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3   **Functional morphology of the gastric mill of the swimming crab *Ovalipes trimaculatus***
4   **(Decapoda: Portunidae)**

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16

17   ABSTRACT

18   *Decapods crustaceans' stomach is a complex structure with a great interspecific variation.*
19   *Several studies suggest that the anatomy of the gastric mill varies according to the diet of species*
20   *in different groups. An alternative view suggests the gastric mill´s structure is related to*
21   *phylogenetic aspects rather than to the diet of a species. The morphology of the gastric mill of*
22   Ovalipes trimaculatus*, a portunid crab target of fisheries in Argentina and Chile, was studied*
23   *through stereo-microscope and scanning electron microscope images.* O. trimaculatus *has a*
24   *stomach that corresponds to a macrophagous and predatory diet. The gastric mill is similar to*
25   *that of other portunids, especially those with predominant animal component in their diet. Our*
26   *results support the idea that this structure has a basic pattern, given by shape and elements*
27   *forming the gastric mill; and upon that pattern, trophic habits adaptively shape certain traits.*

28

29   Keywords: foregut ossicles, predatory decapods, gastric mill structure

30

31   INTRODUCTION

32   Decapoda stomach is a complex structure with a great interspecific variation (Icely & Nott,
33   1992). There, after manipulation of the mouthparts, the secondary processing and the real

34 trituration of the food occurs by the action of the gastric mill (Ceccaldi, 2006). This structure
35 varies between species reaching its highest development (greater number of ossicles and
36 calcification) in Brachiuran crabs (Icely & Nott, 1992), in which the gastric mill was described as
37 a "three-branched claw through which the food must pass in order to reach the pyloric
38 region"(See Ceccaldi, 2006). This "claw" is made up of a pair of lateral teeth protruding from the
39 side walls of the heart chamber, a medium tooth extending from the dorsal wall of the chamber
40 (Allardyce & Linton, 2010) and a number of supportive ossicles. On the other hand, in other
41 groups of Decapoda the stomach can be very simple with just a few calcified ossicles or total
42 absence of them (Felgenhauer & Abele, 1985; Icely & Nott, 1992).

43 Several studies suggest that the anatomy of the gastric mill varies according to the diet of species
44 in different groups of Decapoda (e. g. Kunze & Anderson, 1979; Icely & Nott, 1992; Allardyce &
45 Linton, 2010). According to this hypothesis the gastric mill of macrophagous species is expected
46 to be calcified and dentate with few setae, while those that feed on micro material should
47 present small blunt teeth and high setae density (Caine, 1975; Kunze & Anderson, 1979).
48 Furthermore, the teeth of carnivorous species is expected to present molar processes for
49 grinding soft animal tissue, while herbivores should present high transverse ridges in order to
50 cut fibrous material (Skilleter & Anderson, 1986). Omnivorous species are characterized by
51 ossicles with cusps but also smooth surfaces for grinding (Salindeho & Johnston, 2003). An
52 alternative view suggests the gastric mill´s structure is related to phylogenetic aspects rather
53 than to the diet of a species (Felgenhauer & Abele, 1985), therefore, ossicles and teeth
54 characteristics of the cardiac stomach have been used as phylogenetic markers (e.g.
55 Felgenhauer & Abele, 1985; Sakai, 2004; Brösing et al., 2007). According to this hypothesis
56 phylogenetically close species should have similar gastric mills despite having very different
57 feeding habits. Finally, Brösing and Türkay (2011) propose a synthesis stating that teeth of the
58 brachyuran cardiac stomach have a relatively stable structure, nonetheless this does not exclude
59 the existence of adaptations to food preferences or to different resources use.

60 *Ovalipes trimaculatus* (De Haan, 1833) is a portunid crab distributed from southern Brazil to
61 southern Argentina in the Atlantic Ocean (Vinuesa, 2005; Melo, 2010), and from southern Peru
62 to south of Chile in the Pacific Ocean (Retamal, 1981). In San Matias Gulf, Argentina, it is
63 exploited since 2007 by artisanal fishermen who have historically developed a diving shellfish
64 fishery (Narvarte et al., 2007). The relevance of the activity has been growing ever since because
65 of the products' low cost/benefit ratio, but also because during red tide outbreaks *O.*
66 *trimaculatus* is the only resource the diving fishermen can extract. This new extractive activity
67 involves the need to understand, evaluate and assess biological and ecological aspects of the
68 populations of *O. trimaculatus*. This species has been described as carnivorous and/or scavenger
69 feeding mainly on small benthic invertebrates and fish (Fenucci & Boschi, 1975). Dietary analysis
70 on the San Matías Gulf population has revealed that the more frequent occurrences in stomach
71 contents are small fishes, crustaceans and bivalves, with occasional occurrence of echinoderms
72 (ophiroidea and echinoidea) and chitons (de la Barra et al., 2014). We believe it is necessary to
73 deepen the study of trophic aspects of this population to draw potentiality and consumption
74 patterns.

