Zootaxa 5476 (1): 230–240
https://www.mapress.com/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.5476.1.20
http://zoobank.org/urn:lsid:zoobank.org:pub:B2644666-FF87-41D3-95C7-ACE05CFC7AC5

Ecomorphology of main food processing structures of four ocypodid species: how do they relate to the crabs' trophic habits?

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Abstract

The spoon-tipped (ST) setae coverage and their abundance on the second maxillipeds as well as the morphology of the urocardiac and zygocardiac ossicles from the gastric mills of the four ocypodid species, viz., *Austruca annulipes* (H. Milne Edwards, 1837), *Gelasimus vocans* (Linnaeus), 1758, two typical deposit-feeding fiddler crabs, *Petruca panamensis* (Stimpson, 1859), an atypical herbivorous-cum-'sediment swallower' fiddler crab, and *Ocypode ceratophthalmus* (Pallas, 1772), an omnivorous ghost crab, were described and compared in relation to their respective trophic habits. In the three fiddler crabs, ST setae coverage and abundance generally correlated with their habitats' sediment grain size characteristics—more ST setae in *A. annulipes* ('sandy-habitat crab') and less in *G. vocans* ('muddy-habitat crab'). ST setae were absent in *O. ceratophthalmus*, which suggests that these setae were not needed for food processing. In the two deposit-feeding fiddler crabs, the median tooth of the urocardiac ossicle had tooth-like transverse ridges to grind against the dentition of the lateral teeth of the zygocardiac ossicles. The median tooth in *P. panamensis*, however, had transverse ridges that resemble that of a vascular plant eater as well as some posterior tooth-like transverse ridges, typically found in deposit feeders; and twice the number of incisors than the other three ocypodids, for cutting up ingested algal pieces. The omnivorous *O. ceratopthalmus* had four raised transverse ridges on the round blunt median tooth as well as large premolars and molars on the zygocardiac lateral teeth for maceration of animal tissue. Hence, ST setae abundance as well as the grinding surfaces and dentition of the two gastric mill ossicles are indicative of the habitat adaptations and trophic habits respectively.

Key words: *Austruca annulipes*, Brachyura, deposit feeder, *Gelasimus vocans*, gastric mill ossicles, herbivore, *Ocypode ceratophthalmus*, omnivore, *Petruca panamensis*, spoon-tipped setae

Introduction

The relationship between the ecological role of an organism and its morphological adaptations constitutes the field of ecomorphology. Historically, ecomorphology has been mainly descriptive but there is now potential to use the link between form and function as a tool for prediction of ecological patterns and dynamics. One of the greatest variations in form and function is the dietary habits of organisms—the broad variation in diet (i.e., function) is associated with similarly large variation in gut morphology (i.e., form) (Griffen & Mosblack 2011). Brachyuran crabs display diverse trophic variations, and each species has its own trophic strategy. Hence, the structures involved with the processing of ingested food, namely, the mouthparts and gastric mills, can provide substantial insights regarding the trophic habits of decapod crustaceans (see Icely & Jones 1978; Kunze & Anderson 1979; Skilleter & Anderson 1986; Wolcott & O' Connor 1992; Heeren & Mitchell 1997; Huespe *et al.* 2008; Allardyce & Linton 2010; Carvalho *et al.* 2018).

Mouthpart setation can reflect the predominant dietary habit in crabs. In general, macrophagous crabs have robust setae while microphagous ones tend to have weaker, flexible setae such as plumose setae (Kunze & Anderson 1979; Heeren & Mitchell 1997). There are several studies in which sympatric fiddler crab species were reported to differ in the mouthpart setation, namely spoon-tipped (ST) setae abundance on the second maxilliped, in relation

Accepted by S.H. Tan: 4 Sept. 2023; published: 4 Jul. 2024

to their respective habitats (e.g., Icely & Jones 1978; Yamaguchi & Ogata 2000; Lim 2004; Lim & Kalpana 2011; Colpo & Negreiros-Fransozo 2013; Lim & Goh 2021). Based on the ability to extract organic material, ST setae are reported to improve extraction of food from coarser sediments in sandy habitats (Miller 1961). Crane's (1975: 455) generalization that modification of ST setation on the second maxilliped is correlated with sediment characteristics, i.e., species living in sandy habitats generally have more ST setae c.f. those living in muddy habitats, has since been validated by several quantitative studies on fiddler crabs from different geographical locations (see Yamaguchi & Ogata 2000; Lim 2004; Lim & Kalpana 2011; Lim & Goh 2021).

After food is manipulated by the mouthparts, the secondary processing and actual trituration of the ingested matter occurs in the gastric mill. There is evidence that the morphology of the foregut of fiddler crabs, which are deposit feeders (i.e., mainly feeding on detritus, algae, and bacteria), may be modified in closely related species with rather similar trophic habits (Icely & Nott 1992). Icely & Jones (1978) reported that the structure of the gastric mill of four species of brachyuran fiddler crabs sampled from the same East African shore, reflected the differences in sediment particle size distribution and organic content on which they feed.

Several studies have also suggested that the morphology of the gastric mill varies according to the diet of decapod species (e.g., Kunze & Anderson 1979; Icely & Nott 1992; Allardyce & Linton 2010). The gastric mill ossicles of macrophagous species tend to be calcified and dentate with few setae compared to the small blunt teeth and high setation in microphagous crabs (de la Barra *et al.* 2018). Carnivorous species are also expected to have molar processes for grinding and crushing of soft animal tissues whereas herbivores possess high transverse ridges for cutting fibrous material and less calcified teeth (Kunze & Anderson 1979; Skilleter & Anderson 1986). In contrast, omnivorous species have ossicles with both blunt ridges (for crushing and pulverizing hard food material) as well as cusps (for mastication) (Salindeho & Johnston 2003).

