

The Functional Morphology of *Anodontites trapezeus* (Spix) and *Anodontites trapesialis* (Lamarck). (Bivalvia: Mycetopodidae)

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RESUMO

Anatomia Funcional de *Anodontites trapezeus* (Spix) e *Anodontites trapesialis* (Lamarck). (Bivalvia: Mycetopodidae).

A anatomia funcional comparada de duas espécies de bivalves límnicos, é analisada. *Anodontites trapezeus* e *Anodontites trapesialis*, pertencem à família Mycetopodidae e são comuns no interior do Estado de São Paulo. Vivem no mesmo local e são adaptadas ao ambiente de águas calmas. Foram, pela primeira vez, estudadas sob o ponto de vista da anatomia funcional e, o estudo do estômago contribuiu com valiosas informações, mostrando que, de maneira geral, a estrutura interna é de grande uniformidade nesses animais, tal como ocorre entre os Unionacea, estudados por outros autores.

ABSTRACT

The confronted functional anatomy of two species of limnic bivalves, is analysed. *Anodontites trapezeus* and the *Anodontites trapesialis*, of the Mycetopodidae family, are common in the interior of the State of São Paulo. They live in the same environment and are adapted to the still water environment. Their functional anatomy, was studied for the first time providing valuable informations about the stomach and showing in a general way, that the internal structure is of great uniformity in these animals, such as it occurs among the Unionacea, which were studied by other authors.

1 — INTRODUCTION

In South America there are four sub-families of the Mycetopodidae Gray, 1840, among them the Anodontitinae Modell, 1942, to which the genus *Anodontites* Bruguière 1792 (Parodiz and Bonetto, 1963) belongs.

This genus belonged previously to the Mutelidae Gray family, 1847 (Simpson, 1914; Ortmann, 1921; Hass, 1930, 1931; Modell, 1942, 1949, *apud* Parodiz and Bonetto, 1963), with a large distribution throughout South America, particularly in Brazil (Parodiz and Bonetto, 1963).

So as to contribute to a greater knowledge of our malacofauna, especially with reference to the functional anatomy of the limnical bivalves, species were studied which can be found easily in the interior of the State of São Paulo — *Anodontites trapezeus* Spix, 1827 and *Anodontites trapesialis* Lamarck, 1819.

Nothing is known regarding the functional anatomy of the limnical bivalves in Brazil. Systematic studies were made (Ortmann, 1911, 1921; Frierson, 1922; Marshall, 1928, 1928a, 1930, 1932; Thiele, 1935; Haas, 1939, 1939a, 1945, 1949; Mendes, 1939; Lange de Morretes, 1949; Bonetto, 1954, 1962, 1965, 1967; Parodiz and Bonetto, 1963; Penna and Leme, 1964; Parodiz, 1968; Bonetto and Mansur, 1970; Mansur, 1970). The larval development of several species of bivalves, among them the *A. trapezeus* and *A. trapesialis* (Bonetto, 1951, 1959, 1961, 1962, 1963; Bonetto and Ezcurra, 1962; Parodiz and Bonetto, 1963) was studied.

As for the other fresh-water species, there are some papers about the functional anatomy, but all of them dealing with only isolated aspects in species that belong to different genera and even to different families. Thus, a survey about all the aspects of the functional anatomy of the *A. trapezeus* and *A. trapesialis* is fully justified.

To the major aim of this study, the compared functional anatomy of these limnical species, are added some ecological aspects and the attempt to check whether certain characteristics are caused by an adaptation to the environment, by a convergence, or by genetical factors, since both species live in the same environment. The observations with live specimens were made at the Department of Zoology at the Faculdade de Filosofia, Ciências e Letras de Rio Claro and in the Department of Zoology of the Instituto de Biociências of the Universidade de São Paulo.

2 — HABITAT

A. trapezeus and *A. trapesialis* are found almost totally buried (Fig. 1) either in a muddy bottom or in a muddy-sandy-bottom, formed by large quantities of very fine particles (silt-clay) in regions of small rapids in the rivers or in the ponds submitted to periodical floods during the rainy season.

Both species occur together, and they were collected from the Tiete River and adjacent ponds, near the town of Barra Bonita, in the State of São Paulo, Brazil.

