

J. W. Martin · P. Jourharzadeh · P. H. Fitterer

## Description and comparison of major foregut ossicles in hydrothermal vent crabs

Received: 10 December 1996 / Accepted: 13 November 1997

**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

Communicated by M.F. Strathmann, Friday Harbor

J.W. Martin (✉) · P. Jourharzadeh  
Natural History Museum of Los Angeles County,  
900 Exposition Boulevard, Los Angeles,  
California 90007, USA

P.H. Fitterer  
U. S. Department of Agriculture, 11 Golden Shore,  
Suite 460, Long Beach, California 90802, USA

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 *Austinograea 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 therymydron* 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 *Cyano-graea praedator* (see Hessler and Martin 1989).

For gross comparison with other brachyuran families, we used the foregut of a small local (California) grapsid 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.

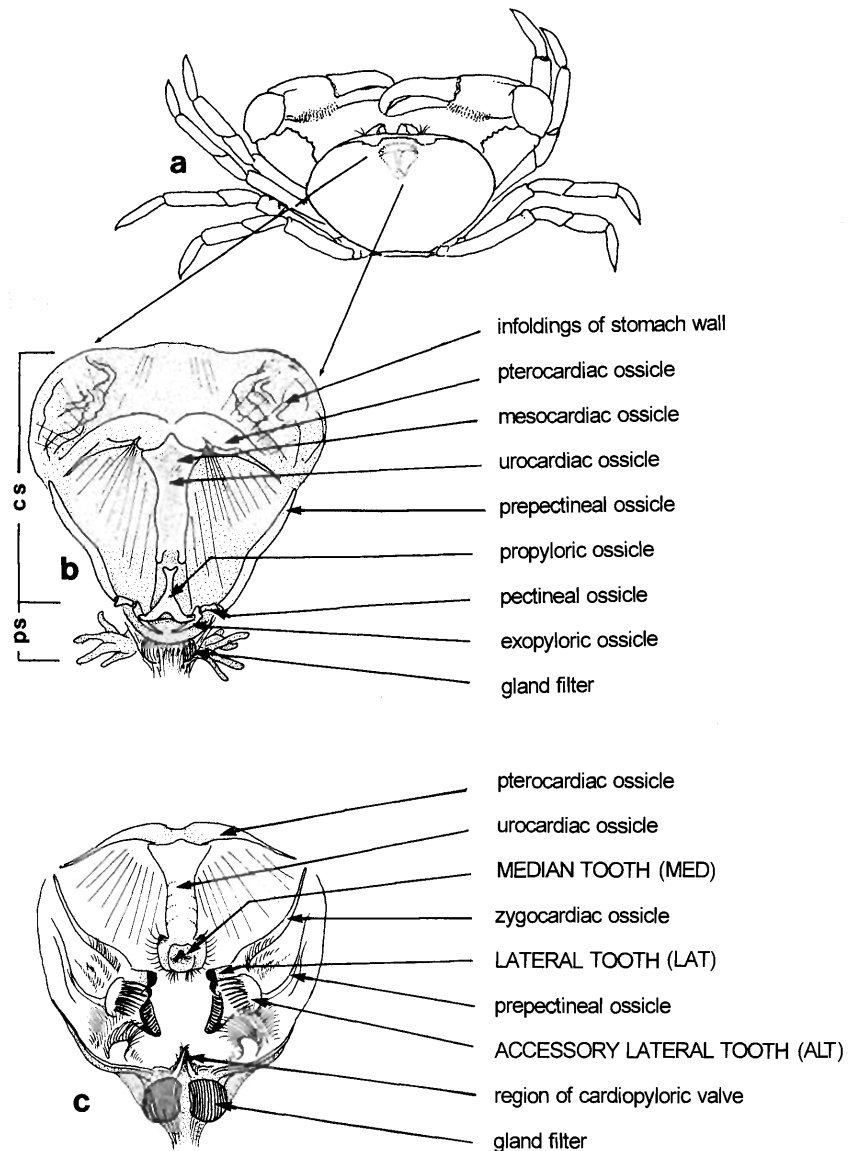
Internally, although the details and overall complexity of the brachyuran stomach are far greater than the scope of our study indicates (see Maynard and Dando 1974 for a more detailed overview), there are basically four large and readily identified and homologized components of the gastric mill that 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 zygo-cardiac 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 cardiopyloric 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 *Austinograea williamsi*, with comments concerning *Bythograea therymydron* 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 therymydron*). The sides of this basal flange are scalloped,

