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# Gastric Teeth of Some Thoracotreme Crabs and Their Contribution to the Brachyuran Phylogeny

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*ABSTRACT* The gastric teeth of three ocypodoid species were investigated using scanning electron microscopy, and the morphological results were discussed with respect to the known food preferences. The species were chosen in particular because of contrasting ideas about their relationships within the Thoracotremata. For the genera *Heloecius*, *Dotilla*, *Mictyris*, and "*Uca*" (s. str.), we find a specific correlation of the gastric teeth with the suspension feeding. The lateral gastric teeth of *Uca* have no prominent lateral teeth cusps, and most of their teeth surface consists of transverse comb-like lamellae. However, this possible food adaptation does not exclude the usability of specific teeth characters to distinguish species of suspension feeders. The closer relationship of the Dotillidae to grapsoid lines of gecarcinid or sesarmid crabs suggested by molecular data is not supported by the gastric teeth. For the genus *Ucides*, we found several characters that distinguish *Ucides* from the remaining ocypodoid genera *Heloecius*, *Dotilla*, *Mictyris*, and "*Uca*." In particular, the structures of the lateral and the dorsomedian teeth show some similarities to genera of the Gecarcinidae and Sesarmidae. Our results suggest that foregut characters can be used for phylogenetic analyses. J. Morphol. 272:1109–1115, 2011. 

KEY WORDS: gastric teeth; ocypodoidea; grapsoidea; SEM

## INTRODUCTION

During the last decade, new morphological characters such as the foregut structures (gastric teeth and foregut ossicles) have been introduced into brachyuran phylogenetic discussions. Their morphology is receiving increasing attention as a valuable character complex to separate brachyuran taxa of different ranks (Sakai et al., 2006; Brösing et al. 2007; Huespe et al., 2008; Allardyce and Linton, 2010; Alves et al., 2010; Brösing, 2010; Naderloo and Schubart, 2010).

The foregut of brachyuran decapods is divided into two regions: the cardiac foregut with the oesophagus and the pyloric foregut. The anterior portion of the cardiac foregut is a thin-walled, noncalcified, sack-shaped structure. It is stretched between several cardiac ossicles and cardiac plates. Some of these cardiac ossicles bear teeth, forming the chewing apparatus of the gastric mill. The posterior portion of the cardiac foregut and the pyloric foregut are supported and strengthened by a number of small pyloric ossicles and plates (Maynard and Dando, 1974; Meiss and Normann, 1977; Felgenhauer, 1992; Ceccaldi, 1997; Brösing 2002; Brösing et al., 2002; Brösing, 2010). In contrast to the outer mouthparts, the teeth of the gastric mill are mainly responsible for crushing and cutting ingested food particles.

A correlation of the foregut structures with described food preferences and their usability for phylogenetic reconstructions in decapods have been discussed by several authors within the last decades, especially in relation to anomuran crabs (Caine, 1975), parastacid crayfish (Growns and Richardson, 1990), lower decapods (Abele and Felgenhauer, 1986; Felgenhauer and Abele, 1983, 1985, 1989), and brachyuran crabs (Crane, 1975; Kropp, 1986; Yang, 1986; Sakai et al., 2006; Brösing et al., 2007). These authors concluded that the gastric mill is more affected by phylogeny that by the animals' diet. This conclusion is strongly supported the observation that the phylogenetic groups built on gastric mill morphology are the same as those built on the examination of other phylogenetically important characters, such as the gonopods (e.g., Sakai et al., 2006).

This article focuses on the gastric teeth of a set of selected thoracotreme species that has been placed in different families in the past. Species selection has been made to contribute to the ongoing phylogenetic discussions as to the classification of the Ocypodoidea and Grapsoidea.

## MATERIAL AND METHODS

### Animals

Animals used in this study are listed in Table 1.

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*TABLE 1. Investigated species*

| Species | Catalog Number | Location | CW/CL (mm) |
|---|---|---|---|
| *Dotilla fenestrata* (Hilgendorf, 1869) | SMF 9109 | Kenja, Küste, S. Malindi, Mida-Creek, Insel, Mangrove, Okt. 1979, leg Grasshoff | 11/9 |
| *Ucides occidentalis* (Ortmann, 1897) | SMF 4139 | No locality data available | 66/45 |
| *Heloecius cordiformis* (H. Milne Edwards, 1837) | SMF 921 | Australien, Queensland, Jacobs Well ca. 50 km S. Brisbane, Salzwiese, 30. V. 1980, leg. M. Türkay | 24/16 |

## Methods

Gastric teeth of 70% ethanol-preserved specimens were dissected using a stereo microscope (LEICA MZ8) and prepared for scanning electron microscopy according to Brösing et al. (2002). For scanning electron microscopy, we used AC digital scanning electron microscope (CamScan, Elektronenoptik GmbH) at the Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt.