The smaller specimens live on the banks, with the water level ten centimeters approximately above the substratum where they are buried. As the animals grow they gradually move to greater depth, and at the depth of 80 cms, the larger sized specimens were found.

In spite of being practically sedentary, these animals, during the dry period of the year, migrate toward deeper regions because the water level is lower. It is during this period that the grooves left by the move-

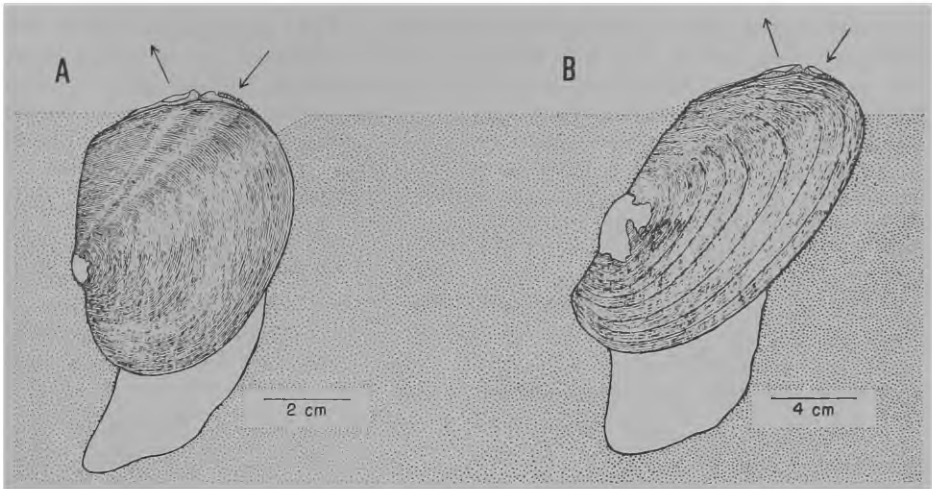


Fig. 1 — Animals in their natural habitat; external view of the left side: A, *Anodontites trapezeus*; B, *Anodontites trapesialis*. The arrows show the direction of the inhalant and exhalant currents.

ment of the animals toward the deeper regions appear on the mud. *A. trapesialis* has difficulty in contouring an obstacle to its movement. This is fatal to the animal if the water level lowers rapidly. Besides, the animal can not always follow the reflow of the waters during the great drought periods. This was proved correct during an excursion to the Tiete River, near the town of São Paulo, in April, 1969, where a large number of *A. trapesialis* valves was found half buried in the banks along the river.

Clark, *apud* Coker *et al.* (1919-1920) observed that the bivalves feed more on plankton than those living in the rivers, for the latter show, in the stomach, a greater percentage of detritus or organic matter, finely divided. Preliminary qualitative analysis of the gastric content obtained from *A. trapezeus* and from *A. trapesialis*, kept alive in the laboratory, revealed a large quantity of microscopical creatures; among them the most common are: *Diatoma* sp., *Navicula* sp., *Oscillatoria* sp. (fragments), *Lyngbya* sp., *Gloeocapsa* sp., *Scenedesmus* sp., *Peridinium* sp., *Penium* sp., *Cosmarium* sp., *Micrasterias* sp., *Phacus* sp., *Euglena* sp., *Amoeba* sp. and *Paramecium* sp. The existence of *Navicula* sp., *Lyngbya* sp., *Oscillatoria* sp., *Scenedesmus* sp. and that of *Cosmarium* sp., had already been verified by Allen (1914) and Coker *et al.* (1919-1920), within the stomach of some fresh water bivalves in the northern hemisphere.

The species studied were found together with *Diplodon rotundus gratus* (Bivalvia, Hyriidae). Limnic Acarids, in a large quantity, live in the branchia of the animals studied. It is a new species of Acarids belonging to the genus *Unionicola*, sub-genus *Pentatax*.

According to Webb (1958), the variation of the water amount in a sediment, as well as the easiness with which it flows among the different grains, can limit the distribution of the animals which live in the sediment.

