

FUNCTIONAL ANATOMY OF BRACHIDONTES SOLISIANUS
(ORBIGNY, 1846) (BIVALVIA: MYTILIDAE)

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RESUMO - A anatomia funcional de *B. solisianus*, foi estudada com especial atenção ao funcionamento dos sífões, palpos, ctenídios e estômago. Procurou-se dar ênfase às adaptações daquelas estruturas ao meio em que o animal vive. Foram analisados com detalhe a motilidade e sensibilidade dos sífões, a estrutura muscular, o pé e o bisso, a movimentação e ciliação dos palpos, a forma e ciliação dos ctenídios, a estrutura e funcionamento do estômago e os órgãos excretores. Em *B. solisianus*, os sífões são do tipo A (II) (Yonge, 1948), os ctenídios do tipo B (I) (Atkins, 1937a); a relação entre os palpos e ctenídios pertence a categoria I (Stasek, 1963), as estruturas labiais são do tipo simples (Bernard, 1972). O estômago é do tipo III (Purchon, 1957), ou da Seção I de Dinamani (1967), apresentando mecanismos de triagem dos tipos A e B de Reid (1965).

ABSTRACT - The morphology of *Brachidontes solisianus* was studied, with special attention to the functional patterns of the siphons, palps, ctenidia and stomach. The similar adaptive relationships of these structures with the particular environments where the animal lives were emphasized. The following aspects were analyzed in detail: the motility and responsiveness of siphons, muscular structures, foot and its byssus, movements and ciliation in the palps, morphology and ciliation of the ctenidia, and structure and functioning of the stomach and excretory organs. The siphons belong to type A (II) (Yonge, 1948), the ctenidia to type B (I) (Atkins, 1937a), and the relationship between palps and ctenidia should be assigned to category I according to Stasek (1963). The lip structure is of the simple type (Bernard, 1972) whilst the stomach is allotted to type III (Purchon, 1957) or to the Section I of Dinamani (1967): the mechanisms for particle selection in the stomach are classified as type A and B of Reid (1965).

INTRODUCTION

According to Klappenbach (1965) the Genus *Brachidontes* is represented by three sub-genera with four species and one sub-species in Brazil, *Brachidontes (Brachidontes) rodriguezi* (Orbigny, 1846), *B. (Hormomya) exustus* (Linné, 1758), *B. (Hormomya) darwinianus mulleri* (Dunker, 1875) and *B. (Mytilaster) solisianus* (Orbigny, 1846).

Lange de Morretes (1949) and Gofferjé (1950) noted its occurrence in Paraná. Klappenbach (1965) cited its appearance in Campeche (México) and in Brazil from Rio Grande do Norte to Torres, Rio Grande do Sul. Rios (1975) noted the presence of this species in Brazil from Fortaleza to Torres, and even as far as Uruguay.

In Brazil only few genera of the Mytilidae have been studied with respect to functional anatomy: *Mytella charruana* (Orbigny, 1846) (Narchi & Galvão Bueno, 1983) and *Brachidontes darwinianus darwinianus* (Avelar & Narchi, in press).

In this study we correlate the animal's structures, ciliary food currents and other functional adaptations to their life surroundings.

MATERIAL AND OCCURRENCE

The animals were collected on the "Lamberto" beach in Ubatuba (23°30'S, 45°04'20"W) and on the "Cabglo Gordo de dentro" beach in São Sebastião (23°48'07"S, 45°23'22"W). They live fixed by byssus threads to rocky substratum in the intertidal zone of creeks and bays, where they can form agglomerates of many hundreds of individuals.

In order to collect these Bivalvia we used a spatula to cut the byssus filaments by which they stick to the substratum.

The animals were kept alive, under good conditions, for about two months in aquaria seawater in circulation, at a temperature of 22°C. Thus, it was possible to study the functional anatomy.

Shell

The shell is rather small, mytiliform, equivalve, inequilateral. It has an angle on the back, the posterior edge curved and the ventral side slightly concave and the umbo is subterminal, characteristic for this species.

The dorsal angle of *B. solisianus* (Fig. 1) is of about 30°, differing from the *B. darwinianus darwinianus* specimens of the same size (Avelar & Narchi, in press). This fact also drew the attention of Wilson (1967) for *Xenostrobus pulex* and *X. inconstans*. The posterior region of *B. solisianus* is truncated and forms an angle of about 90°, with the dorsal and ventral mantle margins. This gives it a rectangular aspect, the dorsal and ventral margins being parallel in the posterior region. The anterior ventral part is slightly con-

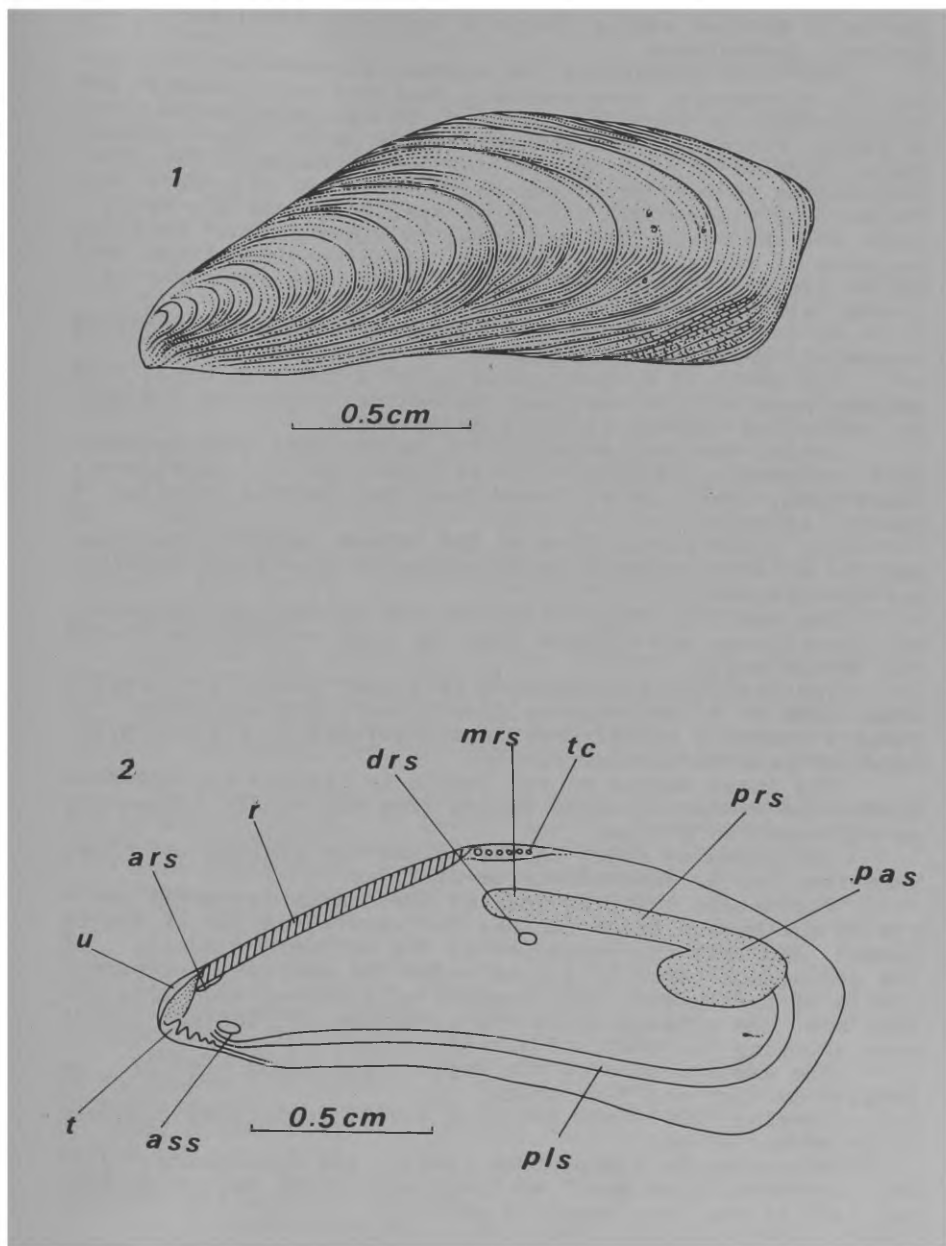


Figure 1 - *Brachidontes solisianus*. External view of left shell. Figure 2 - *Brachidontes solisianus*. Internal view of the shell valve.

vex as in *Mytilus edulis* (Yonge & Campbell, 1968) and *B. darwinianus darwinianus*.