**Fig. 1** *Austinograea williamsi*. **a** Schematic figure of bythograeid crab (based on photograph of female allotype in Hessler and Martin 1989), showing approximate location of foregut; **b** slightly enlarged illustration of whole stomach, dorsal view; **c** ventral view of internal stomach, drawn from 28.1 mm carapace-width individual from Mariana Back-Arc Basin, western Pacific (*Ossicles labeled in capital letters are those examined in present study; cs cardiac stomach; ps pyloric stomach*)



and bear, at the extremity of each cuticular extension, stout spinulose spines that curve gently forward toward the base of the urocardiac ossicle (Fig. 2b,c). The ventral surface of the urocardiac ossicle leading to the tooth is gently curved and bears slight grooves at irregular intervals as it approaches the area from which the tooth arises (Figs. 1c, 2a, b). The situation in *B. thermydron* differs in that the surrounding flange is less nearly rectangular, giving the base of the tooth a more rounded appearance (Fig. 4a, b), and in the lack of the basal anterior thickening or ridge (cf. Figs. 4b and 2b). Additionally, the spines arising from the scalloped margins of the flange appear to taper less and are in general slightly more delicate (Fig. 4c, far right).

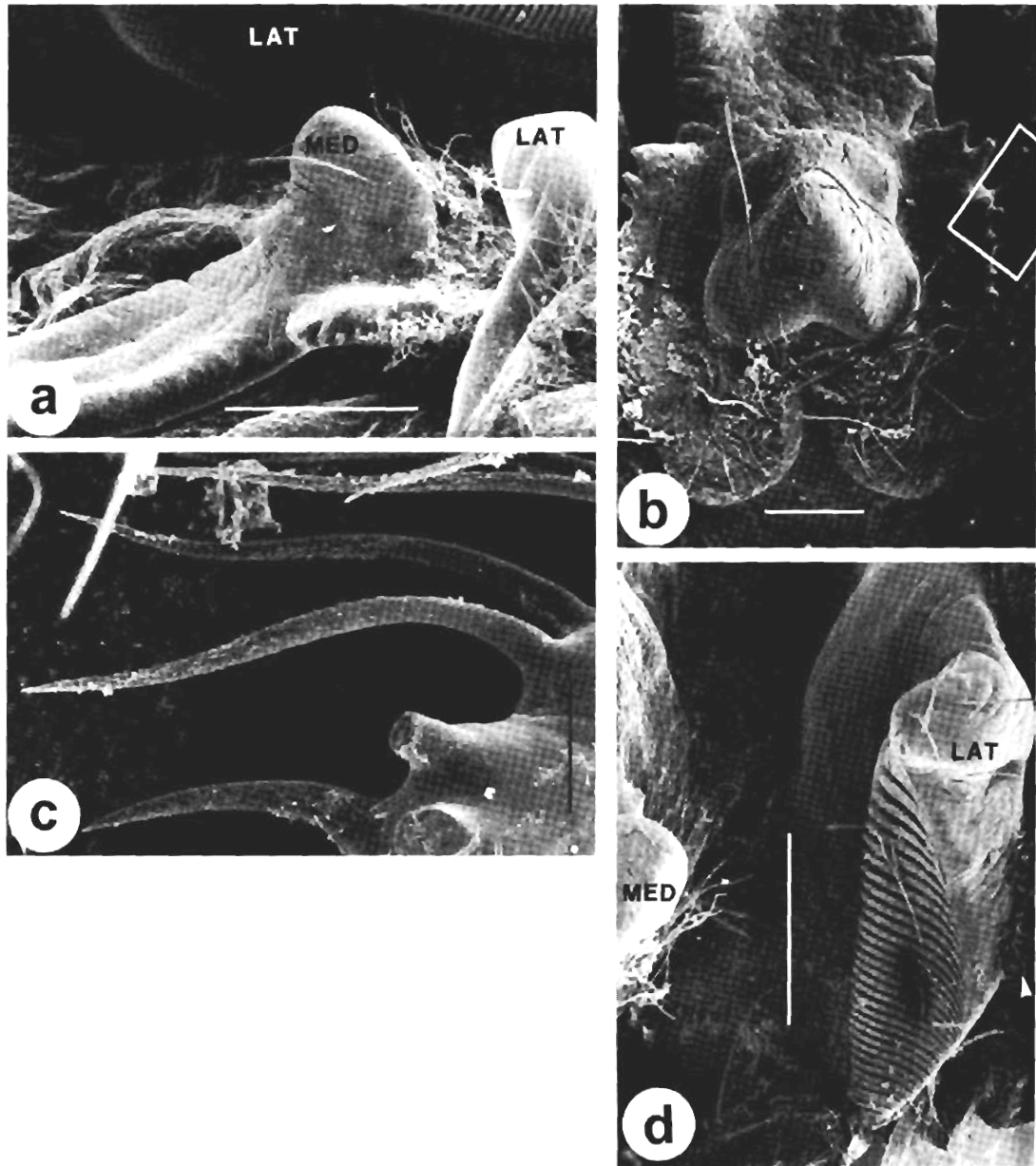
#### Lateral teeth

Both of the well developed lateral teeth bear one large, blunt, anterior denticle (Figs. 1c, 2a, d, 3a). The poste-

rior region bears  $\approx 30$  deep grooves (Fig. 2d). The more anterior grooves are slightly wider than those found in the central or posterior areas. The ventral border of this grooved region is nodulose and bears a small field of stout, cylindrical spines covered with setules and scales (Fig. 2d: arrowhead on lower right; Fig. 5a). These spines appear to have a central lumen and may serve some sensory function. Similar spines and setae are found also at the posterior terminus of each lateral tooth. The lateral teeth of *Bythograea thermydron* differ only in that there are fewer (20 or so) grooves in the posterior region (cf. Figs. 2d and 4d, e), and each groove appears to be slightly wider than those seen in *Austinograea williamsi*.

