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Functional morphology of comminuting feeding structures of *Trichodactylus borellianus* (Brachyura, Decapoda, Trichodactylidae), an omnivorous freshwater crab

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A B S T R A C T

Crustaceans exhibit great diversity of feeding structures with morphological traits that are useful to infer the general trophic habits of species. In this study, we analyzed the functional morphology of comminuting feeding structures (mandibles, chelipeds, gastric mill) of the freshwater crab *Trichodactylus borellianus* directly related with the food fragmentation. The heterochely and mechanical advantage (MA) of the chelae were also studied. In both analyses, we considered the relationship between morphology and the natural diet. We expected to find a consistent relation between feeding habits and morphological traits. In general, we found simple structures armed with uniform setal systems and feeding appendages without pronounced teeth or spines. Mandibles have primarily cutting functions, helping with the food anchoring and fragmentation with mandibular palps armed with pappose setae. Chelipeds were covered with spines and simple setae. Adult males exhibited right-handedness with high MA of the major chelae. The ingested, relatively large pieces of food are finally chewed by a gastric mill equipped with sharp cusps characteristic of decapods with low ingestion of crude fiber material. The morphology of the feeding apparatus revealed that it is well adapted to an omnivorous diet, being able to cope with dietary changes.

1. Introduction

The majority of decapod crustaceans live in aquatic environments and evolved morphological adaptations for a broad variety of food types, from suspended particles to hard animal prey (Watling, 2013; Saborowski, 2015). Feeding in Decapoda is a complex process that involves integrated actions of internal and external structures that finally culminates in the absorption of nutrients. According to Watling (2013 p. 237) "the process of digestion in all animals involves breaking down the food material into even smaller components that, under the action of digestive enzymes, results in molecules small enough to be absorbed by specialized cells in the digestive tract".

Externally, chelipeds and mouth appendages capture and sort the food particles, initiating the crushing of the aliments. The mouth apparatus is composed of six pairs of appendages: one pair of mandibles, two pairs of maxillae (1-2) and three pairs of thoracic appendages (maxillipeds 1-3). Functionally, mandibles are the main comminuting elements (Factor, 1989; Maitland, 1990) for cutting, tearing and crushing food (Garm and Høeg, 2001; Jaszkowiak et al., 2015). The remaining appendages are involved in other functions such as the transporting, holding, current generation, sorting of the food. Internally, the coordinated movement of the gastric mill ossicles (Heinzel, 1988; Heinzel et al., 1993) and the action of the digestive enzymes further reduce the size of particles (Factor, 1989; Felgenhauer and Abele, 1989; Watling, 2013) for more chemical breakdown, absorption of nutrients and waste production (egestion and excretion) (Icely and Nott, 1992). In this study, we focus the efforts on the morphological traits of three feeding structures (mandibles, chelipeds and gastric mill) directly involved in the food fragmentation. These structures may contain

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important information about the feeding habits of species and even provide clues for the trophic preferences when the diet spectra are unknown.

In the Neotropic region, Trichodactylidae is a family of freshwater crabs associated to river basins of Center and South America with exception of Pacific slope rivers (Magalhães, 2003; César et al., 2004). Studies about trophic aspects of these lowland crabs revealed that their diet is mainly omnivorous, including prey types of different sizes and hardness (from rotifers to mollusks), algae and vegetal material of variable relative importance according to the species (Collins et al., 2007). Among trichodactylid species, *Trichodactylus borellianus* is a crab of broad distribution in South America (from 0° to 35° S) (Magalhães, 2003). It is a small-sized crab with abbreviated larval development (Vogt, 2013). Generally, it forms abundant populations associated with aquatic macrophytes of the floodplain littoral zone (Collins et al., 2006; Carvalho et al., 2013a). The natural diet of this crab is well documented and composed of a wide range of food types, being characterized as omnivorous, generalist and opportunist (Williner and Collins, 2013; Carvalho, 2014; Carvalho et al., 2016).

The trophic spectra of juveniles and adults have similar components with some differences in the relative importance of food items (Williner and Collins, 2013). The main prey types found in stomach contents are also those with great availability in the environment, such as oligochaetes, chironomid larvae, algae and vegetal remains (Carvalho et al., 2016). However, the consumption of vegetal remains increases with the size of the crab, while juveniles seem to consume more algae and chironomid larvae (Williner and Collins, 2013). Other frequently found items in gut contents are rotifers, microcrustaceans, insect larvae, mollusks and even terrestrial invertebrates. In this way, the attempt to understand the morphological adaptations that allow juveniles and adults to eat a great variety of items of animal and vegetal origin and successfully occupy floodplains of large rivers within a broad geographical distribution (Magalhães, 2003) proves interesting.

Many studies support the close relationship between diet and feeding structures (Schaefer, 1970; Caine, 1975; Kunze and Anderson, 1979; Garm, 2004a,b; Allardyce and Linton, 2010; Ashelby et al., 2015). When species are macrophagous with predatory habits, the maceration structures are well developed with few robust setae and well calcified ossicles for grinding and crushing (Caine, 1975; Kunze and Anderson, 1979; Heeren and Mitchell, 1997; Allardyce and Linton, 2010). Otherwise, the feeding apparatus of filter feeders are setose with maceration structures weakly developed (Caine, 1975; Kunze and Anderson, 1979). In herbivores, the fibrous nature of the food requires structures capable of cutting and crushing the piece to help the disruption of the vegetal cell (Linton and Greenaway, 2007; Watling, 2013). Incisor mandibles and a gastric mill with sharp ridges are very useful in this case (Allardyce and Linton, 2010; Watling, 2013). Otherwise, carnivores have blunt and smooth structures suitable to break down less fibrous structures such as animal items (Allardyce and Linton, 2010). Conversely, some authors support the hypothesis that structures such as the foregut have a conservative form related to the phylogeny of the taxon (Felgenhauer and Abele, 1989; Brösing and Türkay, 2011). Although there are no specific studies that quantify the correlation between phylogeny and the gastric mill, the morphology of the gastric teeth often appears to be adjusted toward a specific function related with the diet of species.

Although the functional morphology of feeding structures is a field of research widely studied in freshwater true crabs (Brachyura), there are fewer contributions and even less in trichodactylid crabs. In trichodactylid species, the contributions were made in descriptive studies of the foregut ossicles (Alves et al., 2010), seta morphology (Vieira et al., 2013), and a study of feeding selective behavior (Torres et al., 2013). We propose in the present study to analyze the functional morphology of comminuting feeding structures (mandibles, chelae, gastric mill) of *T. borellianus* directly related with the food fragmentation. The morphology of these structures was analyzed in relation to the natural diet previously described in the literature. We expect to find that our results support the hypothesis that those feeding structures directly related with the food comminuting are consistent with the feeding habits of *T. borellianus*. In this way, we predict that juveniles and adults of *T. borellianus* have intermediate morphological traits of herbivorous and carnivorous crabs given their similar trophic spectra.

