult in penaeids because homologies with those of reptant decapods are not always apparent (e.g. in the ventral portion of the proventriculus) and regions of chitin become more calcified in large specimens.

Based on the six specimens studied, the proventriculus of *P. plebejus* was found to have 19 ossicles. The supralateral teeth (Fig. 2) may be considered as an anterior projection of the zygocardiac ossicle and not as part of the posterior lateral cardiac plate, as this plate is homologous with a strip of calcified chitin between the upper and lower cardiac grooves. Bounded by the two lower cardiac grooves is a setose, posteriorly pointing spear-shaped surface, the hastate plate (Tirmizi and Khan 1970). The posterior supra-ampullary ossicle

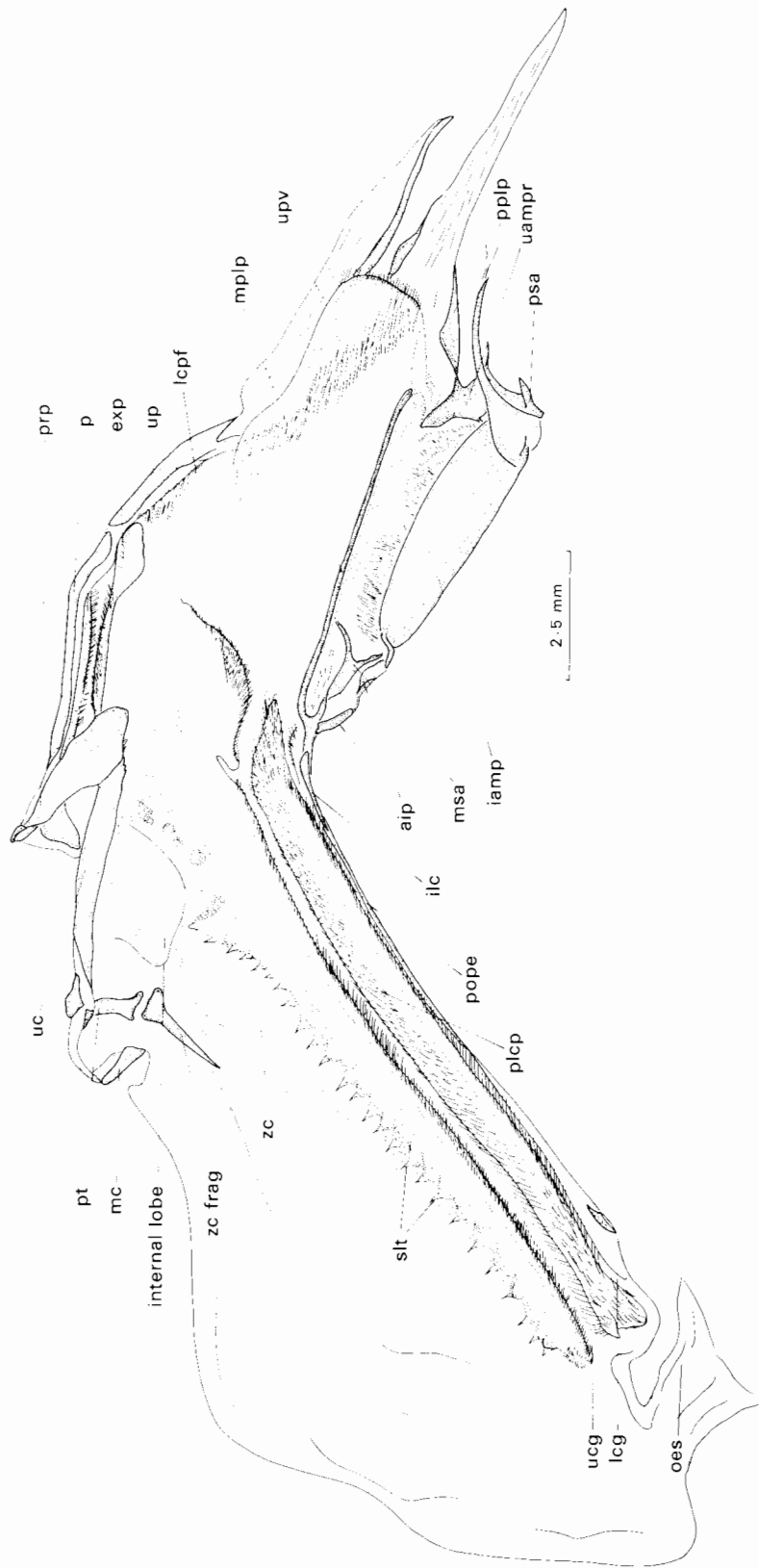


Fig. 2. Proventriculus of *P. plebejus*; internal lateral view. Abbreviation of ossicles: *aip*, anterior inferior pyloric; *exp*, exopyloric; *iamp*, inferior ampullary; *ilc*, inferolateral cardiac; *lcg*, lower cardiac groove; *lcpf*, lower cardiac fold; *mc*, mesocardiac; *mplp*, middle supra-ampullary; *msa*, middle supra-ampullary; *oes*, oesophagus; *p*, pyloric; *plcp*, posterior lateral cardiac plate; *pope*, posterior lateral cardiac plate; *prp*, posterior supra-ampullary; *pt*, pterocardiac; *slt*, supralateral teeth; *uampr*, upper ampullary roof ossicle; *uc*, urocardiac; *ucg*, upper cardiac groove; *up*, urocardiac groove; *upv*, urocardiac valve; *zc*, zygocardiac; *zc frag*, zygocardiac fragment.

is composed of a dorsoposterior projection, the posterior pleuropyloric, a dorso-anterior projection, the upper ampullary roof ossicle (which is also fused to the posterior supra-ampullary ossicle in the Reptantia), and a ventral bar joining both posterior supra-ampullary ossicles, the posterior inferior ossicle.

The working gastric mill of *P. plebejus* is characterized by a violent, pumping action, which is more vigorous when the proventriculus is partially empty. The simpler gastric mill action of a full gut will be described first.