Complementing these observations, Narchi (1974) asserts that for the animals living within but not feeding on the sediments, in a direct way, the study of their behaviour would not be complete without data on the granulometry of the substratum. This is true because the animals transferred from one type of sediment to another, either could not bury themselves or only managed it after a great effort. Through the analysis of substratum of the pond where the animals studied live, we could see that approximately 85% of the particles in weight, are from 0.002 to 0.031 mm., i. e., silt-clay, and 15% of sand, with grains from 0.062 to 0.5 mm. We also found out that each 5 cms. deeper, the total weight of sand, silt and clay, is practically doubled, since we worked with samples of constant volumes. Thus, the interstitial water diminishes considerably from the surface toward the deeper regions or, in other words, the sediment becomes more compact in depth.

Therefore, we must admit that *A. trapezeus* and *A. trapesialis* respectively living in the first 10 and 15 cms. below the surface, occur preferentially in substrata with sediments composed by a great amount of silt-clay and that *A. trapezeus* is specifically adapted to sediments where the amount of interstitial water is great. On the other hand, *A. trapesialis*, being larger, is able to dig more deeply, and with its foot "it settles down" where the sediment is more compact.

3 — SHELL

The *A. trapezeus* shows the heavy, thick, equivalent, equilateral, sub-circular shell, with its dorsal and rear borders almost straight (Fig. 2). Two not prominent keels arise from the umbos toward the posterior region, the most dorsal of them ending at the diaphragmal region of the siphons. The valves are inflated, touching each other throughout the external border, and the joint has no teeth.

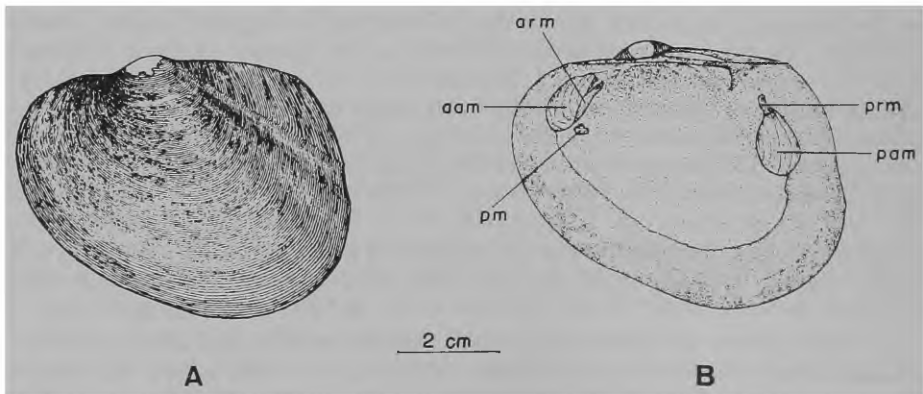


Fig. 2 — *Anodontites trapezeus*. A, External view of the left valve, showing the lines of growth. B, Internal view of the right valve, showing the muscles scars: aam, anterior adductor muscle; arm, anterior retractor muscle of the foot; pam, posterior adductor muscle; pm, protractor muscle of the foot; prm, posterior retractor muscle of the foot.

The periostracum is opaque, with its coloration ranging from the dark-green to the yellowish brown. The lines of development are too close, even anastomosing with each other in some points of the rear region. They are elevated, with a lamellar aspect along the borders of the valves in the adult individuals, and almost on the whole surface in the young ones.

The ligament of connective tissue is amphidetical and the umbo is distended, raised above the joint line, with the periostracum worn out. Internally, the nacreous layer is blueishwhite, mixed with yellowish-cream, iridescent in the sub-marginal region.

The scars of the anterior adductor muscle (aam) and the anterior retracting muscle of the foot (arm) are united, the latter posteriorly. The scar of the protractor muscle of the foot (pm) is posteriorly and ventrally placed in relation to the scars of the anterior adductor muscle. They are connected in the young individuals and separated in the older ones. The scar of the posterior adductor muscle (pam) is elliptical, slightly larger than that of the anterior adductor and it is connected to the scar of the posterior retracting muscle of the foot (prm). There is no paleal sinus.

According to Ortmann (1921), the maximum length recorded for this species was 7.5 cms., which is the size of the largest specimen found within the reservoir at Barra Bonita.

The *A. trapesialis* has a light, thin, equivalent, equilateral, sub-trapezoidal shell, prolonged in the posterior region (Fig. 3). As in *A. trapezeus*, two not prominent lines raise from the umbonal region toward the posterior region, the ligament of connective tissue is amphidetical, and the umbo is raised above the hinge line, with an eroded periostracum.

