Description and comparison of major foregut ossicles in hydrothermal vent crabs

Abstract  Major foregut (gastric mill) ossicles, including the dorsal median tooth, lateral teeth, accessory lateral teeth, and cardiopyloric valve, of hydrothermal vent crabs were dissected and examined during the summer of 1996 from specimens housed at the Natural History Museum of Los Angeles County. Ossicles are described for two species of hydrothermal vent crabs (family Bythograeidae Williams, 1980). The western Pacific Austinograea williamsi Hessler and Martin has an unusual dorsal median tooth. The surrounding cuticular flange is scalloped and bears spinulose setae at the tip of each of the protruding edges, a condition perhaps unique in the Brachyura. The lateral teeth are mostly unremarkable, bearing the typical large anterior denticles and deep serrations seen in other crab families, but with a higher number of serrations than is known for any species previously described. The accessory lateral teeth bear flattened, plate-like spines that are widest basally and that taper to a cylindrical tip. The basic armature of the foregut of Bythograea thermydron Williams, known only from vents in the eastern Pacific, is very similar. Scalloping of the median tooth borders is less pronounced, however, and the shape of the tooth itself and of the plate from which it arises is slightly different. The lateral teeth bear fewer and more widely spaced grooves, and the cardiopyloric valve entrance appears less setose at its extremity. Comparison with foregut ossicles in other crab families based on earlier studies, most of which have not employed SEM, reveals some similarities between bythograeids and some xanthids, but does not clarify the phylogenetic position of the bythograeids. Because of the paucity of other SEM studies of the brachyuran foregut, it is difficult to ascertain whether some of the many spine and setal types in the bythograeid foregut are unique or even unusual compared to those of other crab families. Nothing about the foregut of the vent crabs is indicative of their unusual habitat. Anecdotal observations of feeding in vent crabs indicate that they are opportunistic scavengers and omnivores, which is in keeping with the non-specialized nature of the foregut. The debate between adaptation vs phylogeny as determinants of the form of the gastric mill components is briefly discussed.

Introduction

Hydrothermal vent crabs constitute a unique family of the Brachyura (Williams 1980), the Bythograeidae, about which relatively little is known. Concerning morphology, our knowledge to date comes almost exclusively from studies on external features, usually in a taxonomic framework (e.g. Williams 1980, 1988; de Saint Laurent 1984, 1988; Guinot 1988, 1989, 1990; Hessler and Martin 1989). As far as internal morphology is concerned, we are aware of only one previous study, that of Secretan and Guinot (1988) on the axial skeleton of the Pacific Cyanograea praedator de Saint Laurent. This paucity of information is somewhat surprising in the light of the fact that (1) phylogenetic information often can be gleaned by study of the internal stomach (foregut) ossicles of decapods (e.g. see Felgenhauer and Abele 1983, 1989) and (2) the taxonomic and phylogenetic placement of these interesting crabs is not known. However, it is understandable when one realizes how difficult to capture and relatively rare these vent crabs are. We welcomed the opportunity to remove and dissect the stomach from some hydrothermal vent crabs in a preliminary effort to describe in detail the four most common brachyuran foregut ossicles. Although the brachyuran foregut contains an extremely complex array of ossicles, membranes, and
associated setae and musculature (e.g. see Maynard and Dando 1974), it is unclear to what extent these structures are homologous among the many extant crab families, other than the four rather large and universally found ossicles that form the basis of this report.

Materials and methods

Four adult specimens of *Austenograea williamsi* Hessler and Martin were borrowed from G. Somero, Hopkins Marine Station, Pacific Grove, California, who had previously removed the appendages for physiological work. These crabs ranged in size from 20.8 to 28.1 mm carapace width and from 14.8 to 20.8 mm carapace length. All were females. Identification to species is certain, as this is the only crab species known that completely lacks eyestalks, and because these specimens were collected with the type series from the Mariana Back-Arc Basin in the spring of 1987 (see Hessler and Martin 1989 for collection data). Stomachs were removed under a dissecting microscope, slit along the vertical surface, and flushed with 70% ethanol to remove contents. Contents were examined but, with few exceptions (see “Discussion – Feeding behavior of vent crabs”), could not be identified. Foreguts from three specimens were gradually hydrated to distilled water and sonicated briefly (10 to 15 s) in a Branson™ Model 1200 ultrasonic cleaner. After dehydrating to pure (100%) ethyl alcohol in a series of ethanol baths, the specimens were immersed in HMDS (hexamethyldisilazane; see Nation 1983), air-dried, and mounted on stubs prior to sputter-coating with gold and viewing with a Cambridge Stereoscan 360. The foregut from the fourth and largest crab (28.1 mm carapace width) was not subjected to these SEM preparatory, but was instead used for illustrations made with a Wild M5APO dissecting stereomicroscope equipped with drawing tube.