## RESULTS

### Gastric Teeth of *Dotilla fenestrata*

The lateral teeth are characterized by an antero-lateral straight margin without teeth cusps on the first two-thirds of the lateral teeth. The posterolateral third of the lateral teeth has three to four small teeth cusps (Fig. 1A). The median margin consists of 19 transverse comb-like lamellae (Fig. 1A,B). The urocardiac ossicle (VII), carrying the dorsomedian tooth, has a triangular shape and widens at the posterior end. The dorsomedian tooth at the posterior quarter of the ossicle consists of two transverse teeth cusps. The anterior and lateral margins of the first quarter of the urocardiac ossicle have a row of setose hairs (Fig. 1C). Antero-laterally, with respect to the lateral gastric teeth there are at least 14 long extended pointed accessory teeth (Fig. 1D). The cardio-pyloric valve has antero-dorsally a remarkable single tooth cusp surrounded by brush-like setae (Fig. 1E). Its dorsal surface is trapezoidally shaped, with one pair of posteriorly directed, long bristles and one pair of laterally fringed bulges (Fig. 1F).

### Gastric Teeth of *Ucides occidentalis*

The lateral gastric teeth have well-developed and transversally arranged tooth cusps and become smaller toward the anterior. The transverse cusps of the posterior half have small anteriorly directed comb-like processes as in *Heloecius* (Fig. 2A,B). The dorsomedian tooth consists of 12 transverse tooth cusps, becoming smaller toward the anterior (Fig. 2C). Anterolaterally with respect to the lateral gastric teeth are situated 15 accessory teeth with lancet-shaped tips (Fig. 2D). The cardiopyloric valve is dorsally triangular with bristles on its posterodorsal margin and an anterodorsal single strong median tooth (Fig. 2E). The anterior margin of the cardiopyloric valve is covered by brush-like setae (see also Fig. 2E). Furthermore, the dorsolateral margin has a pair of laterally fringed bulges as in *Dotilla* (Fig. 2F).

### Gastric Teeth of *Heloecius cordiformis*

The lateral gastric teeth are oval-shaped and lack raised tooth cusps. Most of the 22 transverse lamellae consist of small, comb-like processes pointing toward the anterior (Fig. 3A,B). The lamellae of the posterior half of the lateral teeth end mid-laterally in a bunch of elongated bristles. The anterior third of the dorsomedian tooth is oval-shaped, followed posteriorly by a pair of wing-like plates, which are connected in the midline and elongated toward the posterior third. The remaining dorsomedian tooth-structure looks like a raised transverse ridge (Fig. 3C). Anterolaterally with respect to the lateral gastric teeth are situated 15 accessory teeth with mostly rounded tips (Fig. 3D). The dorsal part of the cardiopyloric valve is triangular and has two teeth pointed toward the anterior. Laterally of these teeth there are brush-like setae (Fig. 3E,F).

## DISCUSSION

The two mangrove species *Heloecius cordiformis* (Milne Edwards, 1837) and *Ucides occidentalis* (Ortmann, 1897) as well as their phylogenetic placement have been discussed controversially during the last decades. The genus *Ucides* was placed within the Gecarcinidae for a long time since its description. Due to the swollen branchial regions, which were considered as the prime character of the Gecarcinidae, Chace & Hobbs (1969), correctly pointed out that this character is correlated with the terrestrial life and, therefore, is more of an ecological feature than an indicator of phylogenetic relationships. They stated that all other characters, especially those as the mouthparts and legs, were more similar to ocypodids than to gecarcinids and moved the genus to the OcypodidaeThe relationships within this family remained, however, uncertain. Türkay (1970) agreed with the conclusions of the former authors and kept the genus in the ocypodids. When re-examining the taxonomic position of the Australian mangrove crab genus *Heloecius*, Türkay (1983) discovered the coxosternal position of the male genital openings of this genus and therefore removed it from the relationship with the purely sternotreme genus