Felgenhauer & Abele (1985) presented an alternative general viewpoint to suggest that the gastric mill structure is related to phylogenetic aspect rather than to the diet of a species. It is pertinent to note that they based their conclusions on the foreguts of *Atya innocous* (Herbst, 1792) and *Potimirim glabra* (Kingsley, 1878) (two lower decapods), with the argument that the foreguts of these two shrimps have strong, well-developed ossicles and gastric mills, yet both feed on small particles, including diatoms and filamentous algae. In contrast, *Macrobrachium americanum* Spence Bate, 1868 another caridean, has reduced ossicles and lacks a gastric mill or any grinding structures, although the species is a voracious predator. In 1989, Felgenhauer & Abele surveyed more than 50 species of lower decapods and concluded that the morphology of the foreguts can be a useful taxonomic character that may be more related to the phylogenetic history of the taxon than to diet.

With Felgenhauer & Abele's work (1985, 1989) on lower decapods, there arose an interest in researchers to explore the potential of using the morphology of the gastric mill as a phylogenetic tool in brachyurans (e.g., Brösing *et al.* 2007; Brösing 2010; Naderloo *et al.* 2010; Shih *et al.* 2015). Ng *et al.* (2008) in their comprehensive catalogue of Brachyura, suggested that taxonomic revisions could be carried out using both gastric mill morphology and molecular analysis. Naderloo *et al.* (2010) revised the taxonomy of the wide-front fiddler crab species of the *Uca lactea*-group using external morphology, as well as characteristics of the gonopod and median tooth on the urocardiac ossicle of the gastric mill. They reported that the urocardiac ossicle characteristics grouping was parallel with the gonopod morphology and genetic grouping, as reported by Shih *et al.* (2009) on the *Uca lactea* species complex from the Indo-West Pacific, and advocated that the morphology of the urocardiac ossicle should be used as a routine character in crab systematics. In 2011, Brösing and Türkay stated that although the brachyuran cardiac stomach has a relatively stable structure and is useful for taxonomy, they conceded that the gastric mill characteristics may be indicative of adaptations to trophic habits.

In this study, four ocypodid crabs (three species of fiddler crabs and one species of ghost crab) were selected for our investigation of the link between trophic habits and food processing structures. The deposit feeding fiddler crabs, *Austruca annulipes* (H. Milne Edwards, 1837) and *Gelasimus vocans* (Linnaeus, 1758) feed mainly on detritus and diatoms—albeit from two different habitats, the former inhabits sandy-muddy habitats, and the latter prefers muddy ones (see Crane 1975, pgs. 642–643; Lim 2004); while *Petruca panamensis* (Stimpson, 1859), is an atypical fiddler crab that has adapted to swallowing sediment without sorting (see Takeda & Murai 2003) and also feeds on algae encrusted on rocks, i.e., a herbivore-cum-'sediment swallower'). It is pertinent to note that these three fiddler crab species are placed in different clades by Shih *et al.* (2016) based on molecular evidence from the nuclear 28S rDNA, and the mitochondrial 16S rDNA and cytochrome oxidase subunit I (COI). *Ocypode ceratophthalmus* (Pallas, 1772), the ghost crab, is a typical omnivore, that usually scavenges on sandy beaches but can be an opportunistic carnivore (Yong & Lim 2009). Using these four species of ocypodid crabs with distinctly different trophic habits, our objectives were to relate the morphology of the zygocardiac and urocardiac ossicles of the gastric mill, in conjunction with the abundance and extent of spoon-tipped setation coverage of the second maxillipeds, to their trophic habits.

Materials and methods

Specimens of *Austruca annulipes* and *Gelasimus vocans* used in this study were collected from the lagoonal shore of Pulau Hantu Besar, an offshore island of Singapore (1°13'20.40"N, 103°44'59.99"E) while *Ocypode ceratophthalmus* were sampled from the sandy beaches at East Coast Park, Singapore (1°18'14.24"N, 103°55'34.94"E). *Petruca panamensis* specimens were caught from among the rocks at Punta Culebra, Panama (8°54'45"N, 79°31'48"W). Data on the ST setation for *A. annulipes* (n = 91) and *G. vocans* (n = 100) were extracted from Lim (2004), and that of *P. panamensis* (n = 60) from Lim & Goh (2021). The second maxillipeds of 35 individuals of *O. ceratophthalmus* were examined for the presence of ST setae as described in Lim & Goh (2021).

For the examination and description of the two gastric mill ossicles, each crab was prised open gently along the posterior margin of the carapace and the first abdominal somite. The entire foregut was pulled out using a pair of forceps. A total of 10 specimens (five males and five females) were used for each species. The urocardiac and zygocardiac ossicles were dissected from the stomach, removed and their detailed structures observed under a stereo microscope (Leica M125). The description of the two ossicles followed the terminology used by Yang (1986), Allardyce & Linton (2010) and Shih (2015). Generally, there are three regions in the urocardiac ossicle: anterior basal region, stem region and the posterior tooth plate while the zygocardiac ossicle comprise the lateral teeth (Fig. 1A). The median tooth may have several tooth-like transverse ridges protruding from a longitudinal central ridge on the ventral side of the tooth plate; in some species, it may cover part of the stem too (Shih 2015) or raised transverse ridges/cusps that form part of the blunt end of the tooth (Allardyce & Linton 2010).