#### Accessory lateral teeth

Each of these ossicles bears approximately 10 medially directed spines in a row along the ventral medial border



**Fig. 2** *Austinograea williamsi*. SEM views of median tooth and lateral teeth. **a** Lateral view of posterior region of uropyloric ossicle and median tooth; serrations of left lateral tooth (*LAT*) just visible at upper right. **b** Dorsal median tooth (*MED*), ventral view, same orientation as for Fig. 1c. **c** Cuticular flange and its spinulose setae surrounding median tooth (enlargement of approximate region in box in **b**). **d** Left lateral tooth (*LAT*) rotated slightly outward and downward from position in Figs. 1c and 3a, to show serrations along posterior part of face of tooth; dorsal median tooth (*MED*) is just visible at far left (arrowhead indicates region of scale-bearing cylindrical setae in Fig. 5a) (Scale bars: **a** = 50  $\mu\text{m}$ , **b** = 200  $\mu\text{m}$ , **c** = 50  $\mu\text{m}$ , **d** = 500  $\mu\text{m}$ )

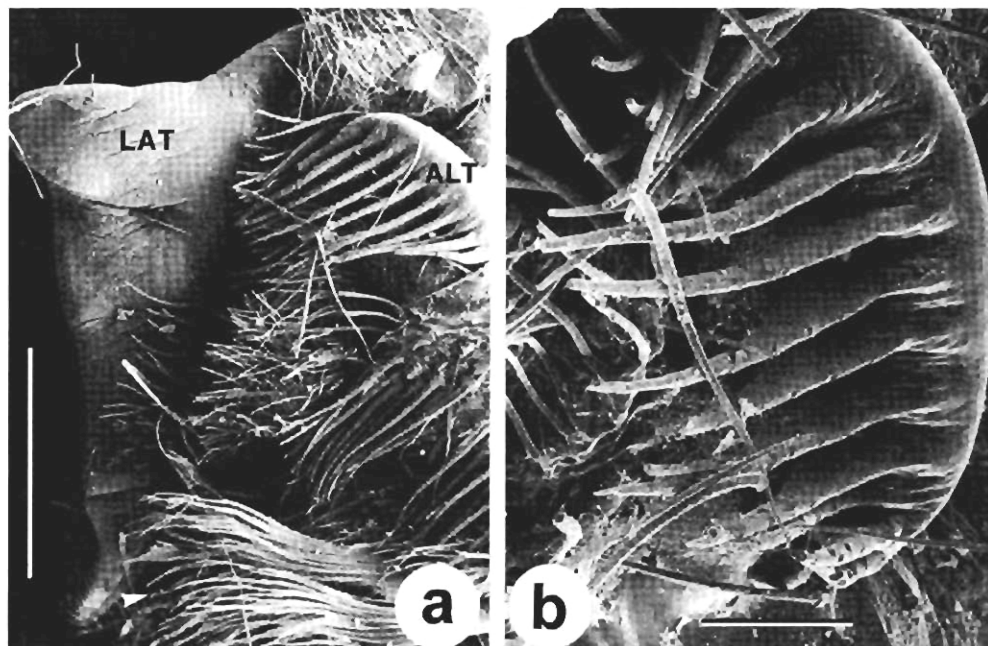
of the tooth (Figs. 1c, 3a, b). Each spine is proportionately wide basally, but only in a dorsal-ventral direction, and at least some of the spines bear small denticles along the distal half. Several additional spines occur on the posterior ventral edge of the tooth and are not in line

with the others; several of these, as shown in Fig. 4f (*Bythograea thermydron*), have broken at their base. There is some variation in the armature of the accessory lateral teeth. The ALT of *B. thermydron* shown in Fig. 4f has shorter and fewer teeth than that shown for *Austinograea williamsi* (Fig. 3d); other specimens of *B. thermydron*, however, had an ALT essentially identical to that of *A. williamsi*.