The outer surface of the valves is smooth and only under the microscope, some scarcely distinct radial lines are recognizable. In very few specimens it was possible to observe radial riblets in the ventral region under the umbonal ridge, because in this species the periostracum in the anterior region is very prominent and often worn. This fact was observed by Klappenbach (1965) in specimens from Rio de Janeiro and São Paulo, and according to him this must be a consequence of the size they reached, since specimens from Mexico, Recife and Alagoas, of smaller size, have their periostracum fairly intact.

On the outer face of the valves we also noted numerous concentric grooves, corresponding to the growth lines.

The shell of *B. solisianus* is of a purplish blue, the periostracum is dark tan, and the ventral region of the valve, below the umbonal ridge, appears white.

Behind the lunula there is a smooth area with an obsolete sculpturing, similar to that formed in *B. multiformis* (Soot-Ryen, 1955) and *B. darwinianus darwinianus* (Avelar & Narchi, in press).

The inner purple face of the valves, slightly nacreous has the anterior ventral surface lighter like in *B. darwinianus darwinianus*.

The resilium (Fig. 2) is similar to that of *B. darwinianus darwinianus* and extends from the umbo to near the top of the dorsal angle.

The marginal scalloping is formed behind the resilium, like in *B. darwinianus darwinianus*, and according to Yonge & Campbell (1968) this is characteristic for the Mytilidae of reduced specialisation.

The inner margin of the lunula is limited by dissodont teeth, the number of which varies from two to six depending on the specimen's size.

The muscular scars in the valves are similar to those described for *B. darwinianus darwinianus*.

That means that the scar of the medium retractor muscle of the byssus never reaches the ventral margin of the ligament, and that the insertion of the retractor muscle of the demibranch (drs) is placed under the medium retractor muscle of the byssus, thus forming an isolated scar (Fig. 2). This scar had already drawn the attention of Ihering (1897) when studying the shell of *B. solisianus*.

The maximum size of the present specimens is 17 mm long, 6 mm high and 8 mm thick.

Ihering (1897) and Goffert (1950) registered lengths of 24 mm and 17 mm.

According to Klappenbach (1965), the specimen's size may vary from 12 mm to 17 mm long, and in the region of Torres (RS) it can even reach 18 mm.

Siphons

The siphons belong to type A (II) of Yonge (1948) They occupy the animal's body; the exhalant siphon is situated in the postero-dorsal region, the inhalant one in the posterior and ventral part of the shell. The branchial septum is situa

ted between the two apertures.

The siphons are brown, inside and outside, darker at the margins.

The inhalant siphon (Fig. 3) whose dorsal edge is formed by the fusion of the inner mantle lobe, has its ventral limit functionally separated from the foot aperture by the apposition of the mantle lobes, as generally in *Mytilacea* (Morton, 1973). It is bigger than the exhalant one and bears a series of papillae around the aperture; the exhalant siphon has a smooth margin.

The papillae are very numerous with spots of an iridescent green. They are similar to those of *Musculista senhauasia* (Morton, 1974) and *B. darwinianus darwinianus* (Avelar & Narchi, in press), i.e. finger-shaped and sometimes have a subdivided top. Their task is to restrain or amplify the inhalant aperture by controlling the water current which reaches the pallial cavity, as in *Mytella charruana* (Narchi & Galvão Bueno, 1983) and *B. darwinianus darwinianus*.

Yonge (1948) and Morton (1974) did not consider this as a real siphon, but only as an aperture, as the mantle edges, separating the inhalant aperture are not fused.

The inhalant siphon has well defined limits, without tentacles on the margin, and its walls can control the water current. The ventral part of the inhalant siphon is continued into the pallial cavity as a tube, which also controls the water current.

Between the apertures of the inhalant and exhalant siphon lies the branchial septum, which, according to Morton (1974) restrains the size of the inhalant aperture and fixes the ctenidium to the mantle, separating the siphon from the inhalant aperture, and thus the upper and lower branchial chambers.

In *B. solisianus* as well as in *B. darwinianus darwinianus* (Avelar & Narchi, in press) and in *Limnoperna fortunei* (Morton, 1974) the branchial septum takes a horizontal position when the siphons are dilated and folds itself up when they retract. It has muscular filaments and a conjunctive tissue by which it is able to diminish the inhalant aperture.

In *B. solisianus* the branchial septum presents itself like two triangular projections, one of them turned to the pallial chamber, and the other, shorter than the first, turned to the exhalant chamber, and limiting also the exhalant aperture so as to control the water current.

The surface of the branchial septum consists of ciliary epithelium with patches of brown pigment, as was observed in *Mytilus edulis* (White, 1937) and by the authors in *B. darwinianus darwinianus*. The ciliary currents on the branchial septum are rejective, as they curve the particles dorsally into the rejection groove at the tangent between the inhalant and exhalant siphons.

In *B. solisianus* the siphons are sensitive and react to the least trepidation or to the slightest observation of the aquarium. This fact had already been observed in various Bivalvia like *Glossus humanus* (Owen, 1953); *Anomalocardia brasiliensis*, *Tivela mactroides* (Narchi, 1972a) and *B. darwinianus darwinianus*.

According to Owen (1953) and Narchi (1972) this sensitivity is connected with the animal's life in quiet waters.