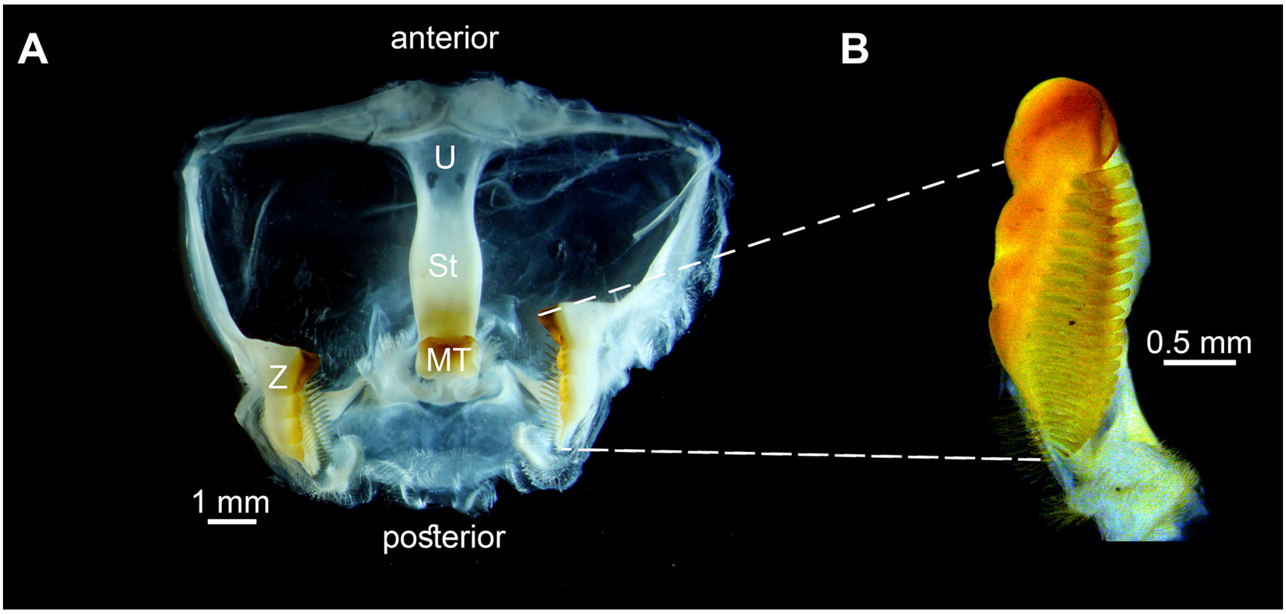

FIGURE 1. Characteristics of the gastric mill of *Ocypode ceratophthalmus* (Pallas, 1772). A, Ventral view showing relative positions of the urocardiac ossicle and the zygocardiac ossicle; B, Dorso-lateral view of the lateral teeth of the zygocardiac ossicles, showing the comb-like structures and some details of the dentition. MT, median tooth; St, stem; U, urocardiac ossicle; Z, zygocardiac ossicle.

Teeth formulae were used to describe the types and the numbers of teeth present on the lateral tooth plate of the zygocardiac ossicles (Fig. 1B) in the four species, largely following the method described by Yang (1986). In Yang's description of the lateral tooth plate, the first and largest anterior tooth was designated as the pre-molar (PM), followed by a series of smaller molars (M), blunt-rounded incisors (I), and ending with small, sharp, posterior canines (C); a series of comb-like structures (CO) on the dorsal surface were also included and separated by a slash from the other tooth types. As the pre-molars and molars were often not easily distinguishable in the three fiddler crabs, we have combined them together as PMM. The number of each type of teeth was appended after each tooth type in brackets. Hence, the zygocardiac teeth arrangement for the ghost crab was PM(*n*)M(*n*)I(*n*)C(*n*)/CO(*n*) and those of the three fiddler crabs were PMM(*n*)I(*n*)C(*n*)/CO(*n*). Variations in the number of the teeth observed in the crabs were indicated by the range of *n* in the formula.

Results

The extent of ST coverage of the muddy-substrate inhabitant, *G. vocans* was similar to that observed in *P. panamensis*, which lives in rocky habitats, whereas there were more ST setae in *A. annulipes* (60–70% c.f. 50% for the former two species) (Table 1). In all three species of fiddler crabs, the number of ST setae on the second maxilliped increased with increasing carapace width (CW) (Fig. 2). However, the rate of increase in the number of ST setae with respect to CW was similar in *A. annulipes* and *P. panamensis*, and higher than that of *G. vocans* (Fig. 2). There were no ST setae on the second maxilliped of all 35 specimens of *O. ceratophthalmus* (Fig. 2 inset; Table 1) that we examined.