#### Cardiopyloric valve

The valve is horseshoe-shaped, as in all brachyurans, with the apex of the horseshoe directed posteriorly such that food travels along the relatively smooth surface of the food groove from the open end toward the posterior terminus (top of Fig. 5b). The valve is rather heavily

**Fig. 3** *Austinograea williamsi*. SEM views of lateral teeth and accessory lateral teeth. **a** Ventral view of left lateral tooth (*LAT*; oriented as in Fig. 1c) and left accessory lateral tooth (*ALT*) (arrowhead indicates sweeping filtering setae; see Fig. 5d); **b** ventral view of left lateral accessory tooth (note basal width of each spine and regular spacing) (Scale bars: **a** = 500  $\mu$ m; **b** = 100  $\mu$ m)



setose around the sides (Fig. 5b,c). The setae of the posterior half of the valve (near the top of Fig. 5b) are long and spinulose; they give way abruptly to fields of shorter setae in the more anterolateral areas. Toward the posterior (narrowest) extremity of the valve, the heavy setae give way to shorter, thicker spines, which in turn become flattened denticles at the apex of the valve (much of which is unfortunately obscured by debris in Fig. 5b). The morphology and setosity of this valve are apparently quite variable. In some individuals the extremity was less setose, and the distal short spines that complete the “horseshoe” across the posterior tip of the valve (Fig. 5b) were lacking with the result that the distal extremity of the valve appeared smoother. The degree to which wear, or time since the last molt, might affect morphology of these structures also is unknown; wear and molting also might explain some of the perceived variability in the valve.

#### Other spines and setae of foregut

The overall complexity of the brachyuran foregut is great, and we have not attempted to discern the morphology and interactions of all components. It is interesting to note, however, that there is a very wide range of setal and spine types. We report some of these here so that future workers employing SEM can compare their results to ours. Nearly all the membranous lining of the foregut bears minute setae, usually found in pairs or triplets, and scattered more or less evenly on and between the major ossicles (e.g. see background cuticle in Fig. 2c). Also widely distributed (that is, found in many places within the foregut but not as universally as the small paired setae just described) are long, tapering setae bearing minute spinules along their entire length (e.g.

along the sides of the CPV; Fig. 5c). These are particularly obvious along the areas of the stomach-wall ossicles posterior to and ventral to the lateral teeth. Other regions, such as the area just between and slightly posterior to the accessory lateral teeth and the lateral teeth, bear extremely dense rows of long, sweeping setae (arrowed in Fig. 3a; Fig. 5d). These setae bear rows of evenly spaced short setules in three or four rows along the primary setal shaft, and would seem to provide a most effective filter mechanism.

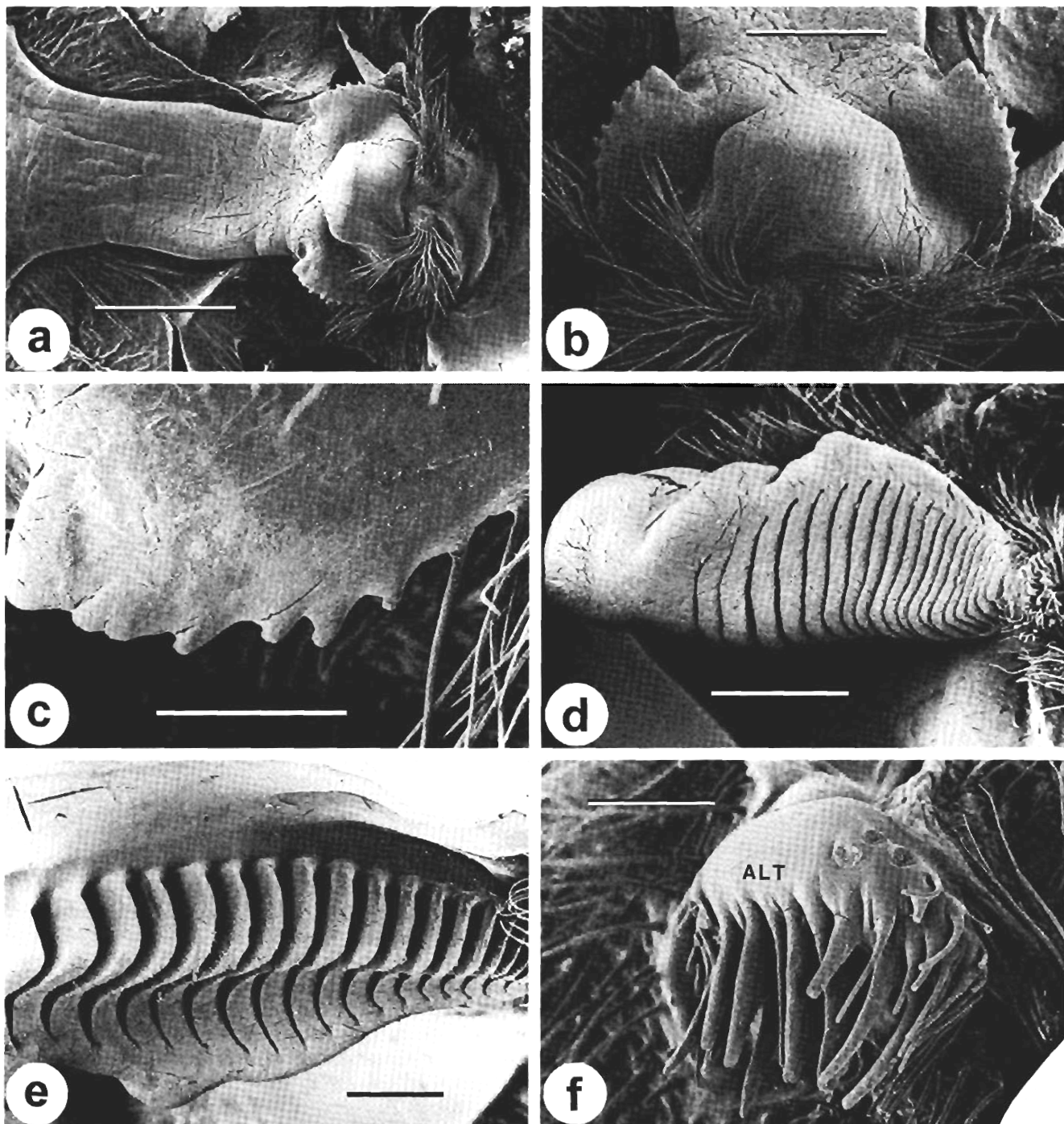
#### SEM comparison with shallow-water grapsid