2. Methods

2.1. Crab collection and dissection

Specimens of *T. borellianus* were manually collected with the aid of a hand net (500 μm mesh size) from the roots of the aquatic vegetation at the shoreline of water bodies of the middle Paraná floodplain (S 31°33′43″, W 60°30′58″). They were anesthetized in ice and sacrificed in alcohol 96%. Crabs were separated in juveniles and adults considering the morphological sexual maturity (Williner et al., 2014). Crabs with more than 7 mm of cephalothorax width were considered adults while those smaller than this size were juveniles.

The carapaces of crabs were opened and stomachs and mandibles were manually dissected under a stereoscopic microscope. Right and left chelipeds were dissected from the crabs' bodies by separating the propodus from the carpus. Gut content, coarse food remains and coarse debris were washed with water with the aid of a squeeze bottle. To remove muscular remains and fine attached debris, feeding structures were cleaned in 10% KOH for 24 h, washed with distilled water and conserved in alcohol 70%. Additionally, chelipeds and mandibles were sonicated in a buffer solution (PBS, pH 7.4) to remove remaining debris. These steps followed the indications of Felgenhauer (1987) with modifications. We observed 10 stomachs, 38 chelipeds (right and left) and 28 mandibles (right and left) under stereoscopic microscope and scanning electron microscope (SEM).

2.2. Preparation of feeding structures for light and scanning electron microscope observation

All dissected stomachs were opened cutting the cardiac sac and exposing the gastric mill. Those stomachs used for visualization under light microscope were stained with Alizarin Red (1%) after the treatment with KOH (10%) (Brosing et al., 2002). Stomachs were submersed in a recipient with alcohol 70% and photographed with a Canon EOS Rebel T2i camera attached to a Leika S8APO dissecting microscope. Specific images were taken of ossicles of the gastric mill: zigocardiac ossicles, uropiloric ossicle, pectineal ossicle and the cardiopyloric valve. The terminology used in the foregut descriptions followed those used by Meiss and Norman (1977) and Brösing et al. (2002). Descriptions of setal system are based on Garm (2004a) and Garm and Watling (2013).

Chelipeds, mandibles and dissected stomachs for analysis with SEM were air-dried in a desiccator containing silica gel with indicator of dampness during at least 24 h. Once mounted on a metal stub using double-sided tape and/or silver paint, samples were gold coated for 120 s using Combined Deposition System metal/carbon, SPI Supplies, AX-12157, operated under argon atmosphere (18 mA) for 120 s. Following, observations were made using a JSM-35C SEM (JEOL, China), equipped with a system of digital image acquisition SemAfore, at an accelerating voltage of 20 kV.

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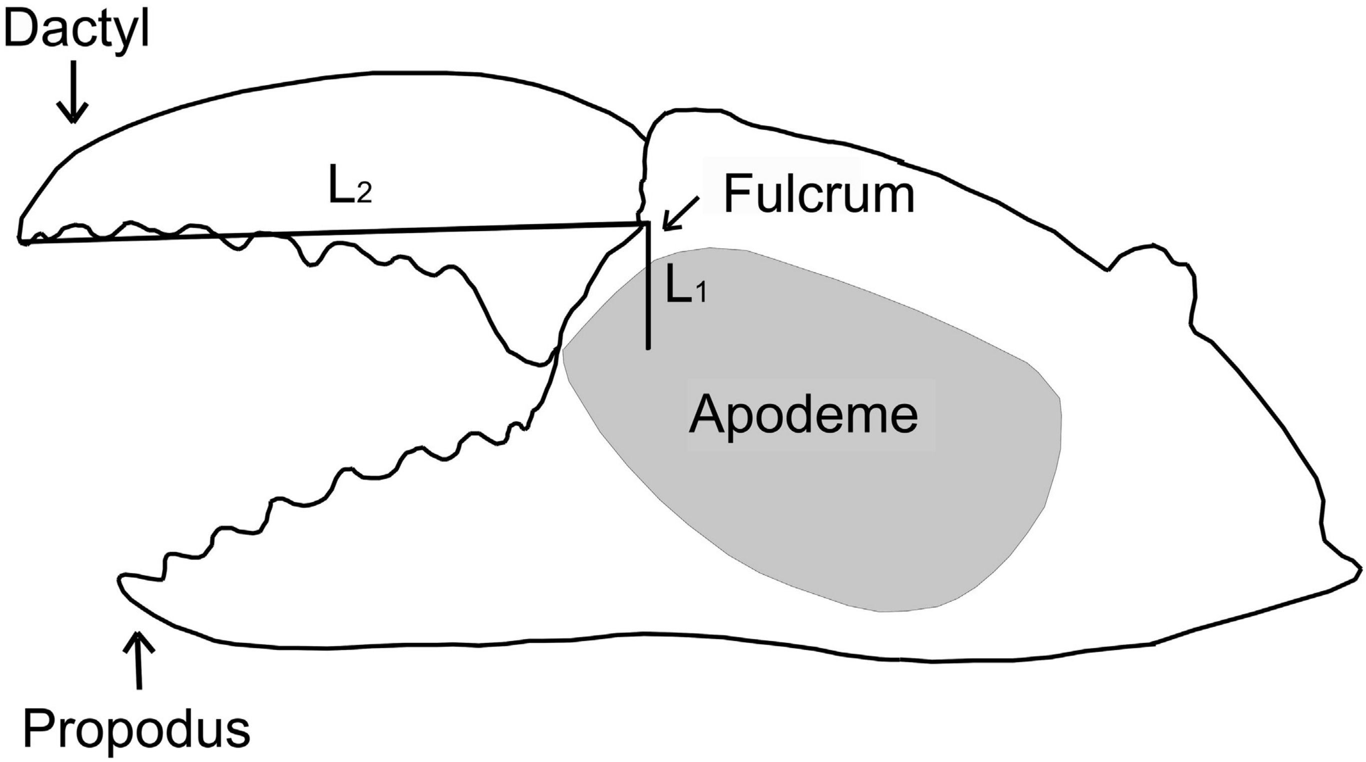

Fig. 1. Parameters used to calculate the mechanical advantage (MA) of chelipeds of *Trichodactylus borellianus*. MA is given by the ratio L_1/L_2 of the dactyl length. L_1: distance between the fulcrum and the proximal apodeme insertion, L_2: the length between the fulcrum and the point on the dactyl.

2.3. Heterochely and mechanical advantage

To quantify the percentage of heterochely and identify right or left-handedness, 58 additional adult specimens of both sexes (33 males and 25 females) were observed qualitatively to verify differences in the gross morphology of chelipeds. The setal system and shape were also compared in chelipeds of all size ranges in specimens observed under SEM.