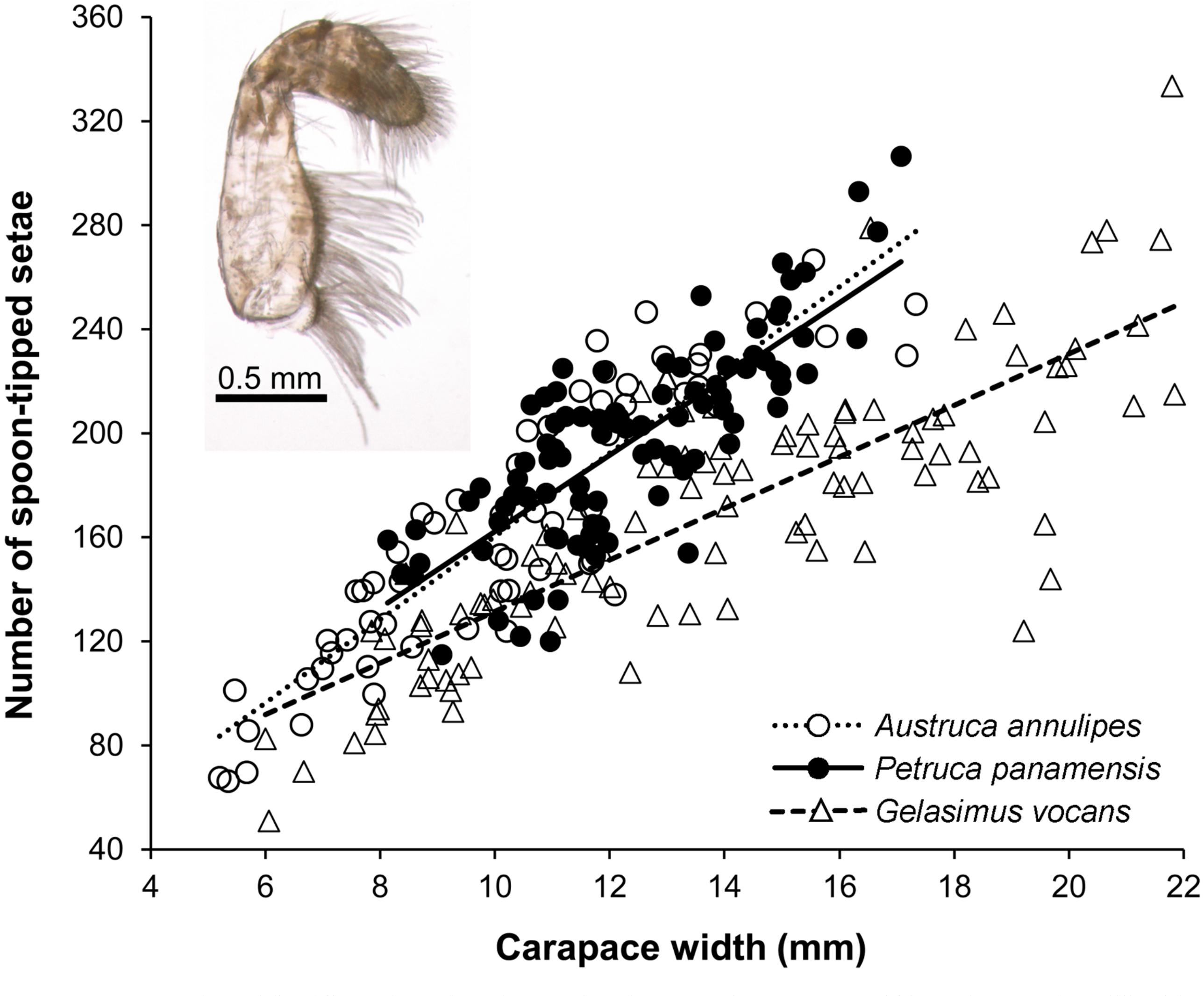

FIGURE 2. Scatterplot and fitted lines of 'number of spoon-tipped setae' against 'carapace width' on the second maxilliped for *Austruca annulipes* (H. Milne Edwards, 1837), *Petruca panamensis* (Stimpson, 1859), *Gelasimus vocans* (H. Milne Edwards, 1837) and the absence of spoon-tipped setae on the second maxilliped of *Ocypode ceratophthalmus* (Pallas, 1772) (inset photograph).

TABLE 1. Spoon-tipped setae coverage on second maxilliped and characteristics of the median tooth and stem of the urocardiac ossicle and the number and types of teeth on the lateral tooth plate of the zygocardiac ossicles in *Austruca annulipes* (H. Milne Edwards, 1837), *Gelasimus vocans* (Linnaeus, 1758), *Petruca panamensis* (Stimpson, 1859) and *Ocypode ceratophthalmus* (Pallas, 1772). C, canine; CO, comb-like structure; I, incisor; M, molar; MT, median tooth; PM, pre-molar; PMM, pre-molar + molar.

<table>
<tr><th>Trophic role</th><th colspan="3">Deposit feeder</th><th colspan="3">Deposit feeder</th><th colspan="3">Herbivore</th><th colspan="4">Omnivore</th></tr>
<tr><td>Species</td><td colspan="3"><i>Austruca annulipes</i></td><td colspan="3"><i>Gelasimus vocans</i></td><td colspan="3"><i>Petruca panamensis</i></td><td colspan="4"><i>Ocypode ceratophthalmus</i></td></tr>
<tr><td>2nd maxilliped</td><td colspan="3"></td><td colspan="3"></td><td colspan="3"></td><td colspan="4"></td></tr>
<tr><td>Coverage of spoon-tipped setation on inner merus</td><td colspan="3">≈ 60–70%</td><td colspan="3">≈ 50%</td><td colspan="3">≈ 50%</td><td colspan="4">0%</td></tr>
<tr><td>Gastric mill</td><td colspan="3"></td><td colspan="3"></td><td colspan="3"></td><td colspan="4"></td></tr>
<tr><td>Urocardiac ossicle</td><td colspan="3"></td><td colspan="3"></td><td colspan="3"></td><td colspan="4"></td></tr>
<tr><td>Median tooth</td><td colspan="3"></td><td colspan="3"></td><td colspan="3"></td><td colspan="4"></td></tr>
<tr><td>Teeth-like transverse ridges</td><td colspan="3">7</td><td colspan="3">5</td><td colspan="3">5</td><td colspan="4">0</td></tr>
<tr><td>Raised transverse ridges</td><td colspan="3">0</td><td colspan="3">0</td><td colspan="3">0</td><td colspan="4">4</td></tr>
<tr><td>Stem</td><td colspan="3">Short and broad</td><td colspan="3">Flattened sheath with setae on the lateral margins</td><td colspan="3">Slightly swollen median part of the stem</td><td colspan="4">Broad, stout and concave at about mid-length</td></tr>
<tr><td>Zygocardiac ossicle</td><td colspan="3"></td><td colspan="3"></td><td colspan="3"></td><td colspan="4"></td></tr>
<tr><td>Lateral tooth plate</td><td>PMM</td><td>I</td><td>C</td><td>PMM</td><td>I</td><td>C</td><td>PMM</td><td>I</td><td>C</td><td>PM</td><td>M</td><td>I</td><td>C</td></tr>
<tr><td>Number of teeth</td><td>1</td><td>1–5</td><td>2–6</td><td>1</td><td>0–4</td><td>4–8</td><td>1–4</td><td>7–10</td><td>0–7</td><td>2–3</td><td>2</td><td>2–6</td><td>0–9</td></tr>
<tr><td></td><td colspan="3">CO</td><td colspan="3">CO</td><td colspan="3">CO</td><td colspan="4">CO</td></tr>
<tr><td>Number of teeth</td><td colspan="3">17–19</td><td colspan="3">17–20</td><td colspan="3">21–23</td><td colspan="4">22–24</td></tr>
</table>