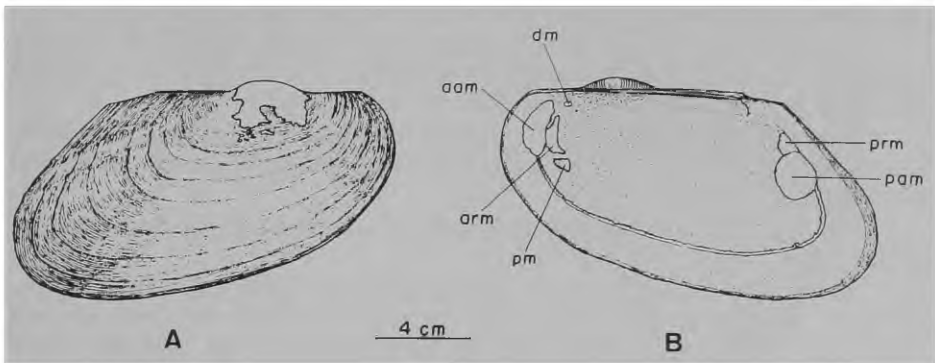


Fig. 3 — *Anodontites trapesialis*. A, External view of the right valve, showing the lines of growth. B, Internal view of the right valve, showing the muscles scars: aam, anterior adductor muscle; arm, anterior retracting muscle of the foot; dm, dorsal muscle; pam, posterior adductor muscle; pm, protractor muscle of the foot; prm, posterior retracting muscle of the foot.

The valves are without teeth and do not touch each other throughout the external border. In the anterior-ventral half from where the foot protrudes, the valves remain kept apart near 0.8 cm in a 15 cm long animal.

The periostracum is bright and its colour ranges from dark-green to a yellowish-brown, with the rear region black. The young are greenish-gray with an opaque periostracum. Lightly prominent dark bands follow the narrow lines of development which rise in the lamellae in the rear region. Weak radial lines appear in the periostracum of some specimens, mainly in the young ones. The nacreous layer is white with blueish-pink reflexes.

The scars of the adductor, retractor muscles of the foot and the protractor muscles, show the same disposition as in *A. trapezeus*. In *A. trapesimalis* there still occur one or two circular scars of the dorsal muscles (dm) which appear in the umbonal cavity. There is no paleal sinus.

4 — SIPHONS

The siphons in *A. trapezeus* (Fig. 4) and in *A. trapesimalis* (Fig. 5) are similar. Like in *Anodonta* (Anthony, 1905), they show an inhalant siphon communicating with the pedal opening and the free exhalant siphon.

In both species studied, the siphons are formed by the internal folds of the mantle and show an intense pigmentation. The inhalant and the exhalant siphons are close together with a muscular diaphragm separation them.

They show a wide base which is dorsally extended to the terminal curve of the intestine and ventrally exceeds the posterior border of the gills. Contrary to what happens in *Leila* (Bonetto, 1963) they are little extensible, short, following the rear region of the shell.

The opening of the inhalant siphon in *A. trapezeus* show a varying number of tentacles, little ramified, gradually reducing in size toward the pedal region, what does not occur in *A. trapesimalis*.

The exhalant siphon has no tentacles around its siphonal membrane which is, nevertheless, when open, externally projected, controlling and directing an exhalant current.

The tentacles of the inhalant siphon are usually turned into the opening and function as selectors.

The activity of the siphons is characteristic: when the valves of the shell are separated, the siphons are projected toward the exterior and they open at the same time. As the differences in the siphons shape reflect the changes in its habits (Narchi, 1974), we shall analyse the siphons studied comparatively.

A. trapezeus seems to evidence the selective function of particles in the inhalant siphon, for the tentacles are ramified and directed towards its opening, interlacing and greatly reducing the possibility of access of large particles into the mantle cavity.

A. trapesimalis does not apparently select particles in the inhalant siphon, for it has no tentacles.

However, both species have sensitive siphons. If we project the shadow of an object on the place where they are, the siphons retract

completely. This was confirmed by several authors for other bivalves (Narchi, 1974 and others). According to Owen (1953) this sensitiveness makes evident that the animal has the habit of living in quiet waters.