The chelae of *T. borellianus* were examined with respect to the mechanical advantage (MA) in order to identify mechanical specialization in the feeding habit. MA was defined as the factor by which the magnitude of the force applied to a lever system is altered by the system. Chelae were regarded as a frictionless lever system and MA was calculated by the ratio L_1/L_2 of the dactyl height (L_1: distance between the fulcrum and the proximal apodeme insertion) and length of the lever arm (L_2: the length between the fulcrum and the point on the dactyl) (Warnes and Jones, 1976) (Fig. 1). Low MA indicated a great speed movement while high MA denotes an increased closing force. To calculate the mechanical advantage (MA), both chelipeds of 28 specimens (males = 14, females = 14) were photographed under a stereoscopic microscope (Leica S8APO) with a camera attached (Canon EOS Rebel t2i). Then, L_1 and L_2 were measured using the software TPSDig2 (Rohlf, 2004).

The MAs of minor and major chelipeds were compared within sexes in adult crabs (more than 7.1 mm) (Williner et al., 2014) using a Kruskal–Wallis (KW) test. These tests were performed with the software PAST (Hammer et al., 2001).

3. Results

The general morphology of the structures studied was similar in juveniles and adults of both sexes. Mandibles in all specimens exhibited a morphology consistent with the structure of early juveniles (megalopa) previously described (Factor, 1982, 1989). Chelipeds exhibited heterochely with different MA values in adult males but the setal system were similar in all specimens. The ossicles of the gastric mill of juveniles and adults were similar with well-chitinized teeth.

3.1. Mandibles

The mandibles were completely calcified and asymmetrically arranged in such a way that, medially, the cutting edge of the right mandible slightly overlaps the left (Fig. 2A and B). Both were similar in form without teeth or setae with a smooth, shield-shaped incisor process and a reduced and cuspidate molar process (Fig. 2B–E). The mandibular palp was a large “J”-shaped process that preserved three distinct elements and was attached laterally on the mandible. The two most distal segments lied between the incisor and molar processes in resting position (Fig. 2B). Rows of pappose setae with infracuticular articulation surfaced from the dorsal side of the two most distal segments (Fig. 2E–G). Pappose setae was long and slender with setules (50–150 μm) randomly distributed and articulated with the shaft (Fig. 2F–H) (Garm, 2004a,b).

3.2. Chelipeds

Trichodactylus borellianus exhibited heterochely in 87.9% of adult males analyzed. Among males with heterochely, 86.2% presented right-handedness and 12.1% left-handedness. Females did not present heterochely (Fig. 3). Handedness becomes evident in specimens with more than 7 mm of cephalothorax width. The minor chelae of both male and female of *T. borellianus* had a series of blunt and sharp denticles on the outer faces of the fingers that were interlocked when fingers close (Fig. 4A). At the tip of the dactyl and propodus, there was a concavity slightly pronounced, like a shallow spoon (Fig. 4B and D). Dactyl (mobile finger) and propodus had eight and nine denticles, respectively (Fig. 4A). The

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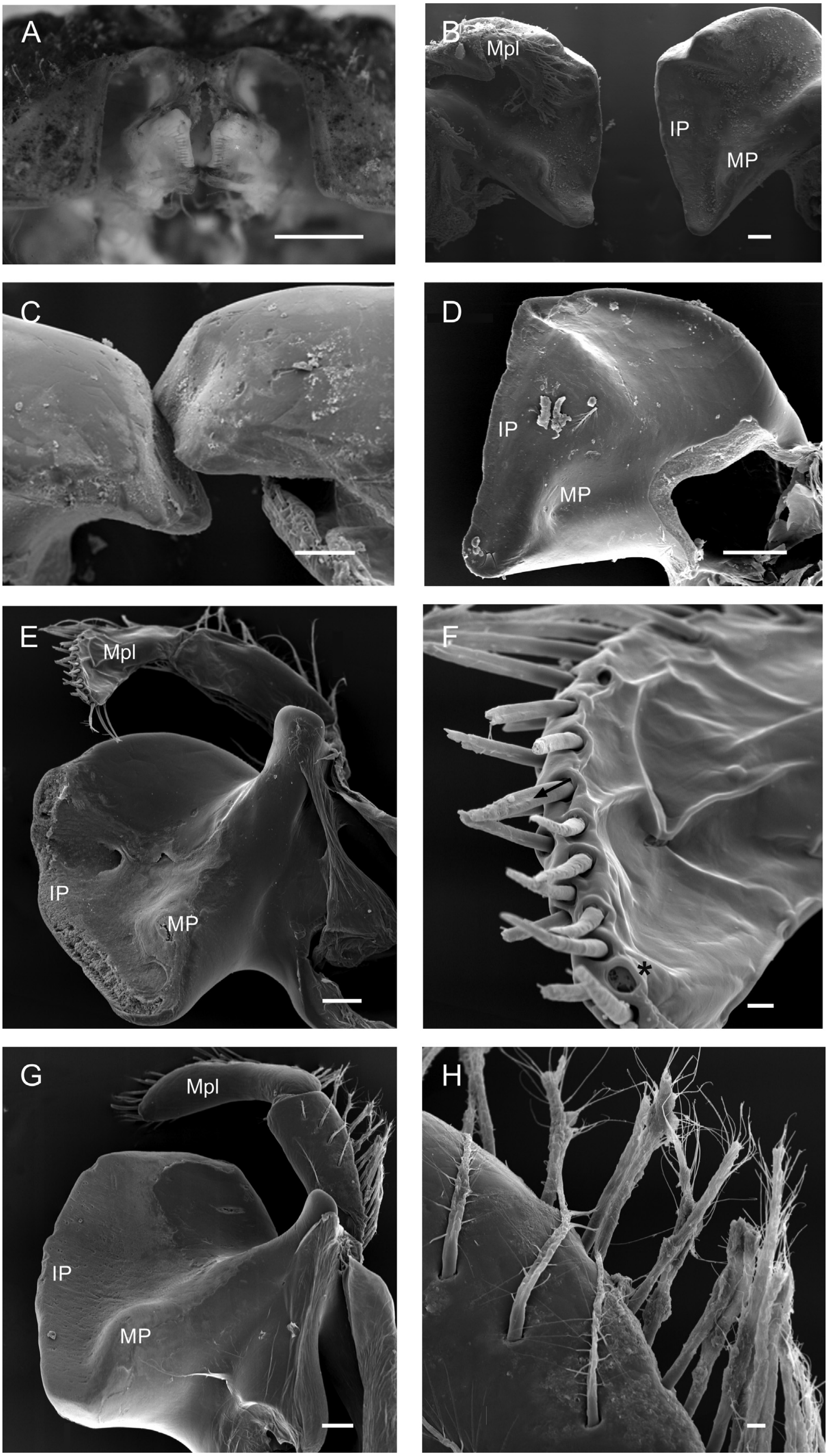