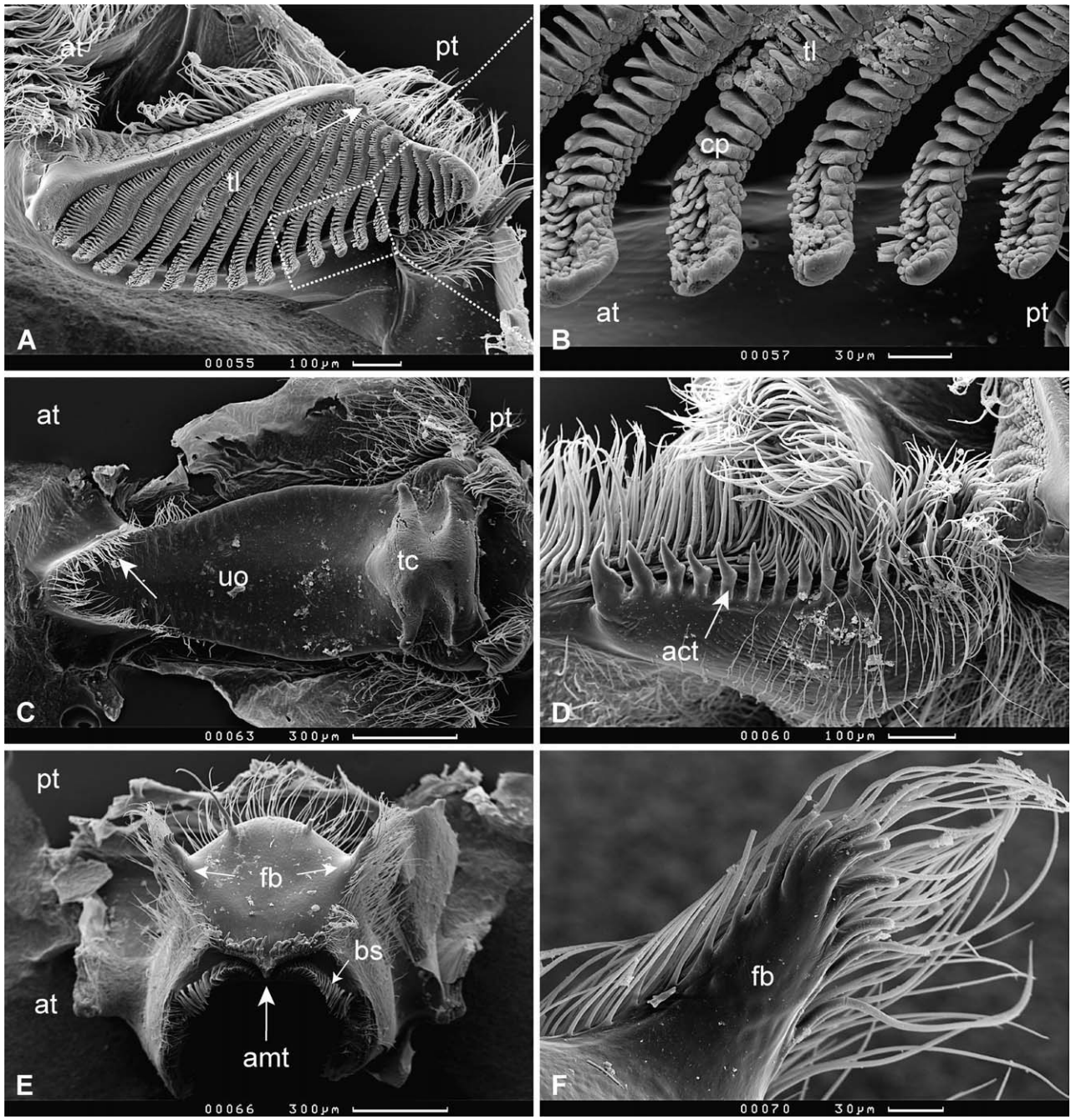


Fig. 1. Gastric teeth of *Dotilla fenestrata*, SMF 9109, (**A**) Dorsomedian view on the lateral teeth. (**B**) Section of Figure 1A, transverse lamellae of the lateral teeth. (**C**) Ventral view on the dorsomedian tooth. (**D**) Lateral view on the accessory teeth. (**E**) Anterodorsal view on the cardiopyloric valve. (**F**) Enlarged view of the fringed bulges. alt, anterolateral teeth; amt, anteromedian tooth; at, anterior; bs, brush-like setae; cp, comb-like processes; fb, fringed bulges; pt, posterior; tc, teeth cusps; tl, transverse lamellae; uo, urocardiac ossicle; wp, wing-like plates.