For gross comparison of the foregut of vent crabs with other brachyurans, we conducted a similar SEM study of the foregut ossicles of a southern California shallow-water grapsid crab, *Pachygrapsus crassipes*, of similar size (carapace width 23.2 mm; Fig. 6). The four major components are easily identified, and the gross appearance of each is similar to what is seen in the vent crabs. Differences, however, in the details of the various ossicles between *P. crassipes* and the vent crabs are immediately noticeable. In *P. crassipes* the cuticular flange around the median tooth is absent; the length and thickness of the spines of the lateral accessory tooth and the general dentition of the lateral tooth also are different.

#### Discussion

##### Feeding behavior of vent crabs

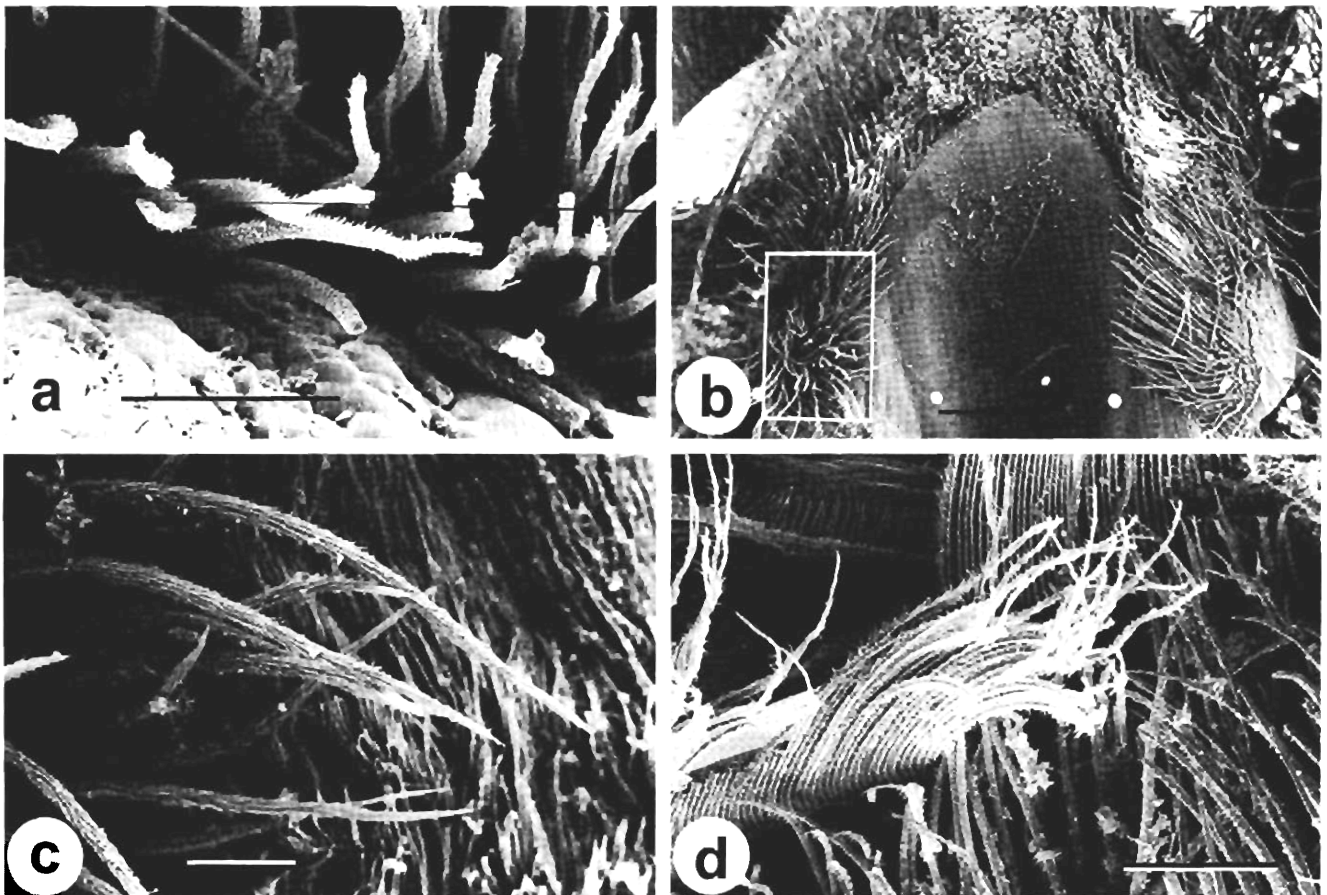
Although we are aware of no previously published observations, vent crabs have been seen to feed on several