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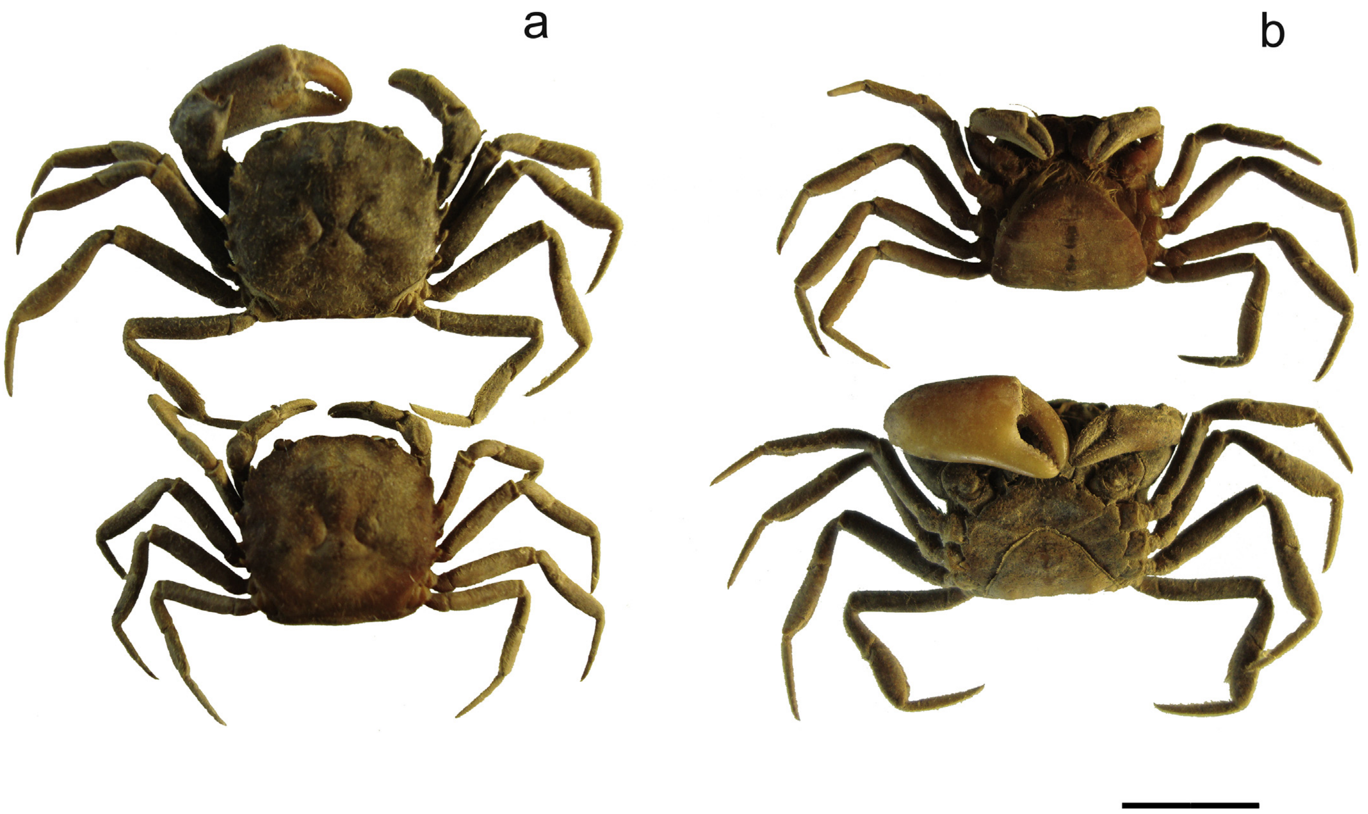

Fig. 3. Dorsal (a) and ventral (b) view of a male (below) and a female (above) of *Trichodactylus borellianus* showing the right-handedness of adult males. Scale bar: 100 mm.

major chelae of adult crabs had a different form being more robust with denticles worn and rounded than younger crabs (Fig. 4C and E). Large specimens of both male and female exhibited the cuticular surface without spines and setae (Fig. 4C and E). In males, the bigger chelae were progressively flattened with the animal size exhibiting broader denticles and no contact between fingers in the proximal part of these appendages (Fig. 3).

The external morphology of the setal system was similar in all sizes and in both sexes. The cuticles of both fingers are filled with small (<15 μm), acute and elongated projections with an articulation that have a direct transition with the general cuticle (Fig. 4F and G). These projections were hollow and classified as spines (Fig. 4G and H). These spines were densely clustered in the region between the interlocking denticles (Fig. 4B and D). Other cuticle specialization was a series of setae distributed linearly in groups of two, three or more along the entire chelae. This type of setae was presented in the occluding face and in the most external region of dactyl and propodus (Fig. 4A). These setae were classified as simple with infracuticular articulation (Fig. 4F and G). Spines and setae were frequently absent in older specimens (more than 9 mm of CW), observing only the insertion areolas of simple setae (Fig. 4C and E).

Morphological differences in adult male chelipeds were also verified in the lever system. The minor and major chelae had a MA (mean ± SD) of 0.22 ± 0.02 and 0.40 ± 0.12 for males and, 0.22 ± 0.03 and 0.22 ± 0.04, for females, respectively. There were statistical differences among MA values of minor and major chelipeds of males (KW: $p = 1.57 \times 10^{-5}$) while females presented MA values of both chelipeds statistically similar (KW: $p = 0.9268$).

3.3. Gastric mill

The foregut of *T. borellianus* is equivalent with the general morphology of Decapoda. The stomach exhibits two well-defined regions: the anterior portion -the cardiac chamber with esophagus, and the posterior portion -the pyloric chamber (Fig. 5A and B). The anterior portion has a thin walled sack-shaped structure where the food is stored for further maceration by the gastric mill. The gastric mill is a chewing apparatus formed by ossicles with chitin-covered teeth and other ossicle with supporting functions. These chitin-covered teeth protruded from the unpaired urocardiac ossicle and from the paired zigocardiac and pectineal ossicles (Fig. 5C, D and F). These structures, plus the cardiopyloric valve (Fig. 5F) composed the chewing apparatus.

3.3.1. Urocardiac ossicle

The urocardiac ossicle, that passed through the dorsal midline of the cardiac stomach, was an unpaired ossicle, strongly calcified, "T"-shaped, dorsoventrally flattened splaying out laterally in the posterior part (Fig. 6A and B). In the posterior end of the uropiloric ossicles bore ventrally the medial tooth (Fig. 6B). It was a plate wider than it was long with a large cubical and flattened process. This process exhibited a semi-hemispherical protrusion at the anterior surface and a "W"-shaped surface posteriorly. Immediately anterior to this process, there was a pair of spines at each lateral edge of the medial tooth, followed by two to three minor ones (Fig. 6B).

Fig. 2. *Trichodactylus borellianus*; light microscope and SEM of adult mandibles. (**A**) Ventral view of the cephalothorax showing the oral disposition of mandibles without other mouthparts. (**B**) Aboral view of mandibles showing the resting position of mandibular palp. (**C**) Dorsal view showing the slight overlapping of mandibles. (**D**) Aboral view of the right mandible of a juvenile crab. (**E, G**) Aboral view of right mandibles with mandibular palp. (**F**) Detail of the mandibular palp showing the infracuticular articulation without pappose setae (asterisk) and the insertion of absent setules (arrow). (**H**) Detail of mandibular palp with pappose setae with evident setules. IP: incisor process; Mpl: mandibular palp; MP: molar process. Scale bars: *A* = 1000 μm; *B, C* = 100 μm; *D, F* = 100 μm; *E, G* = 10 μm; *H* = 1 μm.