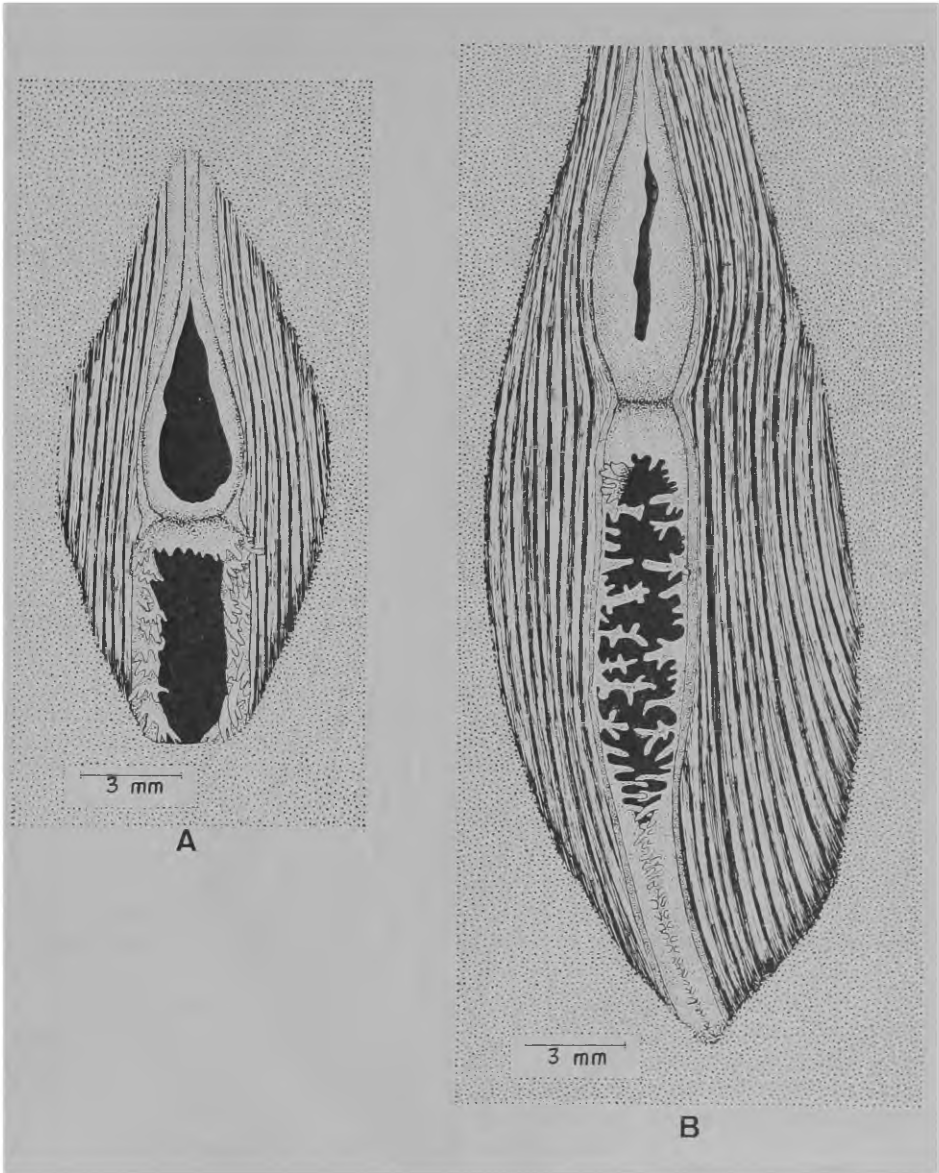


Fig. 4 — *Anodontites trapezeus*. Frontal view of siphons during the water introduction process into the mantle cavity, showing the development of the ramified tentacles of the inhalant siphon. A, an enough buried animal with opened siphons. B, a semi-buried animal with siphons partially opened.