*Uca*, with which the former, indeed, shares a superficial similarity, and accommodated it in a separate subfamily, the Heloecinae. This conclusion was later confirmed by Fielder and Greenwood (1985) on the basis of larval morphology. Türkay (1983) also discussed similarities and differences between *Heloecius* and *Ucides* and showed that the latter is more advanced as to sternotremy based on the fact that the seventh and eighth sternite meet over the base of the penis, but still the shape of the hind part of the sternum is very similar in both genera, as is the general shape of the male pleopod. He therefore included *Ucides* tentatively in the Heloecinae.

Ng et al. (2008) recognized *Heloecius* and *Ucides* as belonging to distinct families [Heloeciidae (Milne Edwards, 1852) and Ucididae (Števcic, 2005)] within

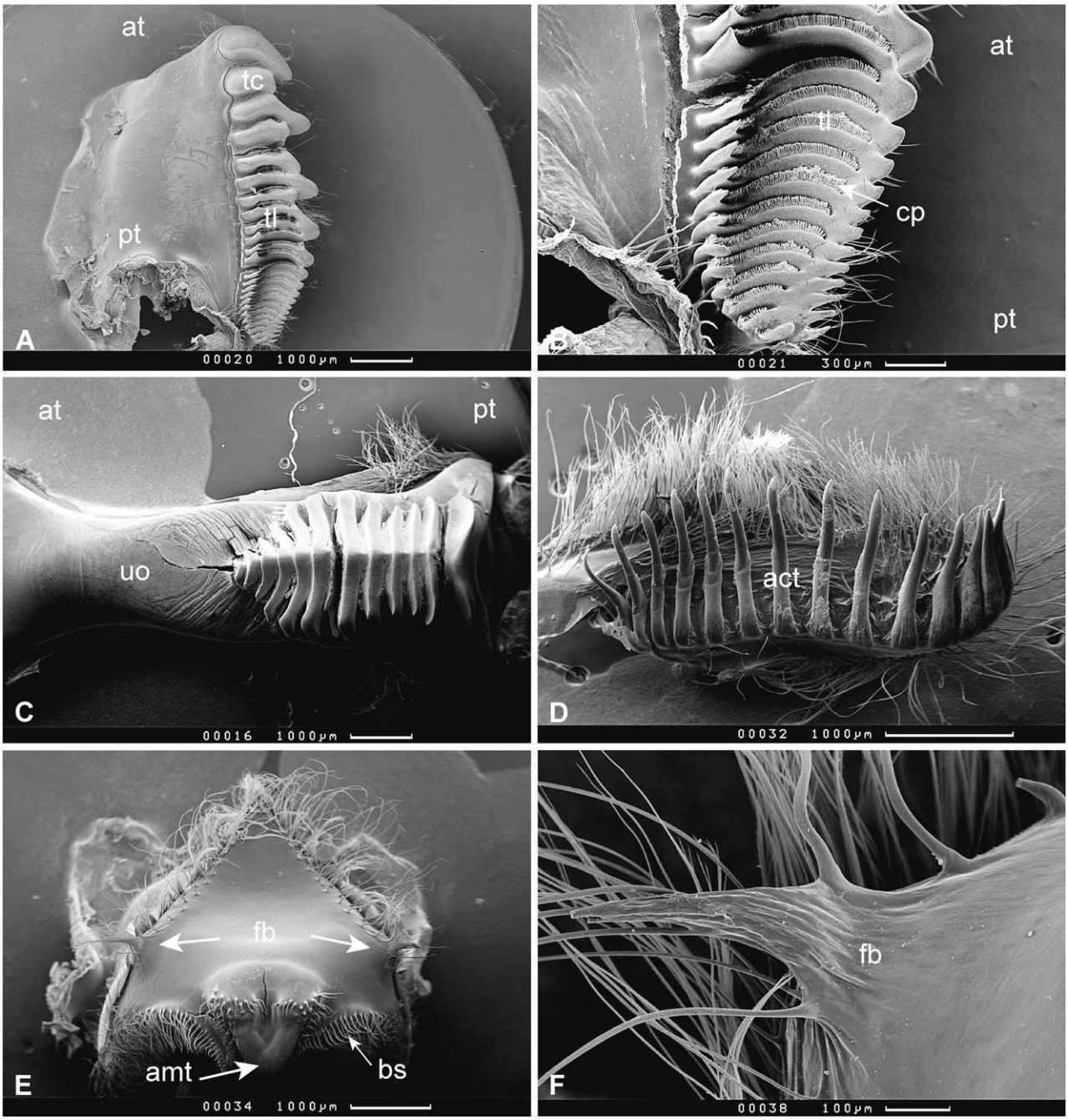


Fig. 2. Gastric teeth of *Ucides occidentalis*, SMF 4139, (**A**) dorsal view on the lateral teeth. (**B**) Dorsal view on the posterior half of the lateral teeth with transverse lamellae. (**C**) Dorsal view on the dorsomedian tooth. (**D**) Lateral view on the accessory teeth. (**E**) Anterodorsal view on the cardiopyloric valve. (**F**) Enlarged view of the fringed bulges.