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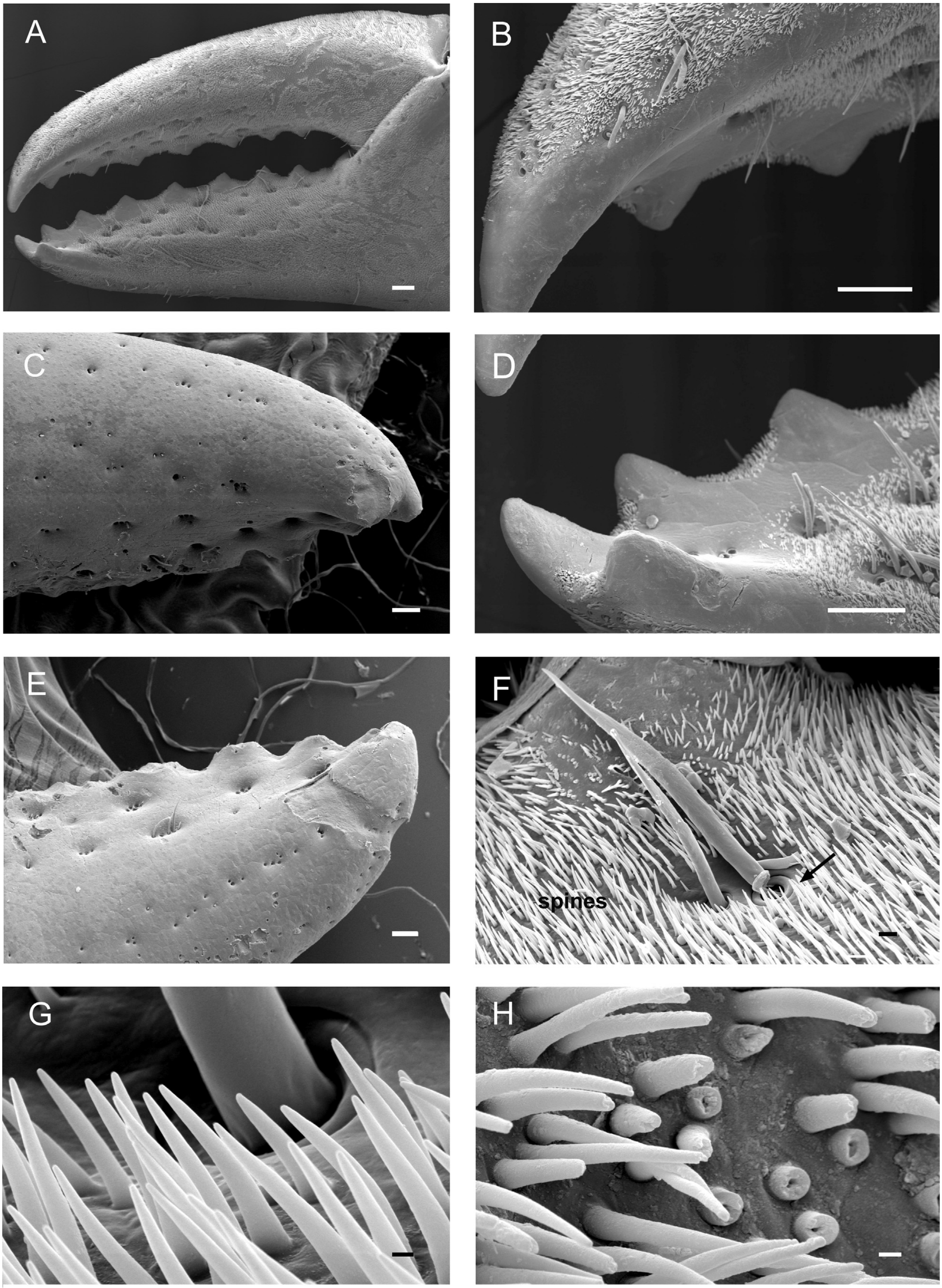

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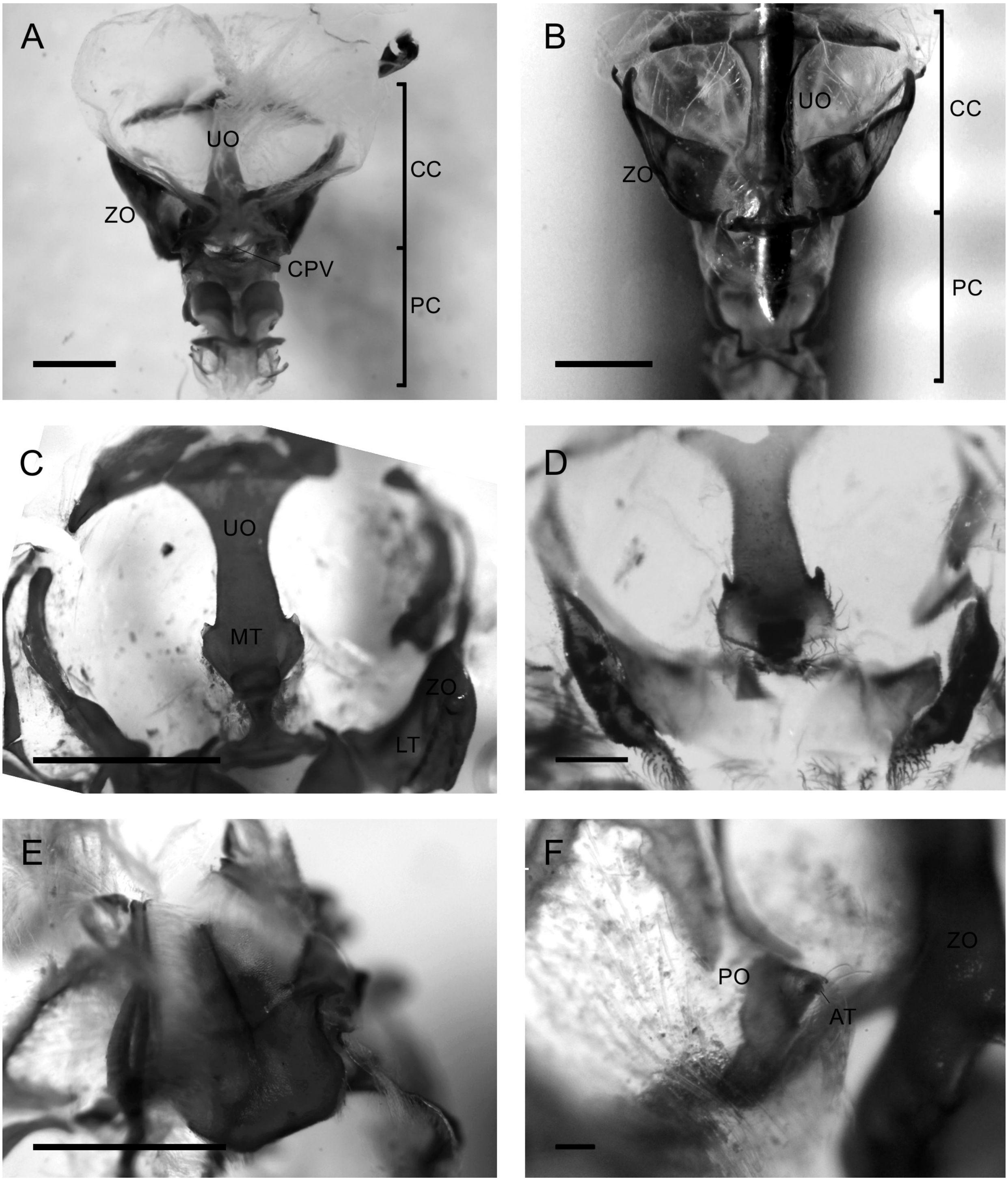