75 The aim of this paper is to describe morphofunctionally the gastric mill of *O. trimaculatus*. In
76 turn, the morphology of the gastric mill is evaluated in light of the species diet and compared

77 with homologous structures in other portunid crabs and other decapods in order to establish
78 the influence of phylogeny or diet on morphology.

79

80 MATERIALS AND METHODS

81 *Ovalipes trimaculatus* specimens were obtained at the north of San Matias Gulf, Argentina
82 (40°58'S, 65°06'W). Crabs were collected manually by SCUBA diving at a depth of 10 to 20 m and
83 preserved at a temperature of -20 °C. Thirty individuals were dissected and their stomachs were
84 preserved in 70% alcohol in order to be put through different treatments afterwards. The
85 stomachs were cleaned and the contents were removed under stereo-microscope. Muscle
86 remains that were attached to the external parts were eliminated. In order to optimize the
87 observation of the structures of interest, 10 stomachs were digested in boiling KOH (10%) for 1
88 h and then stained with Alzarin-red; another 10 stomachs were stained without prior digestion,
89 and the remaining 10 were neither digested nor stained. The different treatments allowed the
90 observation of different structures with more detail and clarity. The stomachs were observed
91 and photographed in a stereo-microscope Leica S8 APO with built-in camera (Canon EOS Rebel
92 t2). Three more stomachs were removed cleaned and preserved as indicated previously and
93 then placed in a desiccator with silica-gel with a moisture indicator for at least 24 hours. After
94 conditioning, these samples were mounted on a metal stub using double-sided tape and/or
95 silver paint, samples were gold coated for 120 s using Combined Deposition System
96 metal/carbon, SPI Supplies, AX-12157, operated under argon atmosphere (18 mA) for 120
97 seconds. Then, observations were made using a JSM-35C scanning electron microscope (JEOL,
98 China), equipped with a system of digital image acquisition Sem Afore, at an accelerating voltage
99 of 20 kV.

100 Descriptions of the structures of the cardiac chamber that could match food processing and
101 outline trophic possibilities were made from the photographs and micrographs using the
102 nomenclature proposed by Ngoc-Ho (1984) and Kunze and Anderson (1979).

103

104 RESULTS

105 The oesophagus connects ventrally with the stomach which consists of two regions: the cardiac
106 and the pyloric stomach. The cardiac stomach is a chitinous, thin-walled translucid chamber, of
107 greater volume than the pyloric stomach. It has a series of well calcified pieces on the walls
108 symmetrically disposed at the posterior end (Figure 1).

109 On the internal laterals of the cardiac stomach's entrance there is a pair of oesophageal valves
110 regulating the opening of the stomach. These valves are elongated, cirrus-like structures, fully
111 covered with setae (Figure 2A). On the ventral wall of the stomach, posterior to the esophageal
112 valves, the medial strip extends reaching the posterior end of the cardiac stomach. On either
113 side of the medial strip there are longitudinal folds of the stomach's floor forming a pair of
114 channels covered by setae called "cardiac filter" (Figure 2A).
115 The gastric mill, the most conspicuous structure of the cardiac stomach is found posteriorly
116 (Figure 2B). It consists of a medial tooth supported by the urocardiac ossicle (Figure 3), two

lateral teeth, supported by the zygocardiac ossicles (Figure 4), a pair of less calcified lateral accessory teeth (Figure 4A, B) and the cardio-pyloric valve (Figure 5).

The urocardiac ossicle extends from the center of the dorsal wall of the cardiac stomach to posterior. It is dorsoventrally flattened and elongated in anteroposterior direction (Figure 3A). Posterior and internally to the chamber this ossicle bears the medial tooth of the gastric mill, a calcified structure pointing toward the anteroventral region from the dorsal wall of the stomach (Figure 3). This tooth has a quadrangular shape and a concave, smooth surface; at each corner of the square there is a projection with round edges (Figure 3C). A setose pad sorrounds this structure (Figure 3B).