the Ocypodoidea (Rafinesque, 1815). Concerning the Dotillidae, molecular data from Kitaura et al. (2002) and Schubart et al. (2006) suggest a closer relationship of *Dotilla* (Ocypodidae) to the Gecarcinidae, Plagusiidae, and Sesarmidae.

Furthermore, the results of our study indicate that the general conclusion of a nonadaptation of foregut structures to the described food preferences needs more differentiation. This means that the morphology of the foregut ossicles and the attached gastric teeth have to be evaluated separately. The comparison of the gastric teeth of at least four different taxa and their morphological similarities suggests a possible correlation to a filter/suspension, herbivore or carnivore feeding behavior, whereas the foregut ossicles appear not to be affected by the food preference. However, this does not exclude the that gastric teeth morphology may be used for taxonomic

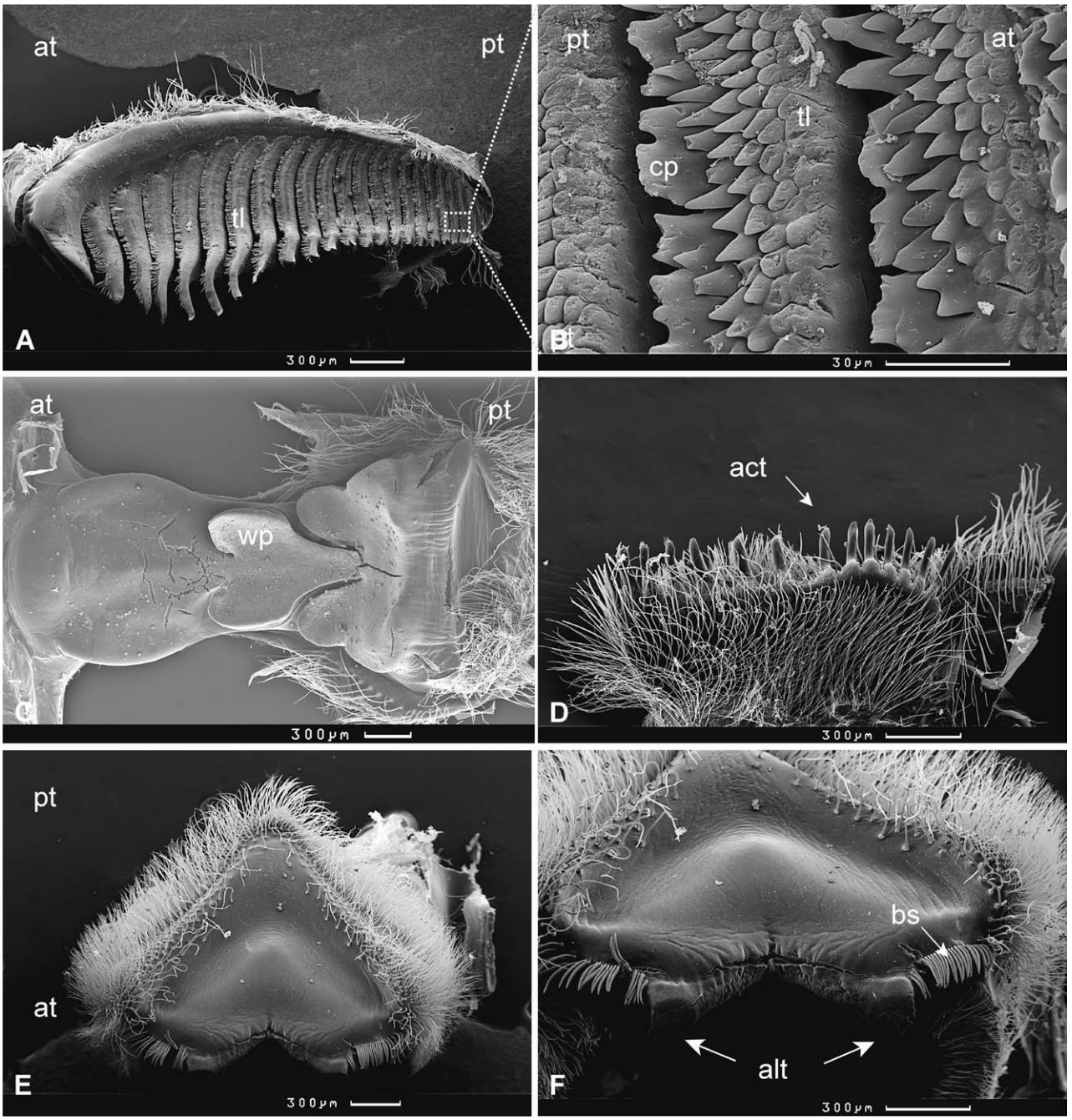


Fig. 3. Gastric teeth of *Heloecius cordiformis*, SMF 921, (**A**) dorsal view on the lateral teeth. (**B**) Ausschnitt von Fig. 3A, Transverse lamellae of the lateral teeth. (**C**) Ventral view on the dorsomedian tooth. (**D**) Lateral view on the accessory teeth. (**E**) Dorsal view on the cardiopyloric valve. (**F**) Anterodorsal view on the cardiopyloric valve.

studies of closely related taxa (e.g., Naderloo and Schubart, 2010; Naderloo et al., 2010).

The present study indicates that in *H. cordiformis* and *D. fenestrata*, as well as in *Mictyris longicarpus* and *Uca* (*Minuca*) *rapax* (Brösing, 2010), the lateral gastric teeth are similarly shaped because of the absence of lateral teeth cusps and the presence of transverse lamellae with comb-like structures on the anterior margin. All of the above-mentioned species are suspension feeders (Table 2), which all occur at tropical and subtropical beaches. However, Maitland (1990) described *Heloecius* also to have well-developed mandibles for feeding on plants or animal material. This raises the question: why *Heloecius* is able to feed on animals and plants with gastric teeth structures suitable for filter feeding? Or is the food preference independent of the structure of these teeth?