Fig. 5. *Trichodactylus borellianus*; light microscope of gastric mill of juvenile and adult gastric mill. (**A**) Ventral and (**B**) dorsal view of a stomach of an adult showing the cardiac and pyloric chambers and the main ossicles involved in the mechanical digestion. (**C**) General ventral view of a dissected stomach of an adult and (**D**) a juvenile showing the medial tooth of the urocardiac ossicle and lateral teeth of zigocardiac ossicles. (**E**) Detail of the anterodorsal face of a cardiopyloric valve of an adult crab. (**F**) Detail of accessory teeth of the pectineal ossicle. AT: accessory tooth; CC: cardiac chamber; CPV: cardiopyloric valve; LT: lateral tooth, MT: medial tooth; PC: pyloric chamber; PO: pectineal ossicle; UO: urocardiac ossicle; ZO: zigocardiac ossicle. Scale bars: *A*, *B*, *C*, *E* = 1000 μm; *D*, *F* = 100 μm.

Fig. 4. *Trichodactylus borellianus*; SEM of juvenile and adult chelae. (**A**) General view of chelae of a juvenile crab showing the interlocking denticles. (**B**) High magnification of (**A**) showing the shallow spoon-like tip of the dactyl of a juvenile crab. (**D**) High magnification of (**A**) showing the shallow spoon-like tip of the propodus of a juvenile crab. (**C**) The flattened dactyl with worn denticles of an adult male. (**E**) The flattened propodus of an adult male. In both (**C**) and (**E**) denticles are worn with absence of cuticular outgrowths. (**F**) Detail of the cuticle specializations of the chela showing numerous spines and simple setae with infracuticular articulation (arrow). (**G**) High magnification of (**F**) showing the detail of the insertion areola of simple setae. (**H**) Detail of the hollow spines. D: dactyl; P: propodus. Scale bars: *A*–*E* = 100 μm; *F*, *G* = 10 μm; *H* = 1 μm.

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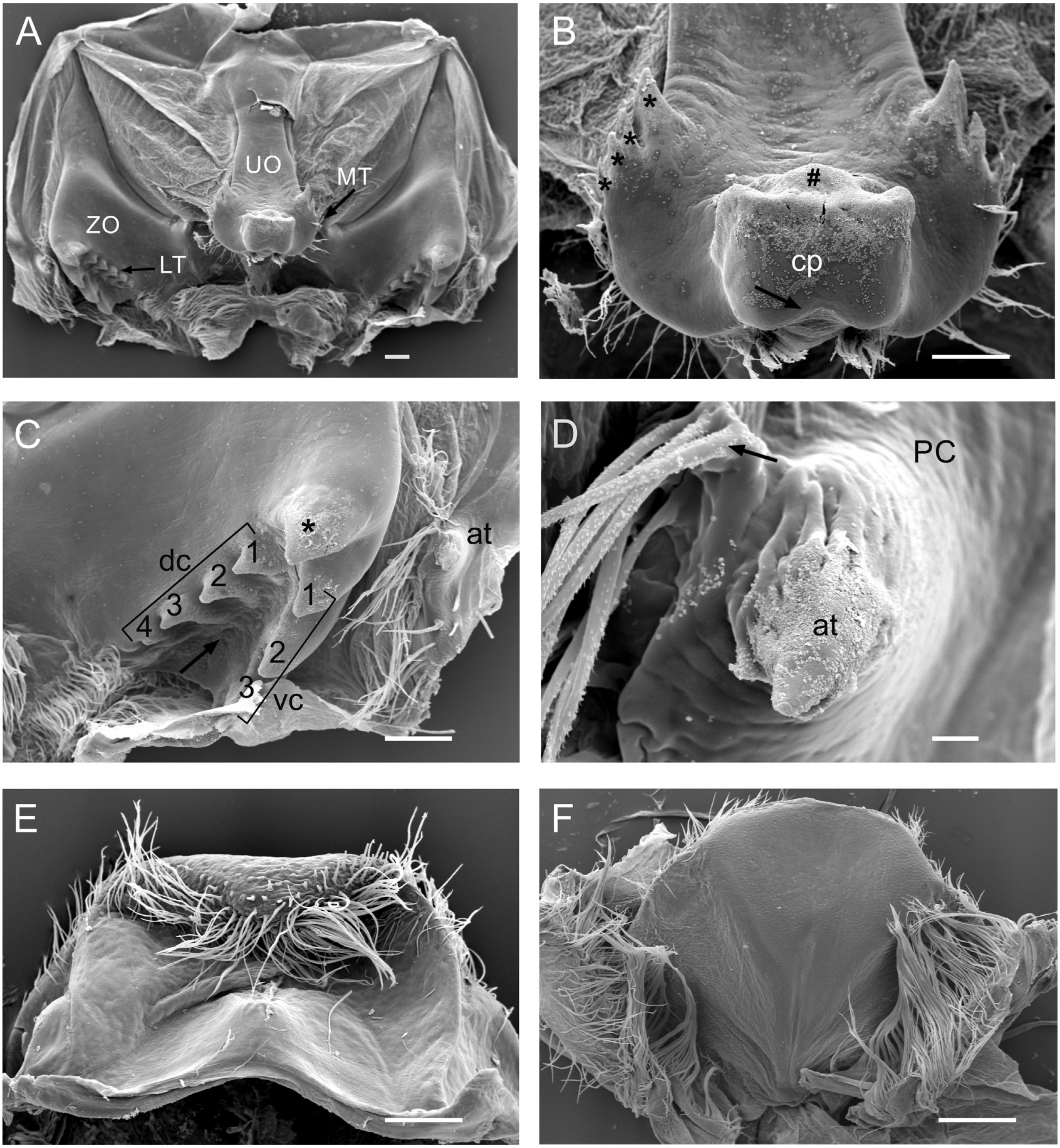

Fig. 6. *Trichodactylus borellianus*; SEM of adult gastric mill. (**A**) General ventral view of a dissected stomach of an adult showing the medial tooth of the urocardiac ossicle and lateral teeth of zigocardiac ossicles. (**B**) Medial tooth with cubical and flattened process, semi-hemispherical protrusion (hash), posterior surface of the cubical process W-shaped (arrow) and spines (asterisks). (**C**) Right lateral tooth with an anterior blunt cusp (asterisks) followed by three ventral cusp and four dorsal cusps separated by a deep hollow (arrow), laterally is the accessory tooth. (**D**) Accessory tooth with a vestigial ossicle and brushes of serrulate setae (arrow). Cardiopyloric valve in ventral (**E**) and dorsal (**F**) view without ridges or bridges. at: accessory tooth; cp: cubical process; dc: dorsal cusps; LT: lateral tooth; MT: medial tooth; PC: pectineal ossicle, UO: urocardiac ossicle; vc: ventral cusps; ZO: zigocardiac ossicle. Scale bars: *A*, *B*, *C*, *E*, *F* = 100 μm, *D* = 10 μm.