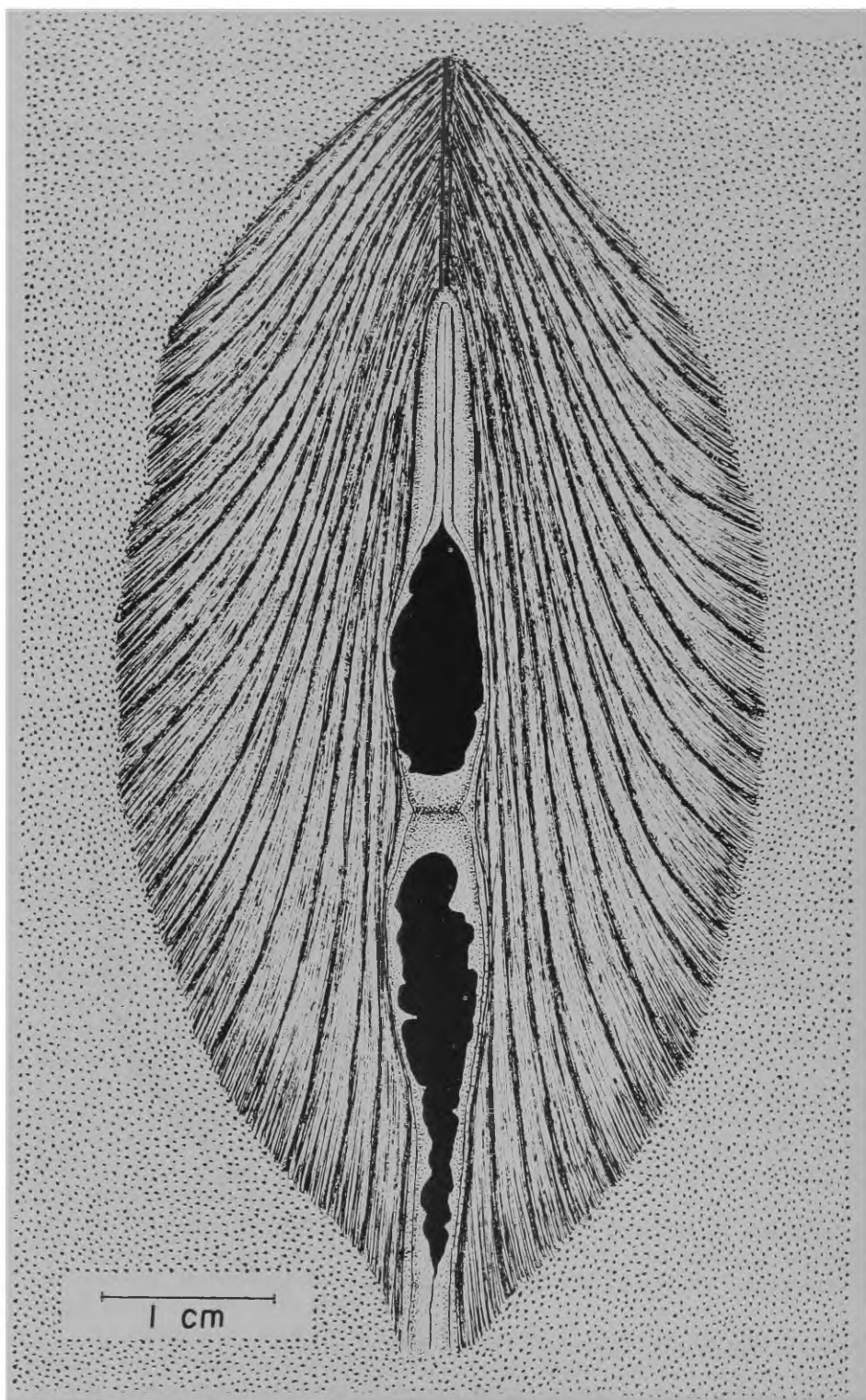


Fig. 5 — *Anodontites trapesialis*. Frontal view of siphons during the water introduction process into the mantle cavity. Dorsal exhalant siphons and ventral inhalant one without any tentacles.

5 — MANTLE

The border of the mantle in these animals is formed by three folds.

A. trapezeus shows a great number of tentacles in the middle fold; they are ramified in the region of the inhalant siphon, while in the central region they are simple and small, occurring up to the foot opening. When the animal is pumping water, the tentacles of one side alternate with those of the opposite side, structured in such a way that they exclude the possibility of access of the granules of sand or larger particles into the mantle cavity.

A. trapesialis has a flat and smooth middle fold, the free border of which makes contact with the adjacent one, and thus, closing the foot opening, when the foot is withdrawn. When moving, as in *A. trapezeus*, they touch the animal foot all over its length.