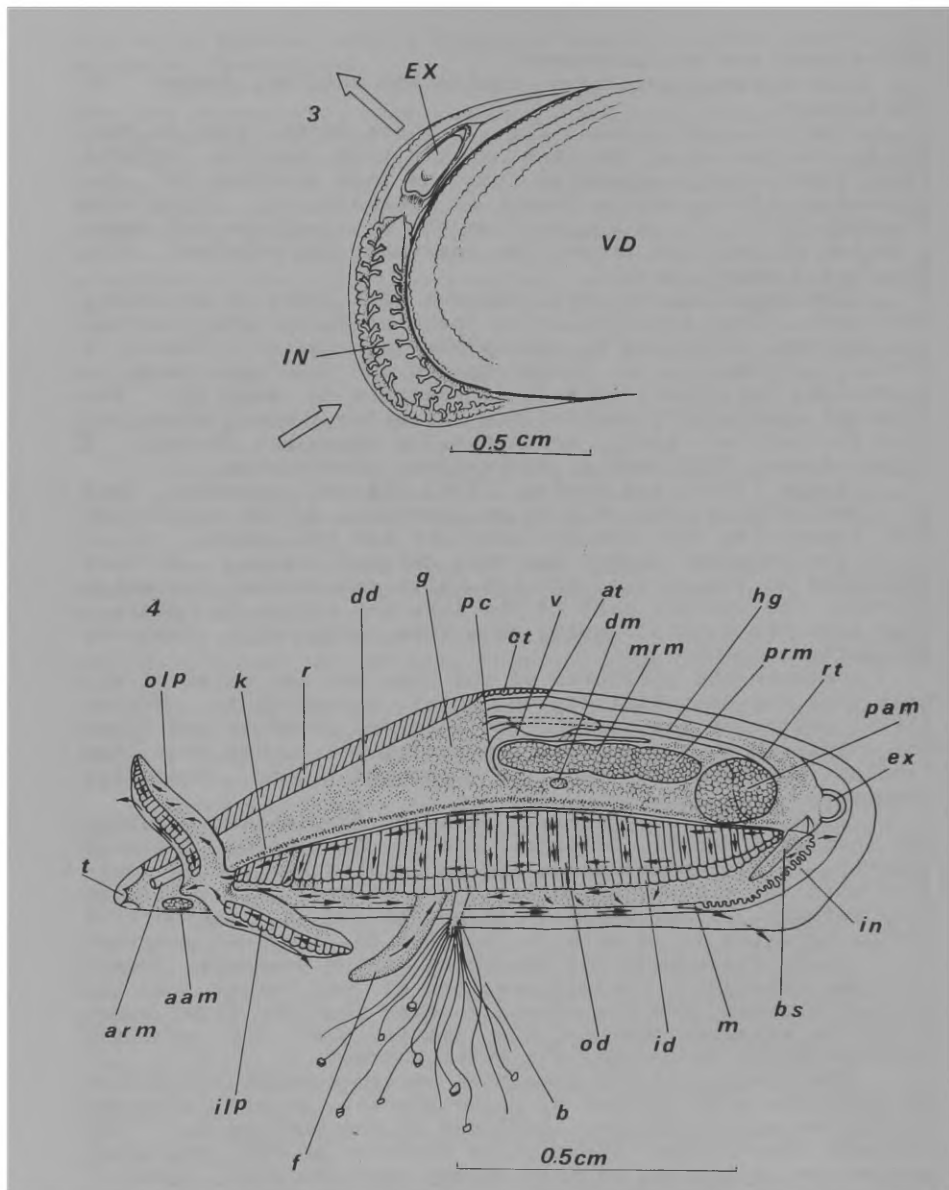


Figure 3 - *Brachidontes solisianus*. External appearance of the siphons showing the inhalant (in) and exhalant openings (ex). Figure 4 - *Brachidontes solisianus*. Mantle cavity viewed from left side after removal of left shell valve and mantle lobe.

Mantle

The mantle edge is similar to that of other known Mytilidae and is similar to the one described for *Mytella charruana* (Narchi & Galvão Bueno, 1983) and *B. darwinianus darwinianus* (Avelar & Narchi, in press).

Mantle cavity

The position of the organs in the mantle cavity (Fig. 4) was exposed by removing the left valve of the shell and the correspondent mantle lobe.

Musculature

The musculature (Fig. 5) is similar to that of the Mytilidae e.g., *Mytilus edulis* (White, 1937), *Musculista senhousia* (Morton, 1974) and *B. darwinianus darwinianus*.

However the muscle of the demibranch (dm) leaves a mark in the shell, under the insertion of the medium retractor muscle of the byssus, different from that of *B. darwinianus darwinianus*. According to Atkins (1944) this muscle belongs to type (b). In these animals the task of the demibranch muscle is to avoid an excess of particle to reach the pallial cavity and fall on the ctenidia.

Foot and Byssus

Anatomy, ciliary currents and general conformation of the foot and byssus (Fig. 6) are similar to those described for *B. darwinianus darwinianus*, with one exception: the distal extremity of the foot groove presents no brown pigment in *B. solisianus*.

Ctenidia

The ciliary currents upon the ctenidia were observed by adding carborundum powder, carmine or aquadaq, in the method used by various authors.

The demibranchs are homorhabdic as Ridewood (1903) Kellogg (1915) and Atkins (1937) observed. They belong to type B (1) described by Atkins and are characterized by the presence of two marginal grooves (Fig. 7), one in the inner and other in the outer demibranch, both of similar aspect and about the same size typical for Mytilidae and Pinnidae.

The marginal groove in *B. solisianus* and *B. darwinianus darwinianus* is rather shallow in comparison with that of *Adula (Botula) falcata* (Fankboner 1971) which can be about 1 mm deep. The depth of this groove varies from 40 to 60 μ m, depending on the degree of distention. According to Atkins (1937a) this groove is connected with the sorting mechanism,

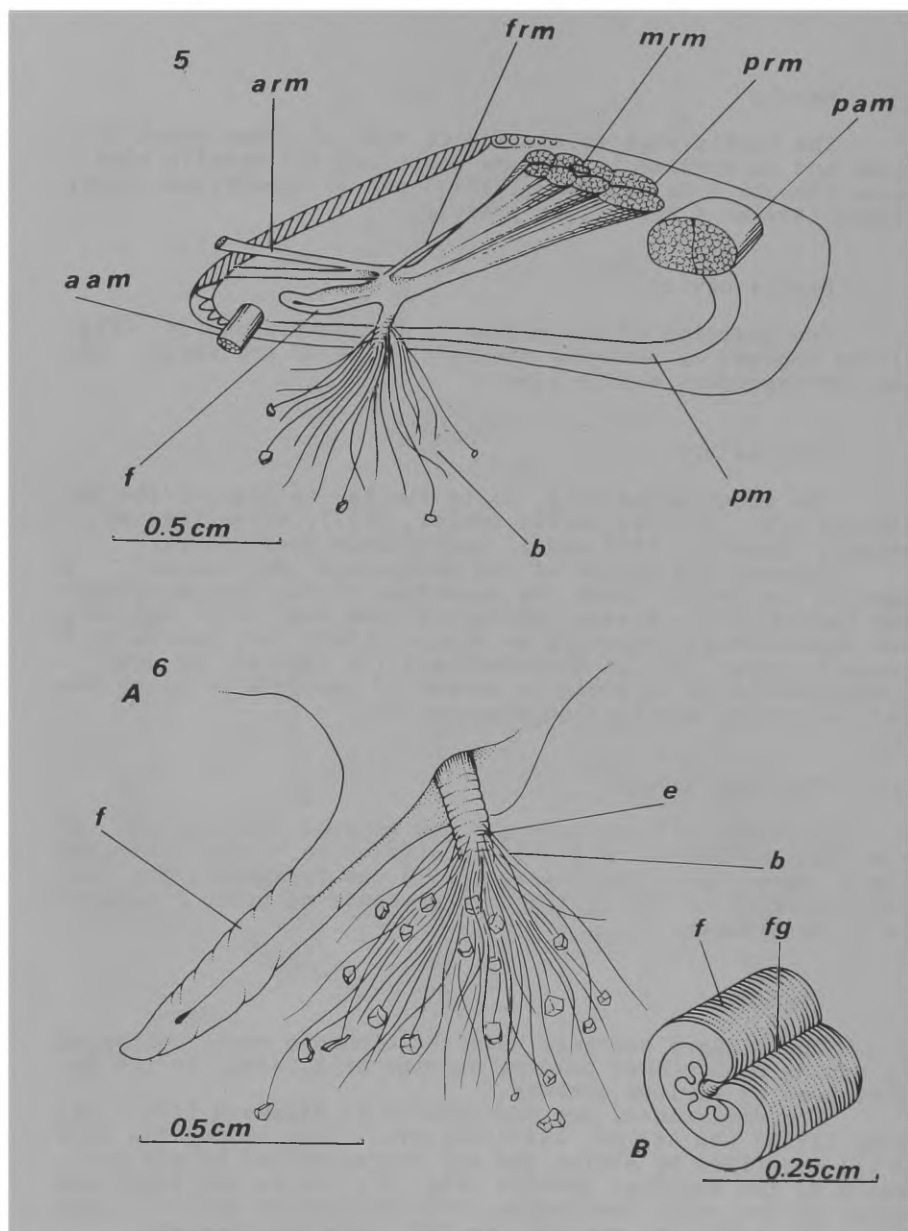


Figure 5 - *Brachidontes solisianus*. Lateral view of muscles, after removal of left shell valve, mantle lobe and visceral mass. Figure 6 - *Brachidontes solisianus*. A, Foot and its byssus. B, Transverse section of foot.

and it restricts the size of the particles by opening or shutting.

We can recognize on the ctenidia five oralward currents (Fig. 7), two in the marginal grooves, one along the axis of the ctenidia between the descendent lamella of the outer and inner demibranchs, one between the ascendent lamella of the outer demibranch and the mantle, and the last between the ascendent lamella of the inner demibranch and the visceral mass. The ciliary currents convey the particles into the free margins of the demibranchs, with exception of a narrow strip in the dorsal region of the inner and outer demibranchs, where the currents are ascendent. This disposition of the ciliary currents is one of the characteristics of the Mytilidae.

In *B. solisianus* the outer demibranch has 8 to 10 filaments less than the inner one. This fact was already known and observed in *Petricola pholadiformis* (Purchon, 1955) *Adula falcata*, *A. californiensis*, *Lithophaga bisulcata*, *Mytilus edulis* (Fankboner, 1971), *Limnoperna fortunei* and *Musculista senhousia* (Morton, 1973, 1974), *Brachidontes darwinianus darwinianus* (Avelar & Narchi, in press). According to Purchon (1955) and Morton (1974) this reduction makes the contact of the marginal food groove of the demibranchs with the labial palps more efficient.