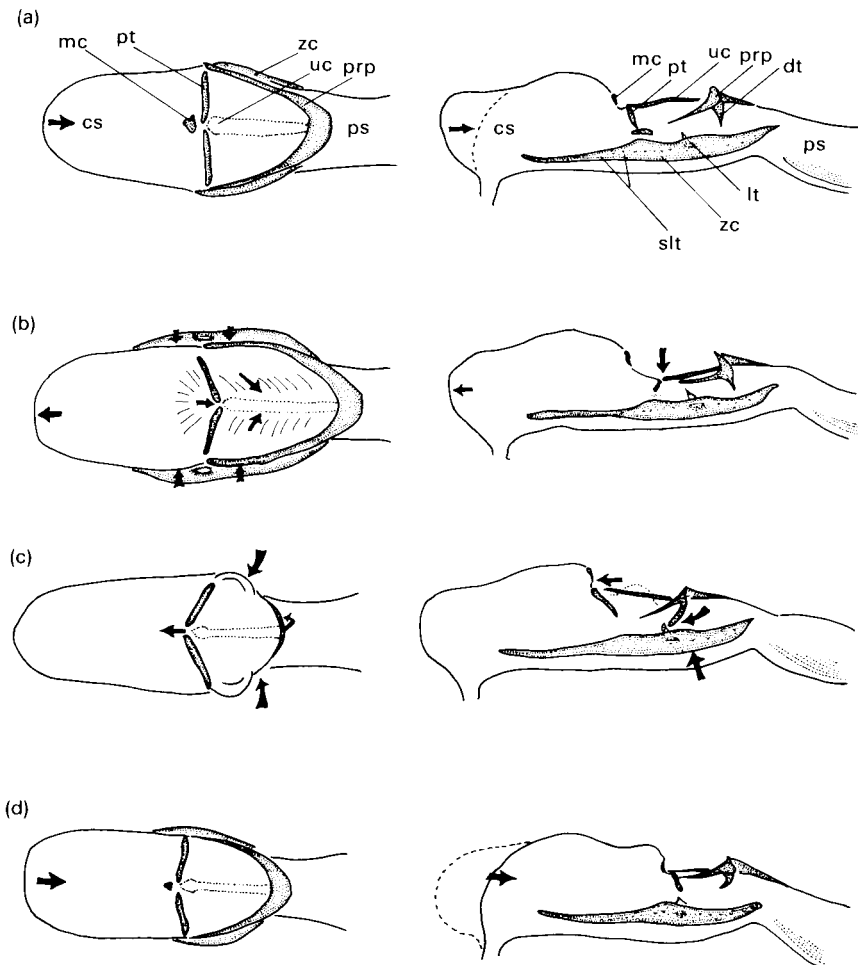


Fig. 3. *P. plebejus*: sequence of movements (a-d) in a single cycle of the gastric mill. Left, dorsal view; right, internal lateral view (diagrammatic). See text for details. *cs*, cardiac stomach; *dt*, dorsal tooth; *lt*, lateral tooth; *mc*, mesocardiac ossicle; *prp*, propyloric ossicle; *ps*, pyloric stomach; *pt*, pterocardiac ossicle; *slt*, supralateral teeth; *uc*, urocardiac ossicle; *zc*, zygocardiac ossicle.

The net result of the various proventricular contractions is to push the food posteriorly into the gastric mill, and then to squeeze the resulting slurry ventrally into the grooves either side of the hastate plate. This is accomplished initially by the posterior contraction of the bulging anterior face to the cardiac stomach (Fig. 3a). The pterocardiac ossicles and the associated urocardiac ossicle then rapidly push down ventrally, packing the food

between the lateral teeth and onto the floor of the cardiac stomach (Fig. 3*b*). Typically there are two to three of these contractions, each interspersed by the posterior contraction of the anterior face. In one swift, smooth motion, the lateral teeth then draw rapidly inwards, followed by the dorsal tooth swinging anteroventrally (Fig. 3*c*). The urocardiac ossicle, attached to the dorsal tooth, consequently moves anteriorly, forming an arrowhead with the pterocardiac ossicles. This grinding contraction is relaxed and followed by the anterior face compaction leading to the next series of ventral compressions (Fig. 3*d*). The entire cycle takes about 4–5 s to complete.

If the gut is partially empty, the compression of the anterior face (Fig. 3*a*) is supplemented by a medial movement by both rows of supralateral teeth and a ventral compression of the anterior dorsal surface, thus completely collapsing the anterior portion of the cardiac stomach. Consequently, the proventriculus has a vigorous, end-to-end, pump-like motion. The use of this action has also been observed in drawing up food from the oesophagus and posteriorly towards the gastric mill. The broad, shovel-like dorsal tooth would enhance this action, pushing food anteriorly and grinding onto the small lateral teeth. On the recovery stroke, the dorsal tooth would presumably grind against the stub-like teeth posterior to the lateral teeth. The lateral cardiopyloric folds (Fig. 2) prevent food from being forced into the pyloric stomach. The supralateral teeth are not easily observed and their function is difficult to determine as there is no masticatory surface. The teeth may have a lacerating function or may aid in holding the food. The penaeid foregut, except ventrally over the hastate plate, is not very setose.

To complement the functional descriptions, foregut contents of 30 individuals are briefly listed here as percentage volume of each item: crustacean remains (amphipod, isopod and euphausiid exuviae and limbs) 31%, detritus 20%, bivalve fragments 19%, sand 9%, unmacerated flesh (including squid tentacles) 11%, polychaetes (*Glycera* sp.; Eunicidea) 6%, foraminifera 2%, and vegetative remains 1%. The stomach contents of the Sydney Harbour sample consisted almost entirely of one particular mysid, *Rhopalophthalmus dakini*.