3.3.2. *Zigocardiac ossicles*

The zigocardiac was a paired ossicle, strongly calcified, triangular plate-shaped with accentuated dorsoventral curvature extending medially into the cardiac stomach (Fig. 6A and C). It was the major masticatory structure of the gastric mill. The medial portion was large with the margins provided with cusps that form the lateral tooth (Fig. 6C). Three to four ventral cusps and four to five dorsal cusps followed a blunt anterior cusp. Ventral cusps were larger and sharpened whereas the dorsal cusps were shorter and sharpened. Each cusp was separated from the other by a deep hollow. Separating the ventral and dorsal cusps was a concave depression along the extension of the lateral tooth (Fig. 6C). This concavity seemed aligned well with lateral spines of the medial tooth.

3.3.3. *Pectineal ossicles and cardiopyloric valve*

The pectineal was a paired ossicle located laterally in the cardiac stomach with strong calcification in the external and internal faces. In *T. borellianus*, it was a pint-sized ossicle positioned below to each

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lateral tooth in the lateral view. Internally, the accessory teeth bore from the pectineal ossicle and had a vestigial denticle on the ventral border of the teeth (Fig. 6C and D). Beside the accessory teeth, there were brushes of serrulate setae (Fig. 6D).

The cardiopyloric valve was an unpaired ossicle, strongly calcified extending up from the ventral side of the stomach to the cardiac chamber floor. It was located just past the posterior end of the zigocardiac ossicle. The valve possessed the anterior surface without ridges or teeth. It was surrounded by numerous serrulate setae measuring about 100 μm long (Fig. 6E and F).

4. Discussion

We expected to find a consistent relation between the studied feeding structures and the natural diet of *T. borellianus* and the intermediate morphological traits of herbivorous and carnivorous crabs. The morphological traits observed in adults and juveniles were similar except for heterochely. Chelipeds exhibited predominantly right-handedness in adult males with morphological differences between minor and major chelae, which was also evident in MA values. Mandible had a reduced molar process and the gastric mill presented smooth medial tooth and cuspidate lateral teeth, indicating a low chewing action. These features are typical of macrophagous crabs with adjustments to cutting and grinding the food, allowing juveniles and adults the handling and mechanical digestion of a diverse range of available food resources with variable relative importance of animal and vegetal material. These results are in concordance with our predictions that the studied feeding structures of *T. borellianus* have morphological traits adjusted to an omnivorous diet.

4.1. Morphology and function of the mandibles

When food is delivered to the mouthparts, mandibles reduce large pieces by moving medially and decreasing the space between incisor processes. This movement also helps to conduct particles to the esophagus (personal observation). The small overlap between mandibles could improve the anchoring of food when mandibles close. Malacostracans present a dual-purpose type of mandibles with cutting and crushing functions (Watling, 2013). However, in *T. borellianus* the reduced molar process and the presence of entire pieces of food in stomach contents (Carvalho, 2014) indicated a limited use of the crushing mode. The lack of teeth in incisor processes and the reduction of molar processes coincides with the morphology of the early juvenile (megalopa) mandibles of decapods described by Factor (1989). *Trychodactylus borellianus* presents an abbreviated larval development and the morphology of mandibles was similar between juveniles and adults. The well-developed mandible of this crab is coincident with a macrophagous diet, and the absence of cuticular outgrowths is a common feature observed in decapods with different diet preferences (Skilleter and Anderson, 1986; Garm, 2004a,b; Sahlmann et al., 2011). In the case of *T. borellianus*, the incisive process may help cut chitin structures, such as insects, and mollusk valves, while the slight overlapping of this structure may facilitate the action of the reduced molar process.

The functional role of the mandibular palps is reported to be directly related in the food manipulation, acting as a transporting mouthpart (Skilleter and Anderson, 1986; Maitland, 1990; Jaszkowiak et al., 2015) and preventing the loss of food particles (Garm, 2004a,b). In the case of *T. borellianus*, the mandibular palps present pappose setae that could be acting as a barrier, preventing the loss of particles, or directing the flow of water as observed in *Penaeus monodon* (Garm, 2004a,b). The consumption of microcrustaceans and rotifers observed in previous studies (Carvalho et al., 2013b; Williner and Collins, 2013; Gutierrez et al., 2014) might be eased through the action of this appendage. Notwithstanding, the effective role of palps should be corroborated with micro recording that allows the accurate observation of such small sized crabs.

4.2. Morphology and function of chelae

Trichodactylus borellianus presents two main strategies to seek for food (Carvalho et al., 2013b; personal observation). In both cases, this crab uses left and right chelipeds, regardless of claw size, to gather and carry food into its mouth, comprising the first handling of the prey item before ingestion. The predominance of right-handedness and MA values between 0.2 and 0.4 are in coincidence with morphological features of brachyuran predators (Vermij, 1977; Lee, 1995). However, despite the similarity of food items exploited by adults and juveniles of *T. borellianus* (Williner and Collins, 2013), morphological differences found in minor (cutter) and major (crusher) chelae imply distinct abilities to get food. Adult males have more strength in the major chela, allowing them to prey on larger and harder items (Warnes and Jones, 1976; Seed and Huges, 1995; Yamada and Boulding, 1998). The minor chelae are slender and mechanically faster (Levinton and Allen, 2005), easing the capture of fast swimming organisms (e.g. zooplanktonic organisms, insect larvae). The shallow spoon at the tip of the cutter chelae can be a helpful tool to scrape algae adherent to surfaces, as algivorous crabs do (Watling, 2013). This feature probably facilitates the ingestion of algae in smaller crabs, such as observed by Williner and Collins (2013).

Despite the heterochely observed in adult males, previous studies did not notice differences in the dietary composition between sexes (Williner and Collins, 2013). The right-handedness observed in *T. borellianus* has an important role in a sexual context, as this weapon is used during courtship and to restrain females during the copulation (Senkman et al., 2015). Although only chelipeds perform a function in the transport of food to the mouthparts, as seen in *Lithodes maja* (Jaszkowiak et al., 2015), the other pereiopods are observed to aid in the immobilization of highly mobile prey (e.g. insect larvae) and in the handling of large and hard prey (e.g. mollusks) (personal observation). One or both claws, with the action of interlocking denticles, hold the prey item while the mouth appendages play a variety of movements to finally carry, crush and cut the food. The functional interpretation of this structure should always be made considering chelipeds as multifunctional organs (Lee, 1995).