In *B. solisianus*, as well as in the Mytilidae in general, the cohesion between the filaments, is maintained by means of ciliary disks.

The descending part of each filament is fused to the ascending part of the same by interlamellar junctions. According to White (1937) these junctions are characteristic for the Mytilacea.

The ciliary arrangement of the branchial filaments (Fig. 8B) in *B. solisianus* is practically the same as that described for *B. darwinianus darwinianus* (Avelar & Narchi, in press) with some small differences, as the presence of sensitive cilia (Fig. 8A, ssc) in triangular tufts of about 20 μm length and a base of 11 μm , which occur principally on the ascending lamella of the outer demibranch. According to Atkins (1937) they are found in *Arca tetragona*, *Glycymeris glycymeris*, *Heteronomia squamula*, *Monia squama* and *M. patelliformis* and probably have tactile function.

The filaments of the ctenidia in *B. solisianus* are separated by the eu-latero-frontal cilia (Fig. 9) of about 19 μm length. These cilia alternate and form a kind of a grate, thus protecting the interfilamentary passage. They were described in the Mytilidae: *Mytilus edulis*, *Modiolus modiolus*, *M. adriaticus*, *Musculus marmoratus*, *M. discor* (Atkins, 1938), *Mytella charruana* (Narchi & Galvão Bueno, 1983) and *Brachidontes darwinianus darwinianus*.

The lateral cilia (lc), situated inwards to the eulatero-frontal cilia, are about 12 μm long and occupy the latero-distal face of the filaments.

All around the filament surface there are the frontal cilia (fc), about 9 μm long, which send food particles to the free margin of the ctenidium.

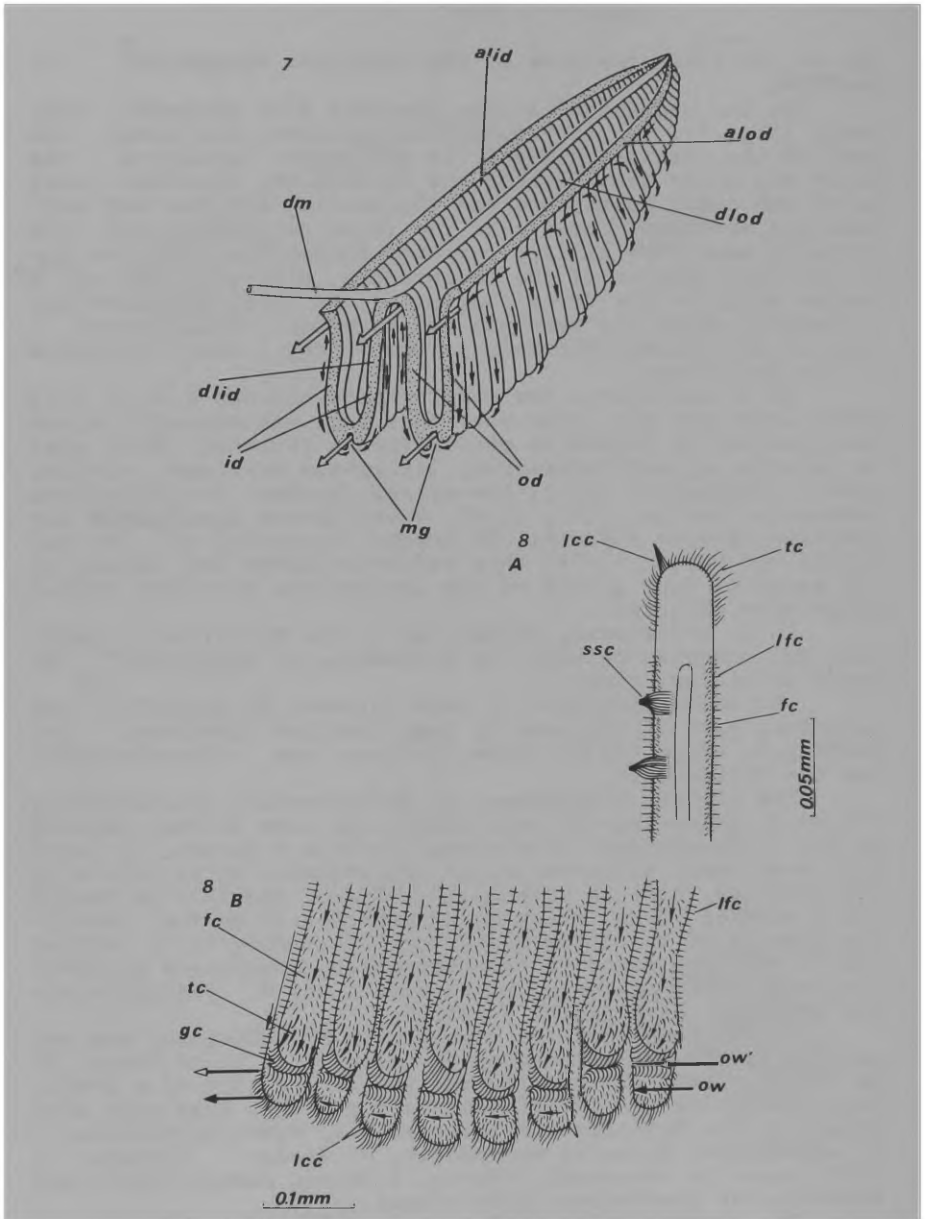


Figure 7 - *Brachidontes solisianus*. Diagrammatic section of ctenidium to show mode of action of frontal cilia, and demi-branch retractor muscle. Arrows indicate direction of ciliary currents, including oral one. Figure 8 - *Brachidontes solisianus*. A, Lateral view of branchial filaments to show sensitive cilia. B, Extremity of filaments showing guarding cilia and the oralward currents.

The frontal cilia give place to the terminal cilia (tc) on the free margin of the filaments, which are bent for wards. The terminal cilia can be as long as $19\text{ }\mu\text{m}$ on the extremity of the filament and are responsible for an oralward current.

No pro-latero-frontal cilia were observed, although they may occur in Bivalvia with eu-latero-frontal cilia. According to Atkins (1938) these cilia always occur in the Mytilidae but are not always laid open owing to the difficulties of observation and preservation of the material. Moore (1971) and Owen (1974) confirmed the presence of these cilia for *Mytilus edulis* with scanning microscope.

B. solisianus has guarding cilia (gc) up to $30\text{ }\mu\text{m}$ long: they occur also in other Mytilidae. These cilia have been registered in *Modiolus*, *Musculus* (Atkins, 1937a), *Adula* (Fankboner, 1971), *Brachidontes* (Avelar & Narchi, in press).

So, the marginal groove has two channels with oralward currents, one formed by the guarding cilia and the other by the terminal cilia.

On the hind third of the demibranchs, at the free extremity of the filaments, there is a triangular tuft of rigid cilia which are called cirrum (lcc). They are $20\text{ }\mu\text{m}$ long and their function is probably correlated with the selection of large particles of sand grains. The presence of these cilia was registered by Atkins (1937) in many bivalves. Yonge (1946) ascribed to them the function of agitating large particles and masses which tend to accumulate on the free margin, thus reinforcing the action of the terminal cilia. In *B. solisianus*, as well as, in *B. darwinianus darwinianus* they are frequent in the hind region of the demibranch and diminish gradually towards the front region.

Labial palps

The labial palps are triangular, flattened, long, and extremely mobile (Fig. 10)

The faces turned to the branches are covered with folds and the opposite ones are smooth.

The inner demibranch keeps in contact with the fold bearing face of both palps, and the initial filaments of the inner demibranch are not fused to the oral groove. That is why the association ctenidium - labial palp belongs to category I (Stasek, 1963), typical for Mytilacea.

The food particles are sorted by muscular or ciliar activity (Kellogg, 1915; Ansell, 1961; Narchi, 1972a)

The particles which reach the palp are sorted according to their size. Those which fall onto the smooth face of the palp are conveyed by the cilia of the dorsal edge to the folded face from where they are carried off the margin of the longitudinal fold.

Small particles which fall upon the folded face are transported rapidly over the surface of the folds to the mouth. Bigger particles are directed from one crest to the other to oral region where they are subjected to selection.