There were multiple teeth-like transverse ridges (5–7) on the median tooth of the urocardiac ossicle in the three species of fiddler crabs (Fig. 3A, B, C, Table 1), whereas *O. ceratophthalmus* had four raised transverse ridges on the round blunt median tooth (Fig. 3D; Table 1). The stem of the urocardiac ossicles of *G. vocans* had a flattened sheath with setae lining the lateral margins which was not observed in the other three crab species (Fig. 3B; Table 1). Variation in the relative length and width of the stem of the urocardiac ossicle was observed across the four ocypodids.

The arrangements of the zygocardiac teeth for the four species were as follow: *A. annulipes*, PMM(1)I(1–5)C(2–6)/CO(17–19); *G. vocans*, PMM(1)I(0–4)C(4–8)/CO(17–20); *P. panamensis*, PMM(1–4)I(7–10)C(0–7)/CO(21–23); and *O. ceratophthalmus*, PM(2–3)M(2)I(2–6)C(0–9)/CO(22–24) (Table 1). In general, the lateral tooth plate of the two deposit feeders (*A. annulipes* and *G. vocans*) had fewer PMM and I than the herbivore, *P. panamensis* and the omnivore *O. ceratophthalmus. Ocypode ceratophthalmus* had at least one more PM than the three species of fiddler crabs and both the PM and M were prominent. The herbivore, *P. panamensis*, had almost twice the number of incisors (7–10) than the two deposit feeders and omnivore (maximum number = 6 in the other three species) (Table 1). Although the range of the number of canines among the three species of fiddler crabs were in similar ranges, i.e., between 2 to 8, the number of canines in *P. panamensis* was highly variable (0–7) (Table 1). Similarly, a high variability in the range of the number of canines was also observed in *O. ceratophthalmus* (0–9) (Table 1). The two deposit feeders, viz., *A. annulipes* and *G. vocans*, had similar ranges of CO structures (17–20) while the herbivore, *P. panamensis* had more (>20) (Fig. 3E–F, Table 1), like the CO of *O. ceratophthalmus* (Fig. 3H). In addition, the edges of the lateral teeth were smooth (Fig. 3E–G), whereas the zygocardiac teeth in the omnivore, *O. ceratophthalmus* can be clearly seen at the edge (Figs. 1B, 3H).