occasions. The eastern Pacific *Bythograea thermydron* has been seen feeding on tube worms and bacterial mats, and the mid-Atlantic *Segonzacia mesatlantica* has been seen feeding on co-occurring shrimp and mussels (C.L. Van Dover and R.R. Hessler personal communication 1996). Gut contents of one individual of our western Pacific specimens of *Austino-graea williamsi* included the leading edge of a small bivalve shell; these crabs also have been seen to scavenge (Hessler personal communication). The setal pads on the inside of the chelipedal carpus and on the branchiostegal areas of females (and to a slightly lesser extent of males) of

**Fig. 4** *Bythograea thermydron*. Major foregut ossicles. **a** Ventral view of urocardiac ossicle and dorsal median tooth, with anterior toward left of figure; **b** higher magnification of median tooth; **c** scalloped border, showing more circular shape and more delicate spines/setae in this species; **d** lateral (inner) view of left lateral tooth; **e** Left lateral tooth shown in **d**, but with angle slightly changed and showing wider separation of serrations than in *Austino-graea williamsi*; **f** left accessory lateral tooth (Scale bars: **a** = 1.0 mm; **b**, **d** = 500  $\mu$ m; **c**, **e**, **f** = 200  $\mu$ m)

*A. williamsi* and *B. thermydron* harbor large numbers of bacteria that may supplement the crabs' diet (Martin personal observation; Williams personal communication



**Fig. 5** *Austino-graea williamsi*. Selected setal types and cardiopyloric valve. **a** Higher magnification of cylindrical, scale-bearing setae along ventral border of lateral tooth, as shown at tip of arrowhead in Fig. 2d; **b** cardiopyloric valve (anterior is toward bottom of figure); **c** higher magnification of setal types in box at lower left of **b**; **d** presumed sweeping/filtering setae found in area indicated by arrowhead at lower left of Fig. 3a (Scale bars: **a** = 50  $\mu\text{m}$ ; **b** = 200  $\mu\text{m}$ ; **c** = 20  $\mu\text{m}$ ; **d** = 100  $\mu\text{m}$ )

1996). Thus, like so many of their shallow-water counterparts, bythograeids can perhaps best be described as omnivorous opportunistic scavengers rather than specialists (Hessler personal communication). Vent crabs probably should be listed among scavengers and detritivores rather than among true predators in future schematic food-web diagrams or general accounts of vent community structure (e.g. Tunnicliffe 1991, 1992; Hessler and Smithey 1993). Predation almost certainly contributes to some degree also. Based on these observations, we might expect that the foregut morphology of these crabs would be of a general nature, and this is what we found. Although we have documented some unique features, we note that there is nothing distinctive about the vent crabs' foreguts that markedly sets them off from other brachyurans, and certainly nothing that might be considered indicative or even suggestive of their unique habitat.

#### Vent crab ossicles compared to those of other crabs

Although there is a relatively rich literature on the stomach ossicles of shrimp (e.g. see reviews by Fryer 1977; Felgenhauer and Abele 1989), less information is available on crabs. Major studies on the foregut ossicles of crabs include the following: Mocquard (1883) on more than 30 species, Pearson (1908) on *Cancer pagurus*, Patwardhan on *Paratelphusa guerini* (1935a) and on

representatives of 11 marine families (1953b), Schaefer (1970) on *Cylograpsus punctatus*, Maynard and Dando (1974) on *Callinectes sapidus*, Factor (1982, 1989) on the ontogeny of the stomach and other components of the feeding system in *Menippe mercenaria*, Nakamura and Takemoto (1986) on 15 crab species representing five families from Japanese waters, and Kropp (1986) on the unique coral gall-crabs (family Cryptochiridae). Basically these studies show that all crabs, even those widely separated taxonomically, have the same major foregut ossicles (two lateral teeth, one median tooth, a pair of accessory lateral teeth, and the cardiopyloric valve), which are seen first in the juvenile stages that immediately follow the megalopal or first postlarval stage (Factor 1982, 1989). Beyond that, comparisons are made difficult by the disparate methods workers have used to discuss or illustrate the more complex components of crab stomachs. For example, the illustrations of Mocquard (1883) were beautifully detailed but, as published, were so small as to be nearly useless, whereas

**Fig. 6** *Pachygrapsus crassipes* (Grapsidae). Major foregut components of 23.2 mm carapace-width specimen of a "typical" (grapsid) brachyuran crab. Note overall similarity to bythograeid foregut components, but obvious differences in details (Scale bar 1.0 mm)



figures provided by other workers (such as Patwardhan 1935a and Maynard and Dando 1974) were meant to be schematic, and so some details were not recorded.