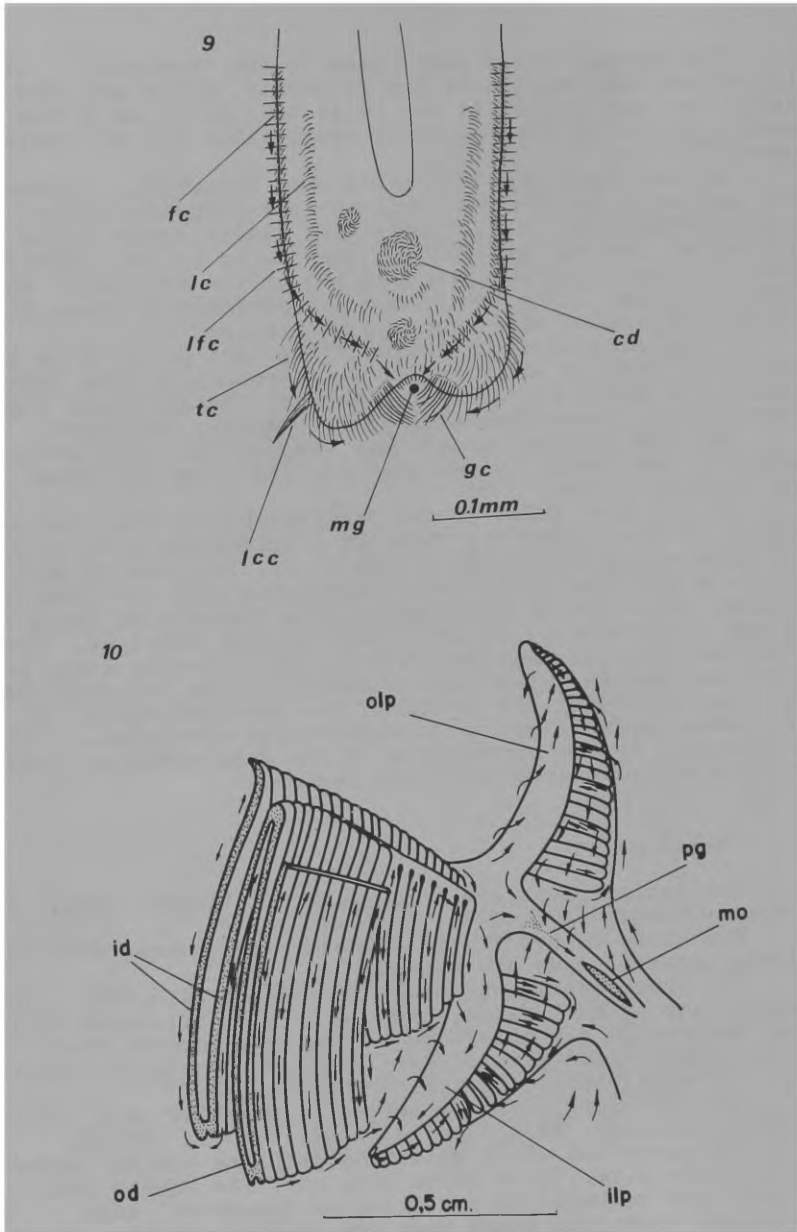


Figure 9 - *Brachidontes solisianus*. Ventral end of living filament in side view showing position of groups of guarding cilia around marginal groove. Figure 10 - *Brachidontes solisianus*. Labial palps and ctenidium of right side showing ciliary currents.

The ciliary currents which were observed, are similar to those of *B. darwinianus darwinianus* (Avelar & Narchi, in press).

The labial structure in *B. solisianus* is of the simple type (Bernard, 1972).

It is rather difficult to observe the ciliary current at the labial region, as the cilia of this region may be subject to nervous control and show a rhythm of activity and inactivity. Hence the possible cessation of ciliary activity in the mouth region may be due to the accumulation of mucus, together with the contraction of the surface tissue (Purchon 1955a).

Food particles which reach the mouth sorted by the labial palps, are not totally accepted as they may be rejected by the lips when the mouth closes and the ciliary palpitations are paralysed.

Analysis of the size of the particles contained in the stomach of *B. solisianus* revealed a more homogeneous sorting of particles than that found in *B. darwinianus darwinianus*. The size of the particles varied from 3 μm to 23 μm in *B. solisianus*, from 3 μm to 160 μm in *B. darwinianus darwinianus*.

On the visceral mass there are rejecting currents, which convey particles sideways, so that they can be either reaccepted by the labial palps or rejected by the visceral mass currents.

The particles rejected by the palps and the visceral mass are transported by the rejecting currents of the mantle to the base of the inhalant siphon, from where they are eliminated.

Ciliary currents on the mantle surface

In order to study the ciliation of the inner mantle surface, the visceral mass and the ctenidium were removed, after which seawater was added to the preparation and it was left standing so as to obtain a certain relaxation of the muscles.

To make the ciliary currents visible, particles of carmine powder were applied.

In *B. solisianus* (Fig. 11) the ciliary currents are rejecting ones. They conduct the particles from the dorsal to the ventral regions, the area being totally provided with cilia.

On the free mantle edge the currents send the particles from the anterior to the posterior region, from where they are eliminated as pseudo-faeces, at the base of the first papilla of the inhalant siphon, by a rapid contraction of the adductor muscle.

Alimentary canal

General structure - The alimentary canal (Fig. 12) was dissected from live specimens, which were anesthetized before hand with magnesium chloride; also animals preserved in

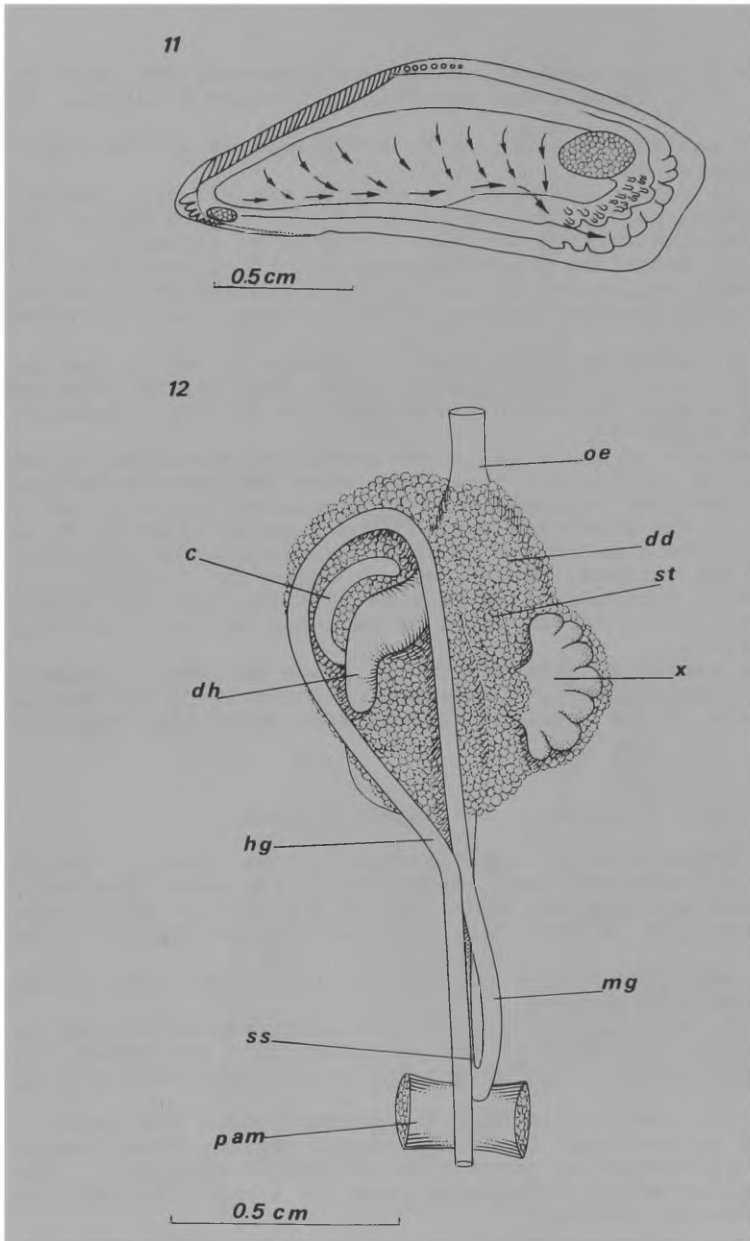


Figure 11 - *Brachidontes solisianus*. Inner surface of right mantle lobe to show ciliary cleansing currents. Figure 12 - *Brachidontes solisianus*. Dorsal view of the alimentary channel.

formol 4% were utilized.