SEM observations highlighted the presence of acute spines throughout the entire dactyl and propodus of chelae and groups of articulated simple setae. Considering only the functions related with trophic aspects, the cuticle outgrowths observed in *T. borellianus* might be related with sensory functions and handling of prey. The morphology of spine-like structures resembles the diagrammatic representation of crustacean hair sensilla in the study of Schmidt and Gnatzy (1984 see Fig. 7g), a mechanoreceptor. Despite Garm and Watling (2013) referred to spines as hollow and unarticulated structures without innervation, a more accurate classification of cuticle outgrowths should be based on ultrastructure and electrophysiology observations. Whether spines observed in the present study are setae lacking differentiation of the socket, they could be mechanoreceptors responding only to strong mechanical stimuli, as observed in the crayfish *Austropotamobius torrentium* (Altner et al., 1983). Functionally, they may help to identify the type of food (e.g. hard or soft) during the rough prey handling and perform a clamp action on a variety of prey types preventing the material loss due to their low flexibility. Simple setae are related with rough prey handling, being chemosensitive depending on location (Mesce, 1993; Garm, 2004b), and are also used for brushing

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the substratum in atyid shrimps (Yam, 2016). If the simple setae are chemoreceptors, crabs could taste with chelipeds.

4.3. Morphology and function of the gastric mill

Despite the cutting action of mandibles, food fragments can still enter the stomach in relatively large pieces (Carvalho, 2014) requiring a further mastication process. However, in rare occasions the material is found intact in stomach contents, indicating an efficient grinding action of the gastric mill. Actual observation revealed that the gastric mill of *T. borellianus* possesses ossicles better suited to chew animal than vegetal material and there is more coincidence with the descriptions of carnivorous and omnivorous decapods (Skilleter and Anderson, 1986; Salindeho and Johntson, 2003; Allardyce and Linton, 2010). Lateral teeth have pronounced ventral and dorsal cusps of similar sharpened shape, without ridge-like structures nor curved spines as observed in herbivorous crabs (Giddins et al., 1986; Allardyce and Linton, 2010). The medial teeth possess a smooth process and a pair of lateral spines without transverse ridges to disrupt vegetal fibers. The morphology of the medial and lateral teeth seems to be consistent with the natural diet previously described (Williner and Collins, 2013).

The other ossicles that compose the gastric mill, the cardiopyloric valve and the accessory teeth, seem to be simple structures compared to other carnivorous or omnivorous decapods (Caine, 1975; Kunze and Anderson, 1979; Williner, 2010). In *T. borellianus*, the cardiopyloric valve has a smooth surface with large serrulate setae anterodorsally located. According to Kunze and Anderson (1979), the breadth, ridge number and flexibility of the ridges of the cardiopyloric valve indicate an increased degree of macrophagy. We did not observe this structure in *T. borellianus*, possibly because it is not a trait at least in trichodactylid crabs (DAC and VW personal observation). Similarly, the increased number of denticles and the reduced abundance of setae of the accessory teeth are related to the macrophagy in anomurans (Caine, 1975). *Trichodactylus borellianus* has an accessory tooth of tiny size with large serrulate setae. However, the reduced size seems to be a recurrent trait in the Trichodactylidae family (DAC and VW personal observation). In this way, these structures might have a more conservative morphology that does not correspond directly with the feeding habit. Conversely, the accessory teeth could have a reduced function in the chewing process.

Once the food enters the cardiac chamber of the stomach, the esophageal valve handles prevent backflow and push the gastric contents into the mill with the aid of accessory teeth (Kunze and Anderson, 1979). The latter structure may also prevent the entry of food to the ventral region of the cardiac chamber (Ngoc-Ho, 1984). Inside the cardiac chamber, shredding begins. The pointed cusps of the lateral teeth indicate that *T. borellianus* is adapted to cut its prey. The joint action of both zigocardiac ossicles, according to Heinzel (1988) and Heinzel et al. (1993) has the function of mixing the content inside the cardiac chamber. However, the movement of "gear" that display the ventral cusps of the lateral teeth could reduce material into smaller fragments. This action may be useful with prey that is swallowed as a whole, mainly of small size (e.g. unicellular algae, protozoa, rotifers, copepods, cladocerans). During the "cut and grind" mode of mastication, the movement of lateral teeth on the smooth process of the medial tooth performs the function of grinding the ingested material. In addition, the depression between the ventral and dorsal cusps of the lateral tooth seems to align with the lateral spines of the medial tooth. This would facilitate the crushing action of any food trapped in this hollow, as suggested in *Geograpsus grayi* and *Geograpsus crinipes* (Allardyce and Linton, 2010). Hereby the exoskeleton of insects, such as chironomid larvae or coleopterans, would be crushed. Hard elements, such as mollusk shells, could be fragmented by the "squeeze" mode, the simultaneous movement of the cusps of the three teeth, in an action such as "mortar-like" process. During mastication, large fragments of food are pushed over the cardiopyloric valve to the gastric mill with the aid of accessory teeth (Caine, 1975). In the case of *T. borellianus*, this structure may have a reduced or a secondary function in the chewing process. The cardiopyloric valve can also function as a chewing ossicle as well as a barrier between the cardiac and pyloric portions of the stomach (Caine, 1975). The ventral movement of the medial tooth, the medial movement of the lateral teeth and the antero-dorsal movement of the cardiopyloric valve provide an additional chewing of hard structures while excluding partially digested items from the pyloric stomach (Caine, 1975; Salindeho and Johntson, 2003). After the complete mechanical digestion of food in the cardiac chamber, the setal system of the post-pectineal ossicles directs particles of different sizes to the channels of the pyloric chamber.

5. Conclusion

Trichodactylus borellianus inhabits ponds with a high spatio-temporal variability that consequently influences food availability. The morphology of the feeding apparatus of *T. borellianus* revealed that it is well adapted to an omnivorous diet, being able to cope with dietary changes. The presence of animal items and decomposed vegetal remains in gut contents indicated a reduced preparation of the food before ingestion. In this way, we found generally simple structures armed with a uniform seta system and feeding appendages without pronounced teeth or spines. Externally, the cutting and crushing chelae have different functional roles during the food handling. Nevertheless, the spine-like structure and simple setae throughout the chelipeds aid the clamp action on a variety of food types. Future studies are necessary to determine whether chelipeds could also detect and identify potential food resources. Mandibles have primarily cutting functions, helping in the food anchoring and fragmentation while mandibular palps, armed with pappose setae, might prevent the loss of particles. The ingestion of relative large pieces of food is finally chewed by a gastric mill equipped with sharp cusps characteristic of decapods with low ingestion of crude fiber material.

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