To our knowledge, no published description of a brachyuran gastric mill shows a median tooth that is surrounded by a plate whose margins are serrate or scalloped, and which has spinulose setae on the tip of each serration. In this regard, vent crabs (at least the two genera we examined) are apparently unique. It is interesting to note, however, that Factor (1982: his Figs. 21, 22) noticed similar but smaller projections around the base of the median tooth in juvenile xanthids (*Menippe mercenaria*), one of the families that Williams (1980) felt might be closely related to the bythograeids. The median tooth in adult xanthids apparently lacks these projections (Factor 1982: his Fig. 24). Another feature that has not appeared in previous descriptions of gastric mills is the large number of grooves in the posterior inner face of the lateral tooth of the vent crabs (up to 30 in *Austinograea williamsi*,  $\approx 20$  in *Bythograea thermydron*). This is more than is seen in adult xanthids (*M. mercenaria*; see Factor 1982: his Fig. 25), and more than is seen in any of the 15 species in 5 families described by Nakamura and Takemoto (1986). In most of the other accounts, the figures are too schematic (or too small, in the case of Mocquard 1883) to permit valid comparisons. We reiterate that relatively few species have been studied to date, and that electron microscopy has been used only sparingly (e.g. Factor 1982, 1989; Kropp 1986). An additional concern is that the appearance of the ossicles changes significantly according to the angle at which they are viewed. Direct comparisons of our findings with those in earlier publications is to some extent unfair.

One area of contention in studies of decapod foreguts has been the degree to which armature of the gastric mill reflects ancestry (e.g. see Felgenhauer and Abele 1983, 1989) vs adaptation to habitat (e.g. see Caine 1975a, b, 1976) vs some combination of the two. The observation that the gastric mill is basically similar in a wide variety of decapod taxa, from crayfish to deep-sea crabs, would seem to support the first school of thought. Certainly the presence of these same teeth in gall crabs, which feed only on the mucus of their coral hosts, would seem to support this idea also, although Kropp (1986) noted that the ossicles in gall crabs were very different from those of other crabs that are not obligate coral commensals. Had the vent crabs fed exclusively on the same bacterial mats that form the basis of so many hydrothermal vent food-chains, examination of their stomach armature might have been a good test of these competing hypotheses. In the light of the apparent generalized nature of feeding in these crabs, the finding of "typical" stomach ossicles in vent crabs in our study adds no fuel to that debate.

**Acknowledgements** We thank Dr. G. Somero, Hopkins Marine Station, for generously allowing us to dissect four specimens of *Austinograea williamsi* for this study and also for providing, while he was at the Scripps Institution of Oceanography several years earlier, the specimens of *Bythograea thermydron*. We also thank A. Thompson (USC Center for Electron Microscopy and Microanalysis) for assistance with the electron microscopy. Dr. R. Hessler allowed access to specimens of both species and shared his personal knowledge of vent crabs and vent community structure. Dr. A.B. Williams discussed vent crab feeding, and G.E. Davis helped at various stages in the laboratory. C.L. Van Dover kindly supplied us with personal observations on feeding in vent crabs made with the D.S.V. "Alvin" in the Atlantic and Pacific oceans. This study was funded in part by a grant to J.W. Martin from the American Philosophical Society, and in part by a Research



Experiences for Undergraduates grant (REU supplement to DEB-9320397) from the National Science Foundation to J.W. Martin (funding the involvement of P. Jouharzadeh).