The short oesophagus (oe) ends in the anteroventral region of the stomach. The style sac (ss) and the intestine are united, separating near the dorsal region of the posterior adductor muscle, like in *B. darwinianus darwinianus* (Avelar & Narchi, in press).

The intestine of *B. solisianus* is similar to that of *B. darwinianus darwinianus* differing only in the position of the anterior intestinal loop which occupies a left-latero-dorsal position. In *Xenostrobus* (Wilson, 1967) the intestinal loop does not reach the stomach.

Into the postero-lateral wall of the stomach opens the multilobate appendix (x).

In *B. solisianus* the dorsal hood, well developed in this species lies in the left dorsal region of the stomach.

Structure of the stomach

The stomach was opened by middorsal incision. The ciliary currents were observed by the use of a suspension of Carmine, Aquadag and very fine Carborundum. The nomenclature is the same as that used by Graham (1949), Owen (1953), Purchon (1955) and Dinamani (1967).

The stomach of *B. solisianus* (Fig. 13) belongs to type III in the classification of Purchon (1957).

The minor typhlosole (mt) ends near the orifice of the midgut on the right posterior wall of the stomach. The major typhlosole (ty) accompanied by the intestinal groove (ig) begins in the posterior region, passes over the floor of the stomach from right to left, and penetrates into the sorting caecum (fc).

The tongue of the major typhlosole (ty') in *B. solisianus* as Dinamani (1967) described for *Perna viridis*, *Modiolus undulatus*, *M. striatulus*, *Arcuatula* sp, forms a curve within the sorting caecum and returns to the stomach. Eight to ten ducts of the digestive diverticulum open into the caecum, similar to *P. viridis* and *B. darwinianus darwinianus* (Avelar & Narchi, in press).

On the anterior wall of the dorsal hood (dh) there is a poorly developed sorting area (sa₄) as in *Neotrigonia margaritacea* and *Lima fragilis* (Purchon, 1957).

In the ventral part of the gastric shield (gs) there is an widened depression that forms the left pouch (lp) into which 3-4 ducts of the digestive diverticulum open like in *P. viridis*, *M. undulatus* and *M. striatulus* (Dinamani, 1967).

The axial fold begins from the floor of the stomach above the sorting caecum. It emits two projections, one towards the left pouch and the other dorsally to the roof of the stomach, ending near the antero-dorsal tract (a).

Beside the lateral fold (lf), which is parallel to the major typhlosole, there are four ducts of the digestive diverticulum (ddd) on the right, and only three on the left.

The posterior sorting area is situated at the right of the lateral fold, being bounded by the rejection tract (rg)

The posterior sorting area does not extend into the dorsal hood like in *P. viridis* and *B. darwinianus darwinianus* (Avelar & Narchi, in press).

The multilobate appendix has eight well visible inner folds and it is situated in front of the posterior sorting area.

The antero-dorsal tract begins on right anterior wall of the stomach and extends to the opening of the dorsal hood, like in *Mytilus edulis* (Reid, 1965).

Between the terminal region of the lateral fold (lf) and the major typhlosole (ty) there is a plain area (sa₃), which Reid denominates tract of the ducts of the digestive diverticulum on the right. This area had been observed in *Lithophaga gracilis* (Dinamani, 1967), *L. nasuta* (Purchon, 1957) and *B. darwinianus darwinianus*.

Functioning of the stomach

The particles not rejected by the ctenidia and the palps are conveyed into the mouth, and reach the stomach through the oesophagus, embedded in mucous in the form of a mucous string that join the crystalline style, where the particles are disintegrated and thrown either towards the sorting caecum or to the opening of the ducts of the digestive diverticulum. Only the small, isolated particles reach the ducts of the diverticulum, whereas the others enter or not into the sorting caecum. Large particles are driven into the dorsal hood by the cilia of the wall of the axial fold, and later are recaptured by the crystalline style. Small particles that reach the sorting area (sa₂) situated on the wide base of the axial fold are conveyed to the dorsal hood either by the ciliary currents of the anterior tract, or by the currents of the axial fold.

The particles triturated by the style, that fall onto the floor of the stomach, are conveyed to the sorting caecum through the major typhlosole or by the lateral fold.

The particles that fall into the widened posterior part of the lateral fold are directed to the sorting area (sa₂) whence the small, light particles are sent into the opening of the ducts on the right. The bigger particles are thrown onto the typhlosole and thence to the sorting caecum.

Particles that fall onto the anterior part of the lateral fold are conducted towards the caecum or the antero-dorsal tract.

The particles that enter the sorting caecum and are rejected there, return to the stomach, along the wall of the axial fold and thence are carried onto the dorsal hood, or are guided by the intestinal groove to the midgut. The material accumulated in the dorsal hood is recaptured by the crystalline style.

Particles broken up in the crystalline style may be led to the left pouch by the ciliary currents of the axial fold.

In the zone of the left pouch two types of currents appear, those which are directed to the posterior region to-

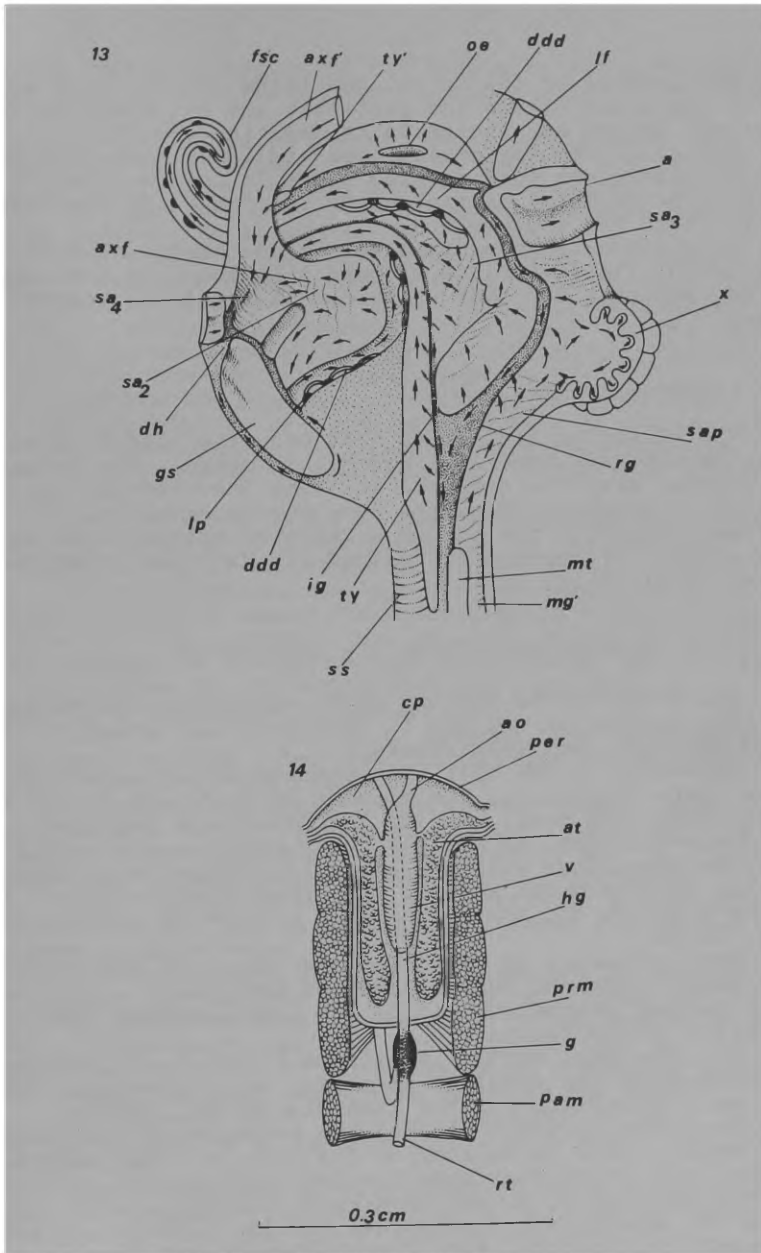


Figure 13 - *Brachidontes solisianus*. Interior of stomach opened by mid dorsal incision passing from oesophagus to midgut. Figure 14 - *Brachidontes solisianus*. Dorsal view of pericardial cavity.

wards the opening of the ducts, and those of the shallow part of the pouch, where the particles are conveyed onto the intestinal groove and thence to the sorting caecum.