The zygocardiac ossicles are paired, calcified structures on the posterior laterals of the cardiac chamber (Figure 1A, 4A). At their anterior end, the zygocardiac ossicles bear the lateral teeth, which are heavily calcified structures that protrude inside the chamber (Figure 4). The lateral teeth are antero-posteriorly elongated. An anterior and a posterior region can be clearly distinguished in the teeth (Figure 4B). The anterior region is wider, with a concave, smooth surface; it has smooth, sharp edges and an anterior concave cusp at the anterior end (Figure 4E). The posterior region of the lateral teeth narrows down from anterior to posterior. It has 6 to 9 sharp vertical ridges on the dorsal side; 2 to 5 rounded cusps of decreasing size can be found ventrally (Figure 4D). The anterior region of the lateral teeth is more robust and somewhat wider than the posterior region, and protrudes inwards, pointing postero-ventrally.

Pectineal ossicles are located on the lateral walls of the cardiac stomach (Figure 1B). From a lateral view, they are found below each zygocardiac ossicle. These paired structures have the shape of a curved rod and articulate anteriorly with zygocardiac and pterocardiac ossicles. On their posterior end, slightly ventroanteriorly to the lateral teeth the lateral accessory teeth can be observed (Figure 4A, F). These are chitinous structures, paired and un-calcified, constituted by 4 to 6 sharp denticles pointing inward and backward of the cardiac chamber. These structures are much smaller and softer than the previously described teeth.

On the posterior end of the cardiac stomach the medial strip curves downward forming the cardio-pyloric valve, a very thin calcareous structure with a semicircular shape, an apical edge covered by setae and a smooth protuberance on the tip (Figure 5).

DISCUSSION

O. trimaculatus' gastric mill is similar to the gastric mills of other Portunidae (Brösing, 2010). It is a complex structure with robust, well calcified teeth. These characteristics would be functional when breaking down large pieces of food, in accordance with a macrophagous diet (Caine, 1975; Kunze & Anderson, 1979).

When food enters the cardiac stomach the esophageal valves and the lateral accessory teeth direct the larger pieces into the mill (Kunze & Anderson, 1979). The function of the lateral accessory teeth is probably to support and/or to direct of the food, rather than that of grinding or processing for they are significantly softer than the other teeth and not calcified. The function of transferring food to the grinder area is consistent with the characteristics described for

carnivorous species of Decapoda (Caine, 1975; Kunze & Anderson, 1979; Salindeho & Johnston, 2003). *O. trimaculatus* lateral accessory teeth are very similar to those described for other carnivorous species of Decapoda that are not closely related to Portunidae, like pagurids *Dardanus setifer* (Kunze & Anderson, 1979) and *Petrochirus diogenes* (Caine, 1975), or like the grapsids *Geograpsus grayi* and *Geograpsus crinipes* (Allardyce & Linton, 2010), and the calappid, *Calappa granulata* (Cartes *et al.*, 2002; Brösing, 2010). Lateral accessory teeth of these species consist on a row of sharp denticles which are in some cases accompanied by groups of setae. Skilliter and Anderson (1986) propose that denticle size of the lateral accessory teeth could be related to the size of the pieces that reach the stomach, for in detritivore pagurids setae seem more relevant than denticles in the structure of lateral accessory teeth, as opposed to what they observed in carnivore pagurids, in which denticles are larger. Nontheless there are predatory species such as *Pseudocarcinus gigas* that do not even present lateral accessory teeth (Heeren & Mitchell, 1997). Whitin portunids, *Nectocarcinus tuberculosus* (Salindeho & Johnston, 2003) and *Callinectes sapidus* (Cochran, 1935) both have lateral accessory teeth conformed by a row of 5 to 7 sharp denticles, not special setae arrangement is mentioned in their description. In this sense, the structures found in *O.trimaculatus* fit a carnivorous diet, but also resembles the morphology of its close relatives.