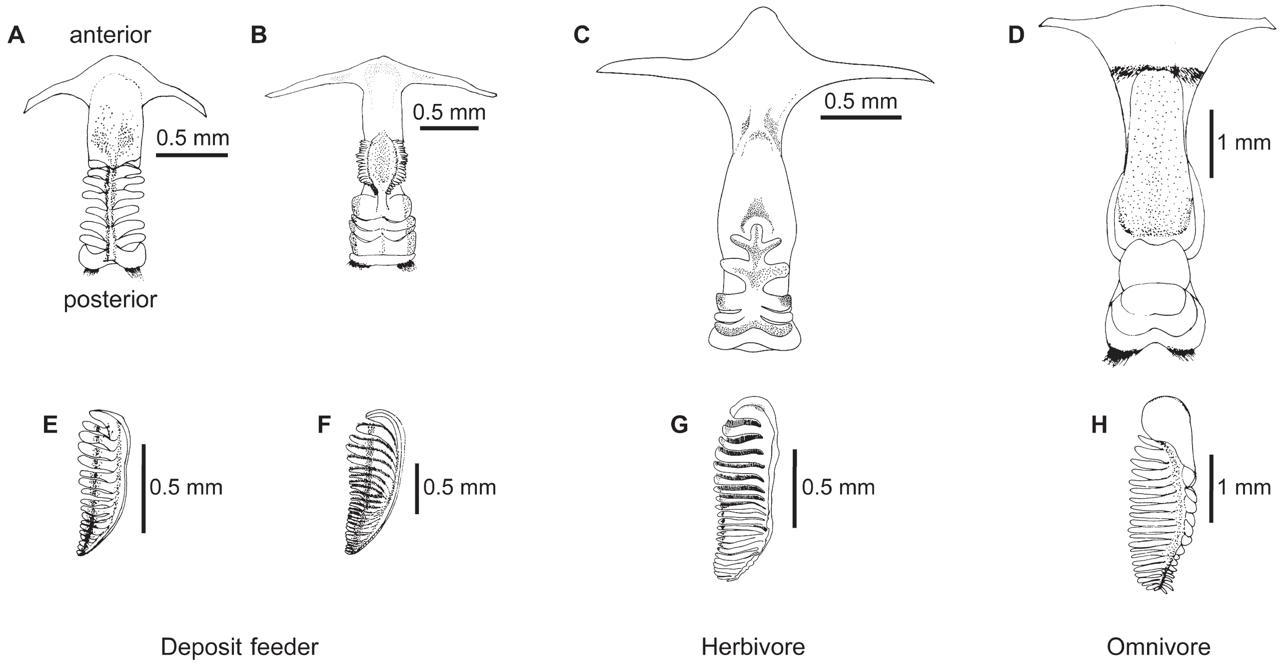

FIGURE 3. Urocardiac ossicle, ventral view (A, B, C, D) and the lateral tooth of the zygocardiac ossicle (E, F, G, H) dorsal view, showing the comb-like structures of the four ocypodid species. A, E, *Austruca annulipes* (H. Milne Edwards, 1837); B, F, *Gelasimus vocans* (Linnaeus, 1758); C, G, *Petruca panamensis*; and D, H, *Ocypode ceratophthalmus* (Pallas, 1772).

Discussion

Ever since Crane (1975: 455) described anecdotally that fiddler crab species that live in sandy habitats have more ST setae on their second maxillipeds than those species living in muddy habitats, there have been several quantitative studies whereby comparisons were made between fiddler crabs from distinctively sandy and muddy habitats (see Yamaguchi & Ogata 2000; Lim 2004; Lim & Kalpana 2011). In the most recent publication on ST setation in fiddler crabs, Lim & Goh (2021) provided evidence that the abundance of ST setae can be an indicator to differentiate between sandy habitats, i.e., down to the level of different sand-grain size—medium sand (particle diameter size of 0.25–0.50 mm) versus fine sand (particle diameter size of 125–250 µm) habitats of *Leptuca terpsichores* (Crane, 1975) and *L. beebei* (Crane, 1975), respectively. In their study, *L. beebei* had significantly fewer ST setae than *L. terpsichores*, possibly because the former species' habitat has sediments with sand grains that are less coarse than the latter's. Hence, the abundance of ST setation on the second maxilliped is indicative of the habitats' sediment grain size characteristics.

In the present study, we compared the coverage of ST in *A. annulipes* and *G. vocans* (data from Lim 2004) with that of *P. panamensis* and *O. ceratophthalmus*. The second maxilliped of *A. annulipes* has a higher percentage coverage (60–70%) of ST setae than the other two fiddler crab species (ca. 50% coverage) (Table 1). It is pertinent to note that *P. panamensis* is atypical in that it does not discard pseudofecal pellets, but swallows the materials directly pinched up from the rocks without sorting (Takeda & Murai 2003), while *G. vocans* sorts and discards pseudofecal pellets like a typical deposit feeding fiddler crab. Takeda & Murai (2003) further suggested that the direct swallowing of the sediments (together with the bits of algae) observed in *P. panamensis* amongst the rocks was a means of reducing loss of stored water by not ejecting wet pseudofecal pellets.

While the coverage of ST setae was similar between *P. panamensis* and *G. vocans*, the abundance of ST (corrected for size) differed (Fig. 2). Instead, the abundance of ST setae of *P. panamensis* was similar to that of *A. annulipes* (Fig. 2). Although it was not possible to sample sediment from the surface of the rocks upon which *P. panamensis* fed, Lim & Goh (2021) inferred (from the comparison of coverage as well as rate of number of ST setae with *Leptuca beebei*) that the sediment was mainly fine sand. In addition, Takeda & Murai (2003) reported that the *P. panamensis* individuals that fed on the sandy substrates directly below the rocks behaved like typical fiddler crabs, whereby small amounts of sand were scooped into the buccal cavity, sorted and discarded as pseudofecal pellets. This could account for the similarity in ST setae abundance between *P. panamensis* and *A. annulipes* for the processing of sandy sediments. Miller (1961) noted that in sandy environments where food is less abundant, ST setae are present in greater numbers for sorting purposes such that only nutrient-rich material is passed to the gut. Although ghost crabs are generally sandy shore inhabitants (i.e., live in habitats with coarse sediment grain size), they are known to exhibit trophic plasticity and are opportunistic carnivores/omnivores. Hence, it is not surprising that *O. ceratophthalmus* did not possess any ST setae on the second maxilliped as they probably do not need to sort coarser inorganic sediment from lighter organic or inorganic matter. This absence of ST setae in *O. ceratophthalmus* is similar to that seen in two other ghost crabs, *O. gaudichaudii* (H. Milne Edwards & Lucas, 1843) (see Lim *et al*. 2016) and *O. quadrata* (Fabricius) (personal observation, AYPY). Both *O. gaudichaudii* and *O. quadrata* are omnivorous (see Lim *et al*. 2016 and do Vale *et al.* 2021 respectively).