Discussion

The omnivorous nature of the diet of *P. plebejus* is confirmed by this study. Most penaeids cannot be placed in a particular trophic category (Moriarty 1977). Racek (1959) noted that *P. plebejus* could capture small fish, and others (Marte 1980; Chong and Sasekumar 1981) concluded that *P. monodon* was more of a predator than a scavenger or detrital feeder, feeding on small crabs, other penaeids, molluscs and fish. Ruello (1973) and Kuttyama (1974) concluded that penaeids are both omnivorous and detritivorous. Dall (1968) argues that on a densely populated prawn ground, the proportion of larger food masses would not be sufficient to feed the entire population and that grazing on the epibenthos would appear to be the main method of feeding. Detrital feeding and digestion have not been filmed but personal observation indicates that the mouthparts function as described in this study, with rapid alternate brushing strokes of all but the mandibles and third maxillipeds (which scrape up material between the ischia). Detritus is swept into the oesophageal region while sand and other indigestible items fall between the slightly rubbing and sorting third maxillipeds. Presumably the proventriculus would also function similarly on both detritus and macromaterial as these items are found mixed in the foregut. Furthermore, the large amount of grit in the diet could not be accidental with the sorting action of mouthparts. This lack of mastication by the mouthparts and the large proportion of sand and bivalve fragments shown in this study are important factors to be considered in the context of gut function.

The mouthpart structure of *P. plebejus*, including the setation of the maxillipeds, displays a similarity with other macrophagous decapods except that stout serrate setae are not apparent, although they are generally present on the third maxilliped of reptant decapods

(Farmer 1974; Kunze and Anderson 1979). The maxilliped exopods and mandibular palps, which are not involved in mastication, reflect the different respiratory, chemosensory or feeding-current adaptations throughout the Decapoda. However, the broad ischium of the third maxilliped in brachyurous forms functions almost identically to that of *P. plebejus*, as do the manipulative carpus, propodus and dactyl. The second maxillipeds and maxillules show little variation in the Decapoda, whereas the first maxilliped shows respiratory adaptations in macrurous decapods, but the masticatory surfaces (the proximal and distal endites) are similar.

The characteristic, well-coordinated tearing action between the third maxillipeds and mandibles has been described in other penaeids (Dall 1967, 1968; Ruello 1973; Alexander *et al.* 1980) and other macrophagous decapods (Farmer 1974; Caine 1975a, 1975b; Warner 1977; Kunze and Anderson 1979; Suthers and Anderson 1981). Such macrophagous feeding behaviour has even been described in starved hermit crabs that are naturally microphagous (Greenwood 1972). Yet the decapod proventriculus displays a general gradation of increasing complexity in the size, shape and number of ossicles from the Penaeidea to the Brachyura—documented by Reddy (1935), Meiss and Norman (1977) and others. The mortar and pestle action of the gastric mill typical of many decapods (e.g. Schaefer 1970; Caine 1975b; Kunze and Anderson 1979) is not universal, as shown by direct observation of the gastric mill function (Powell 1974; Suthers and Anderson 1981; this study). The grinding surfaces of the lateral teeth in *P. plebejus* are small and trituration is feasible only because of the large amount of sand and shell fragments in the diet, along with gastric juices and the motion of the cardiac stomach. The macerating action is similar to that of a gizzard, as suggested by Dall (1967) for penaeids and by Coombs and Allen (1978) for the carid *Hippolyte varians*. Such a mechanism is capable of digesting large fleshy pieces, contrary to the view of Meiss and Norman (1977) and others that mastication in penaeids occurs at the level of the mandibles rather than at the gastric mill. The relationship of an omnivorous diet to the robust mouthparts and more moderate gastric mill is comprehensible within this functional context.

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