Material from the crystalline style may also fall into the posterior right sorting area where it is submitted to selection. The rejected particles are carried on by the rejection tract to the midgut.

B. solisianus presents a sorting mechanism of type A and B (Reid, 1965). Sorting of type A is found in the areas sa_2 , sa_3 and sap , and that of type B in the food separating caecum.

Excretory organs

The kidney is similar to that described for *B. darwinianus darwinianus* (Avelar & Narchi, in press). The pericardial glands, are also disposed as those described for *B. darwinianus darwinianus*. They are very poorly developed in *B. solisianus* and give the atrium a brownish colour, like in *Mytilus edulis*, *Lithophaga cumingiana* and *Musculus marmoratus* (White, 1942) (Fig. 14)

GENERAL DISCUSSION AND CONCLUSIONS

The study of the anatomy of *B. solisianus* has revealed that this species is adapted to that habit of living sticking to rocks in sheltered creeks.

Generally in the Mytilidae the siphons are short and, due to their simplicity, the sorting of particles is not very efficient. The small size of the tentacular papillae of the inhalant siphon, as well as their position and simplicity may be correlated with the animal's life on rocky substratum, the life in quiet waters. The great sensitivity of the siphons would be an adaptation to a habitat in quiet waters (Owen, 1953)

Most probably, in Mytilidae the length of the siphons, their sensitivity and the presence of tentacular papillae are in general characteristic of the family rather than an adaptation to the habitat.

The branchial septum is extremely mobile. It controls the entrance of the inhalant aperture, and, moreover, functions as a protection for the ctenidia (Orton, 1912).

According to Yonge (1943a) the presence of the branchial septum would be related to the life in muddy waters. However it is known that some species of Mytilidae, among them *Mytilus edulis*, *M. californianus* (Kellogg, 1915) as well as *B. darwinianus darwinianus* (Avelar & Narchi, in press), do present this septum, even though they do not live in muddy places.

The musculature is similar to that of the Mytilidae in general and presents the muscle of the demibranch. This muscle is related to the retracting of the ctenidia when a great quantity of particles falls, by the inhalant flux, on

to the posterior region of the ctenidia. Among the Mytilidae this muscle had already been described only for *B. darwinianus darwinianus*.

The labial palps are extremely mobile and efficient for the sorting of particles. They present a prominent muscular activity by preventing undesired particles from entering into the digestive tract. This fact had already been observed by Purchon (1963) and Narchi (1972).

The ctenidia are similar to those of the Mytilidae in general and according to Atkins (1937b) it is very difficult to correlate them with the animal's habitat and manner of life. *B. solisianus* has guarding cilia which Atkins associated with the presence of mud on the substratum. However this is not the case for the present species.

Perhaps the presence of these cilia is related with the feeding habit, as these animals have to use the particles in suspension to the utmost during the immersion period, as they remain exposed during the low tide periods for a long time.

The sensitive cilia on the demibranches may be related with the presence of large particles in the habitat. This correlation had already been mentioned by Yonge (1946).

In *B. solisianus* the quantity of sensitive cilia is smaller than in *B. darwinianus darwinianus* (Avelar & Narchi, in press). This is due to the animal's living in higher levels contrary to *B. darwinianus darwinianus*, which settles on rocks close to the substratum where there is a bigger quantity of particles in suspension.

Like in the Mytilidae in general, the inner demibranch is bigger than the outer one, which helps the sorting of particles to be more efficient.

B. solisianus shows in comparison with *B. darwinianus darwinianus* a smaller number of ciliary disks, perhaps as a consequence of adaptation to the habitat, as *B. solisianus* shows a more homogeneous selection of particles.

Also the mantle surface cooperates in the selection of particles within the pallial cavity, where the currents are uniformly distributed.

The foot contributes to the cleansing of the mantle cavity, since the ciliary currents are rejective, which transport the particles from the anterior to the posterior region. Some of these particles join the branches and are sorted again. When there is an accumulation of particles in the labial palps, the foot cooperates removing the excess.

The stomach of *B. solisianus* belongs to type III of the classification of Purchon (1957) with style sac and intestine fused.

The stomach has sorting areas of types A and B (Reid, 1965). Anatomically the stomach of *B. solisianus* appears more elaborate than that of *B. darwinianus darwinianus*. Probably this greater complexity is related with the size of the particles. The analysis of the contents of the stomach showed that *B. solisianus* deals with homogeneous and small sized material. The presence of an appendix functioning as a basis for stocking and sorting of food reveals that the animal is adapted to a habitat where are many small particles.

in suspension.

In the classification of Purchon (1958) *B. solisianus*, due to its stomach, would be placed in the Gastrotriteia or der of the subclass Polysyringia.

B. solisianus presents conchological characteristics which permit its classification as an intermediate form between the isomyaria, scalloped bivalvia (*Crenella*, Morton, 1974) and anomyaria bivalvia (*Mytilus*, Yonge & Campbell, 1968). One of these characters is the presence of scallopings similar to teeth. The subterminal umbo is also an intermediate character since in *Mytilus* (White, 1937), *Xenos-trobus* (Wilson, 1967) and *Septifer* (Yonge & Campbell, 1968) the umbo is terminal.

The shell is slightly convex in the part before the ventral region, like in *Mytilus* (Yonge & Campbell, 1968). This condition is considered as a particularity among the more specialised Mytilidae.

ABBREVIATIONS USED IN THE FIGURES

a - anterior dorsal tract; aam - anterior adductor muscle ; alid - ascending lamella of inner demibranch; alod - ascending lamella of outer demibranch; ao - anterior aorta; ars - anterior retractor muscle scar; arm - anterior retractor muscle; ass - anterior adductor muscle scar; at - atrium ; axf - axial fold; axf' - terminal portion of the axial fold; b - byssus; bs - branchial septum; c - caecum; cd - ciliar disk; cp - pericardial cavity; ct - crenulation; dd - digestive diverticula region; ddd - digestive diverticula ducts ; dh - dorsal hood; dlid - descending lamella of inner demibranch; dlod - descending lamella of outer demibranch; dm - demibranch muscle; drs - demibranch muscle retractor scar ; e - principal byssus axis; ex - exhalant siphon; f - foot ; fc - frontal cilia; fg - pedal groove; frm - retractor pedal muscle; fsc - food sorting caecum; g - gonad ; gc - guarding cilia; gs - gastric shield; hg - hind gut; id - inner demibranch; ig - intestinal groove; ilp - inner labial palp ; in - inhalant siphon; k - kidney; lc - lateral cilia; lcc - cirrum; lf - lateral fold; lfc - latero frontal cilia; lp - left pouch; m - mantle; mg - marginal groove; mg' - midgut ; mrm - middle retractor byssus muscle; mrs - middle retractor byssus muscle scar; mo - mouth; mt - minor typhlosole; od - outer demibranch; oe - oesophagus; olp - outer labial palp ; ow - oralward current in the region of superficial marginal groove; ow' - oralward current in the region inside marginal groove; pam - posterior adductor muscle; pas - posterior adductor muscle scar; pc - renopericardial channel; per - pericardium; pls - pallial muscle scar; pm - pallial muscle ; pam - posterior adductor muscle; pg - proximal oral groove ; prs - posterior retractor byssus muscle scar; prm - posterior retractor byssus muscle; r - resilium; rg - rejection groove; rt - rectum; sa₂ - sorting area of axial fold; sa₃ - sorting area of right side of stomach; sa₄ - sorting area of dorsal hood; sap - posterior sorting area; ss - style sac;

ssc - sensitive cilia; st - stomach region; t - teeth; tc - terminal cilia; ty - major typhlosole; ty' - major typhlosole tongue; u - umbo; v - ventricle; vd - right valve; x - appendix.