Medial and lateral teeth of the gastric mill grind the larger pieces by performing simultaneous movements: medial tooth moves anteroventrally and lateral teeth swings dorsomedially (McGaw & Curtis, 2013). As these elements are the ones forming the chewing apparatus of the gastric mill, their structure is essential in terms of digestion capacity (Jaszkowiak *et al.*, 2015). In this sense, the aspects in which we focused during this work are directly related to the digestive function of the gastric mill. The presence of smooth concave structures in *O. trimaculatus* gastric teeth suggests a mortar-like action on the food: this feature is usually associated to the action of grinding or softening animal fibers (e.g. Creswell & Marsden, 1990; Heeren & Mitchell, 1997; Salindeho & Johnston, 2003; Allardyce & Linton, 2010). Conversely, in species with higher vegetal content in their diets, the gastric mill is more complex and presents more hooks and sharp peaks to disassemble hard vegetable fibers (e.g. Giddins, 1986; Cannicci *et al.*, 2002).

The medial tooth is not as robust as observed in other species and presents a concave shield where other portunid crabs present ridges (Salindeho & Johnston, 2003). A setose pad is observed at each lateral and dorsally to the medial tooth. Some authors suggest their function could be sweeping the ground particles from the teeth into the light of the stomach (Skilleter & Anderson, 1986; Salindeho & Johnston, 2003). In the anterior region of the lateral teeth there is a concave zone similar to the ones observed in carnivores from other families such as *C. granulata* (Calappidae, Cartes *et al.*, 2002; Brösing, 2010), *G. grayi* and *G. crinipes* (Grapsidae, Allardyce & Linton, 2010); and also in portunids as *C. sapidus* (Cochran, 1935). Other species, such as the omnivore grapsid *Pachygrapsus marmoratus*, present ridges or peaks in the anterior region of the lateral teeth (Cannicci *et al.*, 2002).

The presence of concavities in the medial and lateral teeth could have the function of retaining the food in order to maximize the mechanical action of the mill and the exposure to digestive enzymes. The bulged dimensions of the cardiac chamber along with these concavities could indicate the food ingested requires a considerable amount of time to be processed mechanically and physiologically. It could also be indicative of a trophic strategy, for example the scavenger

crustaceans of the deep benthic habitats can ingest large amounts of food in short time (Eastman & Thiel, 2015). Furthermore, in species that spend a considerable amount of time sheltered as *Thenus orientalis*, the folds that increase the storage capacity are a possible adaptation to optimize the reduced time spent in capturing prey (Johnston & Alexander, 1999). In species with this kind of behavior the calcification of the mill is considerably low although they present a macrophagous diet and a predatory behavior. *O. trimaculatus* is generally buried in sandy bottoms and presents rapid ingestion after quick external processing of food, therefore the dimensions of the stomach and the concavities of the teeth probably respond to its feeding behavior.

At the posterior region of the lateral teeth of *O. trimaculatus* there are vertical ridges, very typical structures of the lateral teeth also found in many other species of Brachyura (e. g. Cochran, 1935; Cannicci *et al*., 2002). Similar structures but with hooked ends can be found in herbivorous species (Giddins, 1986). In micromaterial feeders these teeth present comb like processes (e. g. Brösing & Türkay, 2011) or even a saetiform structure (Kropp, 1986). In *O. trimaculatus* the blunt ends of these structures can be indicative of adaptation to animal tissue processing, which does not require a strong mechanical treatment opposed to vegetal fibers. Also, similar ridges are present in the lateral teeth of other Portunidae and related families (Brösing, 2010).

In some decapods the cardiopyloric valve contributes to the grinding action of the mill by forcing the accumulation of the material and providing a structure on which the food can be disintegrated (Icely & Nott, 1992). The latter seems unlikely in the case of *O. trimaculatus* because of the low calcification of its cardiopyloric valve and the absence of annexed structures that could collaborate with the mechanical destruction of the material. Despite been a carnivorous species, the cardiopyloric valve of *O. trimaculatus* lacks masticatory structures as seen in other carnivores such as the anomuran *Petrochirus diogenes* (Caine, 1975).