In the gastric mill, the ingested food matter is shredded and pulverized mechanically by the coordinated movements of the median tooth of the urocardiac ossicle and the two lateral teeth of the zygocardiac ossicle (Schaefer 1970). From Allardyce & Linton (2010)'s study of six species of decapod crustaceans with carnivorous, herbivorous, and omnivorous trophic habits, they concluded that the morphology of the gastric mill matched the diets well. The two closely related carnivorous species, *Geograpsus grayi* (H. Milne Edwards, 1853) and *G. crinipes* (Dana, 1851), had a blunt, rounded median tooth and flattened lateral teeth with a longitudinal grinding groove, suited to a carnivorous diet of soft animal tissue as well as hard material such as arthropod exoskeleton. The two herbivorous species, *Gecarcoidea natalis* (Pocock, 1889) and *Tuerkayana hirtipes* (Dana, 1851), had a median tooth with raised transverse ridges and lateral teeth with sharp interlocking cusps and ridges which are able to shred fibrous plant materials but lack grinding surfaces. As the representatives of omnivores used in their study were anomurans, *Coenobita perlatus* H. Milne Edwards, 1837 and *Birgus latro* (Linnaeus, 1767), Allardyce & Linton (2010) conceded that the morphology of the gastric mills was significantly different from those of four brachyuran species used to represent carnivores and herbivores, due to them being from different infraorders. Nonetheless, they stated that the morphology of the median tooth and lateral teeth were more generalized towards a mixed diet, with intermediate characteristics between that of a carnivore and an herbivore.

The function of the tooth types on the lateral tooth of the zygocardiac ossicle have been described in detail by Chiu (2006). The premolars and molars are used for grinding food since they are usually wide and rounded in shape; the incisors are used to cut food as their cutting surface is flat and plate-like, while the canines are used for tearing food since their shapes tend to be tapered and sharper. The comb-shaped structures (CO) are used for 'filtering'/sieving food, with the overall shape being comb-like. Chiu (2006) used Principal Component Analysis (PCA) to analyze six morphological characteristics (inclusive of number of tooth plates, molars, incisors, canines, comb teeth, and comb-end hooks) of the gastric mill of 48 species of brachyuran crabs from western Taiwan. Her PCA results showed that the sampled crab species were divided into three large groups, viz., deposit feeders (11 species), omnivores (17 species) and carnivores (16 species), and one small group of four algivorous species. Five out of the 48 species deposit feeders were fiddler crabs within what was then one genus, *Uca*. She concluded that the number of incisors, canines and comb-shaped teeth on the lateral teeth has a high correlation with feeding habits and are less important for taxonomic differentiation. It is pertinent to note that Shih *et al*. (2016) has since reclassified the five fiddler crabs studied by Chiu (2006) into five different genera, viz., *Austruca lactea* (De Haan, 1835), *Gelasimus borealis* (Crane, 1975), *Paraleptuca crassipes* (White, 1847), *Tubuca arcuata* (De Haan, 1835), and *Xeruca formosensis* (Rathbun, 1921). In addition, *O. ceratophthalmus* was considered as a carnivore by Chiu (2006) since she did not detect any plant material in the stomach contents of the specimens that she examined.

In our study, the median tooth of the two deposit-feeding fiddler crabs had teeth-like transverse ridges (Fig. 3A, B) which agrees with Davie *et al*. (2015)'s conclusion that since these crabs consume particulate organic matter derived from vascular plants, microalgae, bacteria, and other small interstitial organisms, the transverse teeth-like ridges are crucial for the fine grinding of such ingested matter. The median tooth of the herbivorous *P. panamensis* observed in our study (Fig. 3C) had combined characteristics between what Warner (1977) depicted as a deposit feeder (Fig. 4A, as represented by *Uca* sp.) and a vascular plant-eater (Fig. 4B, as represented by a sesarmid crab, *Aratus pisonii* (H. Milne Edwards, 1837)). This is not surprising as Takeda & Murai (2003) had observed some *P. panamensis* individuals deposit feeding at the sandy substrate below the rocks, in addition to the usual mode of feeding on encrusted algae on the rocks. Furthermore, our results (Table 1) showed that *P. panamensis* had more incisors (7–10), and premolars/molars (1–4), probably needed for the cutting up as well as the grinding of the algal pieces in its diet, than the other two deposit-feeders (max 4–5 incisors and 1 PMM). In contrast, the teeth-like transverse ridges observed in the fiddler crabs were absent in *O. ceratophthalmus* (Fig. 3D); this absence was also reported in two other ghost crab species: the omnivore *O. sinensis* Dai & Yang *in* Song & Yang, 1985 and the carnivore *O. cordimanus* Latreille, 1818 (see Huang *et al*., 1998). Instead, *O. ceratophthalmus* has raised transverse ridges (Fig. 3D) which are similar to those seen in the varunid, *Helice tridens* (De Haan. 1835), an opportunistic carnivore/omnivore (see Sakai *et al*. 2006) (Fig. 4C). There were also larger and more PM and M at the edge of the lateral tooth—visible even from the dorso-lateral view—in *O. ceratophthalmus* as compared with the fiddler crabs (Fig. 3H). The size and additional number of PM and M are indicative of a diet in which there is a great deal of maceration of the ingested food. This part of our results, thus, indicate that the morphology of the transverse ridges on the median tooth of the urocardiac ossicle (i.e., teeth-like for deposit feeders and raised ridges in omnivores/carnivores) as well as the dentition (tooth type and size) on the lateral tooth of the zygocardiac ossicle are strongly related to the trophic habit of the crabs.