REFERENCES

- ANSELL, A.D. 1961. The functional morphology of the British species of Veneracea (Eulamellibranchia) *J.mar.biol.Ass. U.K.*, 41(2):489-517
- ATKINS, D. 1937. On the ciliary mechanisms and interrelationship of Lamellibranchs. Part. I: New observations on sorting mechanisms. *Q.Jl.microsc.Sci.N.S.*, 79:181-308
- ATKINS, D. 1937a. On the ciliary mechanisms and interrelationship of Lamellibranchs. Part. II. Sorting devices on the gills. *Q.Jl.microsc.Sci.N.S.*, 79:339-373.
- ATKINS, D. 1937b. On the ciliary mechanisms and interrelationship of Lamellibranchs. Part. III: Types of Lamellibranchs gills and their food currents. *Q.Jl.microsc.Sci.N.S.*, 79:375-421.
- ATKINS, D. 1938. On the ciliary mechanisms and interrelationship of Lamellibranchs. Part VII: Latero-frontal cilia of the gill filaments and their phylogenetic value. *Q.Jl.microsc.Sci.N.S.*, 80:345-436.
- ATKINS, D. 1944. On the ciliary mechanisms and interrelationship of Lamellibranchs. Part VIII: Notes on gill musculature in the microciliobranchia. *Q.Jl.microsc.Sci.N.S.*, 84:187-256.
- AVELAR, W.E.P. & W. NARCHI, in press. Anatomia funcional de *Brachidontes darwinianus darwinianus* (Orbigny, 1846) Bivalvia Mytilidae. *Papéis Avulsos Zool.*
- BERNARD, F.R. 1972. Occurrence and function of lip hypertrophy in the Anisomyaria (Mollusca, Bivalvia) *Can.J.Zool.*, 50:53-57
- DINAMANI, P. 1967. Variation in the stomach structure of Bivalvia. *Malacologia* 5(2):225-268.
- FANKBONER, P.V. 1971. The ciliary currents associated with feeding, digestion and sediment removal in *Adula (Botula) falcata* Gould, 1815. *Biol.Bull.mar.biol.Lab.Woods Hole*, 140:28-45.
- GOFFERJÉ, C.N. 1950. Contribuição a zoogeografia da Malaco-fauna do litoral do Estado do Paraná. *Arqs.Mus.parana.*, 8: 221-282.
- GRAHAM, A. 1949. The Molluscan stomach. *Trans.R.Soc.Edinb.*, 61(3):737-778.
- IHERING, H. VON 1897. Os Molluscos Marinhos do Brasil. *Revta. Mus.paul.*, 2:73-113.
- KELLOGG, J.L. 1915. Ciliary mechanisms of Lamellibranchs with descriptions of anatomy. *J.Morph.*, 26(4):625-701.
- KLAPPENBACH, M.A. 1965. Lista preliminar de los Mytilidae brasileños con claves para su determinación y notas sobre su distribución. *Anais Acad.bras.Ciênc.*, 37(supl.): 327-352.
- LANGE DE MORRETES, F. 1949. Ensaio de Catálogo dos Moluscos

- do Brasil. *Arqs.Mus.parana.* 7(1):5-216.
- MORTON, B. 1973. Some aspects of the biology and functional morphology of the organs of feeding and digestion of *Limnoperna fortunei* (Dunker) (Bivalvia: Mytilacea) *Malacologia* 12(2):265-281.
- MORTON, B. 1974. Some aspects of the biology, population dynamics and functional morphology of *Musculista senhousia* Benson (Bivalvia, Mytilidae). *Pac.Sci.*, 28(1):19-33.
- MOORE, H.J. 1971. The structure of the latero-frontal cirri on the gills of certain lamellibranch molluscs and their role in suspension feeding. *Marine Biology*, 11:23-27.
- NARCHI, W. 1972. On the biology of *Iphigenia brasiliensis* Lamarck, 1818 (Bivalvia, Donacidae) *Proc.malacol.Soc.London.*, 40:79-91.
- NARCHI, W. 1972a. Comparative study of the functional morphology of *Anomalocardia brasiliensis* (Gmelin, 1791) and *Tivela mactroides* (Born, 1778) (Bivalvia, Veneridae) *Bull. Mar.Sci.*, 22(3):643-670.
- NARCHI, W. & M.S. GALVÃO BUENO, 1983. Anatomia funcional de *Mytella charruana* (Orbigny, 1846) (Bivalvia: Mytilidae) *Bolm.Zool., Univ.S.Paulo*, 6:113-145.
- OWEN, G. 1953. On the biology of *Glossus humanus* (L.) (*Isocardia cor* Lam.) *J.mar.biol.Ass.U.K.*, 32:85-106.
- OWEN, G. 1974. Studies on the gill of *Mytilus edulis*: the eulatero-frontal cirri. *Proc.R.Soc.London*, 187:83-91.
- PURCHON, R.D. 1955. The functional morphology of the rock-boring lamellibranch *Petricola pholadiformis* Lamarck. *J.mar.biol.Ass.U.K.*, 34:257-278.
- PURCHON, R.D. 1955a. The structure and function of the British Pholadidae (rock-boring lamellibranchia) *Proc.Zool.Soc.Lond.*, 124:859-911.
- PURCHON, R.D. 1957. The stomach in the Filibranchia and Pseudolamellibranchia. *Proc.Zool.Soc.Lond.*, 129:27-60.
- PURCHON, R.D. 1958. Phylogeny in the Lamellibranchia. Proceedings of the Centenary and Bicentenary Congress of Biology, Singapore, p. 70-82.
- PURCHON, R.D. 1963. A note on the biology of *Egeria radiata* Lam. (Bivalvia, Donacidae) *Proc.malac.Soc.Lond.*, 35:251-271.
- REID, R.G.B. 1965. The structure and function of the stomach in bivalve molluscs. *J.Zool.*, 147:156-184.
- RIDEWOOD, W.G. 1903. On the structure of the gills of the Lamellibranchia. *Phil.Trans.R.Soc.Lond.*, B, 195:147-284.
- RIOS, E.C. 1975. *Brazilian marine mollusks iconography*. Fundação Universidade do Rio Grande, Centro de Ciências do Mar, Mus. Oceanogr., 331 p. 91 pls., Rio Grande - RS, Brasil.
- SOOT-RYEN, T. 1955. A report on the family Mytilidae. *Allan Hancock Pacif. Exped.*, 20(1):1-175.
- STASEK, C.R. 1963. Synopsis and discussion of the association of ctenidia and labial palps in the bivalved Mollusca, *Veliger*, 6(2):91-97.
- WHITE, K.M. 1937. *Mytilus*. In: DANIEL, R.J. ed. *Liverpool Marine Biology Committee, Memoirs*. Liverpool, The University Press of Liverpool Ltd. 31:117 p., Liverpool, England.

- WHITE, K.M. 1942. The pericardial cavity and the pericardial gland of the Lamellibranchia. *Proc.malac.Soc.Lond.*, 25: 37-88.
- WILSON, B.R. 1967. A new generic name for three recent and one fossil species of Mytilidae (Mollusca-Bivalvia) in southern Australasia with redescriptions of the species *Proc.malac.Soc.Lond.*, 37:279-295.
- YONGE, C.M. 1946. On the habits and adaptations of *Aloidis (Corbula) gibba*. *J.mar.biol.Ass.U.K.*, 26(3):358-376.
- YONGE, C.M. 1948. Formation of siphons in Lamellibranchia. *Nature*, 161:198-199.
- YONGE, C.M. 1948a. Cleansing mechanisms and the function of the fourth pallial aperture in *Spisula subtruncata* (Da Costa) and *Lutraria lutraria* (L.). *J.mar.biol.Ass.U.K.*, 27(3):583-596.
- YONGE, C.M. & J.I. CAMPBELL, 1968. On the heteromyarian condition in the Bivalvia with special reference to *Dreissena polymorpha* and certain Mytilacea. *Trans.Roy.Soc. Edinb.*, 68:21-43.