An unclear structure of the cardiopyloric valve is found in specimens of *D. fenestrata* and *U. occidentalis*. Both have fringed bulges at the dorsolateral mar-

*TABLE 2. Brachyuran food preferences*

| Taxa | Herbivore | Carnivore | Suspension Filter feeders | References |
|---|---|---|---|---|
| Dotillidae Stimpson, 1858 | | | ✓ | Warner, 1977; Grahame,1983; Henmi and Koga, 2009 |
| Heloeciidae Milne Edwards, 1852 | ✓ | ✓ | ✓ | Griffin, 1968; Maitland, 1990 |
| Mictyridae Dana, 1851 | | | ✓ | Quinn, 1980, 1986 |
| Genus *Uca* (*s. str.*) | | | ✓ | Crane, 1975; Robertson and Newell, 1982 |
| Ucididae Števcic, 2005 | ✓ | | | Nordhaus, 2003, Nordhaus and Wolff, 2007; Nordhaus et al., 2006 |
| Genus *Cardisoma* | ✓ | ✓ | | Herreid II, 1963, Greenaway and Raghaven, 1998 |
| Sesarmidae Dana, 1851 | ✓ | | | Emmerson and McGwynne, 1992; Micheli, 1993; Ng and Sivasothi, 1999 |

gin that are not present in *H. cordiformis*. This means that the two more ancestral genera *Ucides* and *Heloecius* may not be closely related, and the sterna structures are plesiomorphies rather than synapomorphies. Our results also show that the gastric teeth of *U. occidentalis* are similar to the structures described for *Cardisoma armatum* and *Pseudosesarma moeschi* (Brösing, 2010). They all have clear transverse lamellae on the lateral gastric teeth and at least in *P. moeschi,* there are also comb-like structures on the anterior margin of the transverse lamellae. Furthermore, the dorsomedian teeth of *U. occidentalis*, *C. armatum*, and *P. moeschi* consist of transverse teeth cusps. On the basis of these results, we think that the structures of the gastric teeth (the lateral teeth and the dorsomedian tooth) of *U. occidentalis* do not support the removal of this genus, and the family Ucididae, from the Grapsoidea, to which the Gecarcinidae and Sesarmidae belong, and its inclusion into the Ocypodoidea.

Our results also show that the teeth of the brachyuran gastric mill have a comparatively stable ground pattern, which does not exclude adaptation to specific food preferences or resources.

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