## References

- Caine EA (1975a) Feeding and masticatory structures of six species of the crayfish genus *Procambarus* (Decapoda, Astacidae). *Forma Functio* 8: 49–66
- Caine EA (1975b) Feeding and masticatory structures of selected Anomura (Crustacea). *J exp mar Biol Ecol* 18: 277–301
- Caine EA (1976) Relationship between diet and the gland filter of the gastric mill in hermit crabs (Decapoda, Paguridea). *Crustaceana* 31: 312–313
- Factor JR (1982) Development and metamorphosis of the feeding apparatus of the stone crab, *Menippe mercenaria* (Brachyura, Xanthidae). *J Morph* 172: 299–312
- Factor JR (1989) Development of the feeding apparatus in decapod crustaceans. *Crustacean Issues* 6: 185–203
- Felgenhauer BE, Abele LG (1983) Phylogenetic relationships among the shrimp-like decapods. *Crustacean Issues* 1: 291–311
- Felgenhauer BE, Abele LG (1989) Evolution of the foregut in the lower Decapoda. *Crustacean Issues* 6: 205–219
- Fryer G (1977) Studies on the functional morphology and ecology of the atyid prawns of Dominica. *Phil Trans R Soc (Ser B)* 277: 57–129
- Guinot D (1988) Les crabes des sources hydrothermales de la dorsale du Pacifique oriental (campagne *Biocyarise*, 1984). *Oceanol Acta* 38: 109–118
- Guinot D (1989) Description de *Segonzacia* gen. nov. et remarques sur *Segonzacia mesatlantica* (Williams): campagne HYDRO-SNAKE 1988 sur la dorsale médio-Atlantique (Crustacea Decapoda Brachyura). *Bull Mus natn Hist nat, Paris (4e sér.)* 11: 203–231
- Guinot D (1990) *Austinograea alayseae* sp. nov., crabe hydrothermal découvert dans le bassin de Lau, Pacifique sud-occidental (Crustacea Decapoda Brachyura). *Bull Mus natn Hist nat, Paris (4e sér.)* 11: 879–903
- Hessler RR, Martin JW (1989) *Austinograea williamsi*, new genus, new species, a hydrothermal vent crab (Decapoda: Bythograeidae) from the Mariana Back-Arc Basin, western Pacific. *J Crustacean Biol* 9: 645–661
- Hessler RR, Smithey WM Jr (1993) The distribution and community structure of megafauna at the Galapagos Rift hydrothermal vents. In: Rona A et al. (eds) *Hydrothermal processes at seafloor spreading centers*. Plenum Press, New York, pp 735–770
- Kropp R (1986) Feeding biology and mouthpart morphology of three species of coral gall crabs (Decapoda: Cryptochiridae). *J Crustacean Biol* 6: 377–384
- Maynard DM, Dando MR (1974) The structure of the stomatogastric neuromusculature system in *Callinectes sapidus*, *Homarus americanus* and *Panulirus argus* (Decapoda, Crustacea). *Phil Trans R Soc* 268 (Ser B) 161–220
- Mocquard MF (1883) Recherches anatomiques sur l'estomac des crustacés podophtalmaires. *Annls Sci nat (Sér Zool Paleont)* 16: 1–311
- Nakamura K, Takemoto T (1986) Morphology of stomach ossicles in Brachyura. *Mem Fac Fish Kagoshima Univ* 35: 7–15
- Nation JL (1983) A new method using hexamethyldisilazane for preparation of soft insect tissues for scanning electron microscopy. *Stain Technol* 38: 347–351
- Patwardan SS (1935a) On the structure and mechanism of the gastric mill in Decapoda. I. The structure of the gastric mill in *Paratelpusa guerini* (M. Edw.). *Proc Indian Acad Sci (Sect B)* 183–195
- Patwardan SS (1935b) On the structure and mechanism of the gastric mill in Decapoda. II. A comparative account of the gastric mill in Brachyura. *Proc Indian Acad Sci (Sect B)* 359–375
- Pearson J (1908) *Cancer* (the edible crab). *Proc Trans Lpool Biol Soc* 22: 1–554; 18 plates (LMBC Mem No 16)
- Saint Laurent M de (1984) Crustacés décapodes d'un site hydrothermal actif de la dorsale de Pacifique oriental (13° Nord), en provenance de la campagne française Biocyatherm. *C r hebdomadaire Acad Sci (sér III)* 299: 355–360
- Saint Laurent M de (1988) Les mégalopes et jeunes stades crabe de trois espèces du genre *Bythograea* Williams, 1980 (Crustacea Decapoda Brachyura). *Oceanol Acta* 38: 99–107
- Schaefer N (1970) The functional morphology of the foregut of three species of decapod Crustacea: *Cyclograpsus punctatus* Milne-Edwards, *Diogenes brevivostis* Stimpson, and *Upogebia africana* (Ortman). *Zoologica african* 5: 309–326
- Secretan S, Guinot D (1988) Premières observations sur le squelette axial du crabe dit "des fumeurs" *Cyanograea praedator* de Saint Laurent. *Oceanol Acta* 38: 119–124
- Tunnicliffe V (1991) The biology of hydrothermal vents: ecology and evolution. *Oceanogr mar Biol A Rev* 29: 319–407
- Tunnicliffe V (1992) Hydrothermal-vent communities of the deep sea. *Am Scient* 80: 336–349
- Williams AB (1980) A new crab family from the vicinity of submarine thermal vents on the Galapagos Rift (Crustacea: Decapoda: Brachyura). *Proc Biol Soc Wash* 93: 443–472
- Williams AB (1988) New marine decapod crustaceans from waters influenced by hydrothermal discharge, brine, and hydrocarbon seepage. *Fish Bull US* 86: 263–287