To our knowledge, the masticatory structures of the gastric mill of three other portunid crabs have been described to date: *Callinectes sapidus* (Cochran, 1935; Maynard & Dando, 1974), *Ovalipes guadulpensis* (Caine, 1974) and *Nectocarcinus tuberculosus* (Salindeho & Johnston, 2003). Brösing (2010) also described the gastric mill of other portunids but information on the characters of interest to this study lacks. When comparing *O. trimaculatus'* gastric mill with *C. sapidus'*, *O. guadulpensis'* and *N. tuberculosus'* similar structures can be easily found: lateral teeth bearing a front cusp and two lines of posterior denticles, medial tooth relatively quadrangular pointing in anterior direction, semicircular cardiopyloric valve with setous edge (except in *O. guadulpensis*, which lacks description). However certain differences can be observed when comparing *N. tuberculosus'* gastric mill with the gastric mill of *O. trimaculatus*, *O. guadulpensis* and *C. sapidus*. *N. tuberculosus* has a medial tooth that presents ridges and cusps (Salindeho & Johnston, 2003) while in the other three portunids the medial tooth has a smooth surface. When comparing lateral teeth within portunids, *N. tuberculosus* presents more pronounced cusps and more evident grooves than the other species; also, it presents an anterior cusp with a convex surface while the other portunids present an anterior cusp forming a concave region. Although Portunidae are generally predators and scavengers, species have been observed that integrate vegetal material in their diet (Williams, 1981). This is the case of *N. tuberculosus,* which has an omnivorous diet in which sea grasses are a predominant component

243 (Salindeho & Johnston, 2003). Conversely, *C. sapidus* and *O. guadulpensis* have a diet mainly
244 composed of small benthic invertebrates and fishes, with a low presence of algal material (Caine,
245 1974; Laughlin, 1982 4% for *C. sapidus*). The described diet for *O. trimaculatus* is very similar to
246 the ones of *C. sapidus* and *O. guadulpensis*: benthic invertebrates, small fishes and a very low
247 content of algal material (Fenucci & Boschi, 1975; de la Barra *et al.*, 2014). east structures, while
248 the mill of the portunid with more relevant vegetal component in the diet has greater presence
249 of uneven surfaces and structures with more cusps. However, all three species conserve the
250 typical structure of portunidae gastric teeth (Brösing, 2010). These structures can also be found
251 in closely related families such as Cancridae (e. g. Schubart & Reuschel, 2009; Spiridonov *et al.*,
252 2014). In species of this family quadrangular, smooth medial tooth are found along with lateral
253 teeth bearing an anterior cusp, posterior ventral ridges and posterior dorsal cusps *(Cancer*
254 *pagurus* Brösing, 2010; *Cancer novaezelandiae* Creswell & Marsden, 1990). They also present a
255 semicircular cardiopiloric valve crowned by setae. The lateral accessory teeth, on the other hand
256 are much more robust in Cancridae (Brösing, 2010).

257 Gastric mill ossciles have been used in various Decapoda groups to discern their phylogeny (e.g.
258 Brösing *et al.*, 2007; Reimann *et al.*, 2011). Although, mainly, supportive ossicles' traits are used
259 to discern between brachyuran families (see Brösing *et al.*, 2007), medial tooth morphology has
260 proven useful to distinguish even closely related species (e. g. Naderloo *et al.*, 2010; Naderloo &
261 Schubart, 2010). Also, numerous examples exist of closely related species with different traits in
262 their gastric teeth associated to their diets (e. g. Icely & Jones, 1978; Allardyce & Linton, 2010;
263 Brösing & Türkay, 2011). The strength of the relationship between structures and phylogeny or
264 diet most likely depends on adaptive pressure and physical constraints. What is clear is that
265 within brachyuran these structures are very plastic and can take saetiform shape as well as
266 robust hard teeth, although conserving a similar ground pattern (Brösing, 2010). Other feeding
267 structures (i. e. chaelas and mouth appendeges) have also been tested as phylogentically
268 diagnosis (e. g. Naderloo *et al.*, 2010; Sahlmann *et al.*, 2011) and trophic habits (e. g. Sahlmann
269 *et al.*, 2011).

270 The phylogenetic position of the genus *Ovalipes* has been discussed in the past years because
271 molecular phylogenetic reconstructions do not place *Ovalipes* within the Portunidae family
272 (Schubart & Reuschel, 2009; Spiridonov *et al.*, 2014). Schubart and Reuschel (2009) placed
273 *Ovalipes* provisionally in family Geryonidae along with genus *Benthochascon*, and later
274 Spiridonov *et al.* (2014), proposed the new family Ovalipidae with *Ovalipes* as the type genus. In
275 that sense, although in the present study *O. trimaculatus* was considered a portunid crab (Ng *et*
276 *al.*, 2008), it is possible that this classification is not accurate. To our knowledge there is no
277 description of any Geryonidae's foregut traits, and within *Ovalipes* the only description available
278 is the study by Caine (1974).