Frozen specimens of *Bythograea thermydron* on Williams were borrowed from the Scripps Institution of Oceanography, where they were being stored for future physiological work. These samples were collected along the East Pacific Rise, although date and cruise data were lacking. Again, identification to species is certain, as the only other bythograeid known from the eastern Pacific is the considerably larger and morphologically distinctive species *Cyanoograea praedator* (see Hessler and Martin 1989).

For comparison with other brachyuran families, we used the foregut of a small local (California) grass crab, *Pachygrapsus crassipes*, of comparable size (carapace width 23.2 mm, carapace length 20.8 mm) collected from Redondo Beach, California (see Fig. 6). The remains of the vent crabs (adult body, minus the stomach and all appendages) were deposited in the Natural History Museum of Los Angeles County.

Results

General shape of foregut

As in all brachyuran families studied to date (see “Discussion – Vent crab ossicles compared to those of other crabs”), the bythograeid foregut, as viewed from above, is a triangular, trapezoidal, or heart-shaped membranous sac supported by, and shaped by, cuticular components of various thickness and complexity (Fig. 1a, b). These structures are commonly called ossicles. Although various names have been applied to these ossicles, the names of the few components we have labeled seem to be widely used and accepted. Our terminology is taken mostly from the works of Mocquard (1883), Pearson (1908), Patwardan (1935a, b), Maynard and Dando (1974), Factor (1982, 1989), and Nakamura and Takemoto (1986). Viewed from above, the foregut is divided into two regions, the anterior cardiac stomach and the posterior pyloric stomach (Fig. 1b). In all brachyurans, the cardiac portion is by far the larger of the two and contains the sclerotized components that form what is referred to as the “gastric mill” (see following paragraph). The wider anterior portion is little more than a distended membranous sac, and in the vent crabs it bears, internally, two rather large infoldings of cuticle that probably serve to increase the surface area of the foregut. Running laterally across the dorsal surface of the cardiac region, and located just posterior to the cuticular infoldings, is a transverse ossicle termed the pterocardiac ossicle (Fig. 1b). From the center of this ossicle a longitudinal ossicle, the urocardiac, extends posteriorly, and as it does so it becomes hollowed out centrally and produces two small dorsal lobes. These lobes articulate with the anterior medial branch of the propyloric ossicle, which in turn is in contact with the pyloric ossicle (not visible in Fig. 1) and other ossicles, as shown in Fig. 1b and c.

Internally, although the details and overall complexity of the brachyuran stomach are far greater than the scope of our study indicates (see Maynard and Dando 1974 for a more detailed overview), there are basically four large and readily identified and homologized components of the gastric mill that are shared by all crabs studied to date (Fig. 1c): (1) a dorsal median tooth (MED) that descends from the posterior ventral (inner) terminus of the urocardiac ossicle; (2) large, paired lateral teeth (LAT), which arise from the posterior extension of the zygocardiac ossicles and which are anteriorly solid and bear few large denticles, but are serrated or grooved along the posterior half; (3) accessory lateral teeth (ALT), which are paired processes that arise from the posterior terminus of the prepectineal ossicle and are found ventral to and surrounding and cupping the lateral teeth; (4) the variously armed entrance to the cardipyloric valve (CPV), which arises from the floor of the cardiac stomach (and therefore is not visible in Fig. 1c).

The following description of these major ossicles in vent crabs is based on our observations of *Austenograea williamsi*, with comments concerning *Bythograea thermydron* added only when they differ.

Median tooth

The median tooth is smooth and nearly heart-shaped when viewed from directly below (Figs. 1c, 2b). The central portion is widest basally, where it also produces a slight anterior thickening or ridge. Surrounding the basal part of the tooth is a rather wide flange that is distinctly bilobed on its posterior edge, following the curves of the median tooth itself (Fig. 2b). The flange bears two groups of ventrally projecting setae, one on either side (more obvious in Fig. 4a, b of *Bythograea thermydron*). The sides of this basal flange are scalloped,