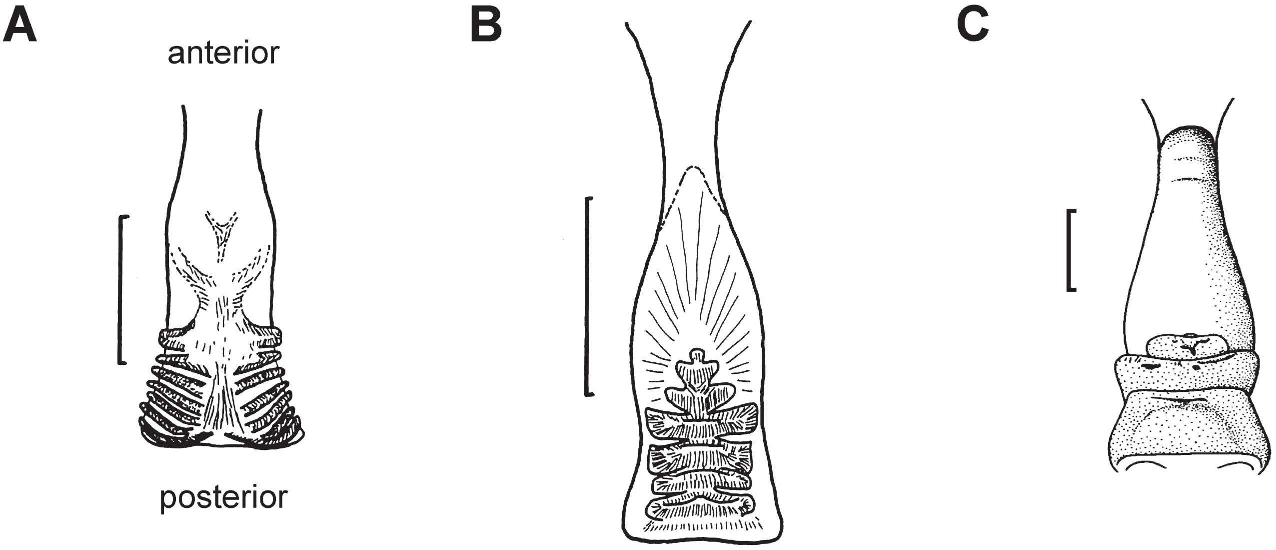

FIGURE 4. Variations in the dorsal urocardiac teeth from the gastric mills of crabs with different diets. A, a deposit-feeder, *Uca* sp. (Ocypodidae); B, vascular plant-eater, *Aratus pisonii* (H. Milne Edwards, 1837) (Sesarmidae); C, an opportunistic carnivore/omnivore (believed), *Helice tridens* (De Haan, 1835) (Varunidae). Scale = 1 mm. (A, B, after Warner 1977: 91, fig. 28; C, after Sakai *et al*. 2006: 6, fig. 4C).

In a study on dotillid crabs, Murniati *et al*. (2023) concluded that there is a tendency for species with more comb-like teeth (e.g., *Dotilla* sp. and *Scopimera* sp.) to inhabit sandy habitats and those with fewer CO teeth (*Ilyoplax* sp.) to live in muddy habitats. Our results showed that while *O. ceratophthalmus* had the highest number of CO teeth (22–24) (suggestive of sandy habitat inhabitant), there is no difference observed in the two deposit-feeding fiddler crab species to differentiate their respective habitats—similar ranges of 17–19 (*A. annulipes*, sandy) and 17–20 (*G. vocans*, muddy) (Table 1). Hence, the trend reported by Murniati *et al*. (2023) for the dotillids may not hold true for ocypodids. In addition, previous work by Huang *et al*. (1998) on two ghost crab species that inhabit the supralittoral zone (i.e., sandy beaches) documented similar ranges of CO teeth as that of the fiddler crabs used in our study: *O. sinensis* and *O. cordimanus* had about 16 and 17 CO teeth respectively, i.e., not as many as that seen in *O. ceratophthalmus*. It should be noted that the sample sizes in Huang *et al*. (1998)'s study were small: *O. sinensis* (n = 4, 2 males and 2 females) and *O. cordimanus* (n = 3, 1 male and 2 females).

It is evident from our results that the morphology of the median tooth and the lateral teeth of the urocardiac and zygocardiac ossicles of the four ocypodids show adaptations for the processing of the ingested food in their respective diets. Especially in fiddler crabs, there is now substantial evidence to show that both the ST setae abundance (e.g., Icely & Jones 1978; Yamaguchi & Ogata 2000; Lim 2004, etc., and present study) and gastric mill morphology, in terms of grinding surfaces of the urocardiac median tooth and dentition of zygocardiac lateral teeth (e.g., Icely & Jones 1978; present study) are indicative of the habitat characteristics as well as trophic habits respectively. Thus, characters of the median tooth which have been cited to be useful in distinguishing among closely related species (see Naderloo *et al*. 2010; Shih *et al*. 2015), can also shed light on the trophic habits of the crabs. Of course, the strength of the relationship between morphology and phylogeny and/or diet, probably depends on adaptive pressure as well as environmental constraints.

Acknowledgements

This paper is dedicated to our dear friend, Ngan Kee, with the fondest of memories as she introduced us to the fascinating topic of gastric mill morphology 13 years ago. Due to our individual busy schedules, it was unfortunate that we did not have the opportunity to deepen our collaboration in this area of research, save for a conference presentation based on some preliminary work on gastric mills of the local Singapore ocypodids, at the ICC7 in Qingdao, China in 2010. We are deeply appreciative of the editors of this Memorial Volume for extending the invitation to two non-taxonomists to be part of this meaningful tribute to Ngan Kee. Comments from two anonymous reviewers contributed to the improvement of the manuscript substantially. Dr John Christy's great hospitality at his laboratory in the Smithsonian Tropical Research Institute, Panama, is gratefully acknowledged. The Authoridad de Recursos Acuáticos de Panamá (ARAP) granted us the ARAP Collection Permit for the collection of *P. panamensis* from Punta Culebra. We thank JC Mendoza for the generous use of his research stereo microscope. Funding was provided by the research grants RI 10/03 SL, RS 04/08 and RI 8/10 SL from the National Institute of Education, Nanyang Technological University, to SSLL.

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