279 The constraint observed between phylogeny and trophic habit is also observed in other feeding
280 structures that have shaped the habits of consumption of portunids as well. Some cheliped traits
281 conserved throughout Portunoidea, for example, are considered the morpho-functional basis of
282 the predatory and scavenger habit typical of this group (Spiridonov *et al.*, 2014). Moody and
283 Steneck (1993) on the other hand, have seen that patterns of behavior in handling and
284 consuming mollusks may vary between phylogenetically related species more than between
285 ecologically similar species. In summary, the results attained in the present work and their

286 comparison with the existing literature on other portunid species and other Decapoda families
287 show that while *O. trimaculatus'* gastric mill shares its main traits with other portunid's, it also
288 shows the typical characters expected for a carnivorous diet. In this sense, our results agree with
289 the views expressed by Brösing and Türkay (2011): there is a stable ground pattern given by
290 shape and elements forming the gastric mill: *O. trimaculatus* gastric mill is probably more similar
291 to *C. sapidus'* or *N. tuberculosus'* than that of *Pseudocarcinus gigas* (Heeren & Mitchell, 1997),
292 but upon that pattern, trophic habits can adaptively shape certain characteristics (e.g. smooth
293 medial teeth, concave lateral teeth). In future work, to thoroughly analyze the morphology
294 modeling trophic habits we should analyze the morphology of the mouthparts and chelipeds of
295 *O. trimaculatus*. In addition, information of digestive enzymes and feeding behavior will further
296 improve the knowledge we have on trophic habits of this species.

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433

434 FIGURE CAPTIONS

435 **Fig. 1.** Stereo-microscopy images of the cardiac stomach of *Ovalipes trimaculatus*. (A) Dorsal
436 view showing urocardiac and pterocardiac ossicles; (B) posterior view showing gastric mill
437 ossicles and pyloric stomach. ANT: anterior direction, CS: cardiac stomach, DOR: dorsal direction,
438 Pc: pectineal ossicles, POS: posterior direction, PS: pyloric stomach, Pt: Pterocardiac ossicles, Uc:
439 urocardiac ossicle, Zy: zygocardiac ossicles. Scale bars: 1 mm.

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Fig. 2. Stereo-microscopy images of *Ovalipes trimaculatus.* (A) Inside ventral view of the cardiac stomach showing oesophageal valves followed by medial strip; (B) frontal view of the gastric mill. Cf: cardiac filter, DOR: dorsal direction, Lat: lateral accessory teeth, Lt: lateral teeth, Ms: medial strip, Mt: medial tooth, Ov: oesophageal valves, VEN: ventral direction. Scale bars: 1 mm.

Fig. 3. (A) Urocardiac ossicle carrying the medial tooth on its posterior region; (B) view of the medial tooth showing setose pads around it; (C) medial tooth detail, showing its smooth concave surface. ANT: anterior direction, Mt: medial tooth, POS: posterior direction, Sp: Setose pads, Uc: Urocardiac ossicle. A-B Stereo-microscopy images; C SEM image. Scale bars: A-B, 1 mm; C, 0.1 mm.

Fig. 4. (A) Zygocardiac ossicle with lateral tooth; (B) posterior view of the lateral tooth showing relative position to lateral accessory tooth, anterior and posterior region; (C) anterior and posterior region of lateral tooth; (D) posterior region of the lateral tooth showing ventral cusps and dorsal vertical ridges; (E) spoon shaped anterior region of the tooth; (F) lateral accessory tooth surrounded by setae. ANT: anterior direction, Ar: Anterior region of the lateral tooth, Cu: cusps, DOR: dorsal direction, Lat: lateral accessory tooth, Lt: lateral tooth, Pr: posterior region of the lateral tooth, VEN: ventral direction, Vr: vertical ridges, Zy: zygocardiac ossicle. A-B are stereo-microscopy images; C- F are SEM images. Scale bars: A- C, 1 mm; D-F 0.1 mm.

Fig. 5. (A) Stereo-microscopy of the ventral view of the cardio-pyloric valve; (B) scanning electron microscopy of the dorsal view of the cardio-pyloric valve. ANT: anterior direction, POS: posterior direction. Scale bars: 1mm.