6 — MUSCULATURE AND THE FOOT

The musculature and the foot are very similar to those in *Anodonta cellensis* described by Brück (1914).

The adductor muscles are inserted in the valves of the shell, ventrally to the line of the hinge. They are sub-equal, the posterior one a little larger than the anterior one in both species studied.

The anterior retractor muscle of the foot is inserted posteriorly to the anterior adductor muscle and most of its fibers are directed toward the rear region of the foot, internally to the posterior retractor muscle. At the distal region, the fibers on each side intersect and join each other as it occurs in *Anodonta cellensis* (Brück, 1914).

The insertion of the protractor muscle of the foot is situated below the insertion of the anterior retractor muscle. The fibers of the protractor muscle are superficially directed, toward the dorsal and posterior regions of the body of the animal.

Muscles which Bonetto (1963) called dorsal muscles and which correspond to the elevator muscles of Brück's (1914) appear only in *A. trapesialis*. They are not seen in small specimens, according to the observation made by Bonetto (1963) and confirmed in this paper. Bonetto reports the appearance from one to three circular scars in the internal face of the umbonal cavity, while we have always observed one or two.

The posterior retractor muscle of the foot is inserted at the rear region of the shell, situated anteriorly and dorsally to the posterior adductor muscle in both species studied. The branches on each side join under the pericardium, and fibres on the left and right sides cross over one another, entering the foot, where the branches are separated and the fibers spread toward the anterior-ventral region.

There exist many branches of circular muscles below the epithelium of the visceral mass and the proximal part of the foot, involving the visceral mass completely. In the distal parts, they are situated transversally, and a large number of others occur going from the epithelium on one side to the epithelium on the opposite side.

The foot is wide and pointed at the anterior region and is adapted to digging. It does not show any cilia on the external surface, while on the visceral mass region ciliary currents are observed, directing the particles toward the siphons.

It is difficult to dig up *A. trapesialis*, for its foot fastens it to the substratum. When buried it remains in the same place for a long time.

The penetration speed in the mud is small when it is compared with the results obtained by Narchi (1972) for sea bivalves. One 2.6 cm long specimen of *A. trapezeus* took 8 minutes to bury itself while another specimen, 4.6 cm long, took 15 minutes. For *A. trapesialis*, this time was 8 and 28 minutes respectively, for specimens 2.8 cms and 14 cms long.

When it digs, the foot pulls the animal down almost vertically and it buries itself after an intermittent series of strong contractions of the pedal muscles. At each contraction of the muscles, the shell raises and falls abruptly, thus lessening the angle with the horizontal and increasing the penetration process. This generalized movement is similar to that a rocking chair and allows the animal to bury itself easily (Trueman, 1968; Narchi, 1969 and others).

Besides the vertical locomotion, both species studied move over the substratum, surface an already observed fact in other bivalves by Vlès (1904), Brafield and Newell (1961), Trueman (1968) and Narchi (1969).

7 — THE MANTLE CAVITY

A — TOPOGRAPHY: The position of the principal organs within the mantle cavity is better indicated in the drawings (Figs. 6 and 7). Other observations are the following:

a — The region of the visceral mass is easily distinguished from that of the foot through difference in colouration. In both species the visceral mass is white and milky, while the foot is yellowish-pink. In the visceral mass one also observes the intense ciliation along, with the appearance of rejection currents that move the particles toward the posterior region.

b — The ctenidia extend backward toward the base of the siphonal process. The supra-axial region does not occur in these species.

c — Both demibranchs for both species, are plicated with a variable number of folds, in accordance with the animal size.

d — The borders of the mantle do not merge on the midventral line. The fusion does not occur in the region of the diaphragm muscle, leaving a wide pedal opening continuous with the inhalant siphon.

e — The labial palps are smaller in *A. trapezeus* and greatly developed in *A. trapesialis*.

B — CTENIDIA: In both species studied, the ctenidia seem identical in many aspects (Fig. 8). A marginal groove (g) is present in the inner demibranch and there is a ciliary current directed toward the oral region in this groove. There are two other currents: one along the axis of the ctenidia and the other at the proximal region of the outer demibranch at the insertion with the mantle.

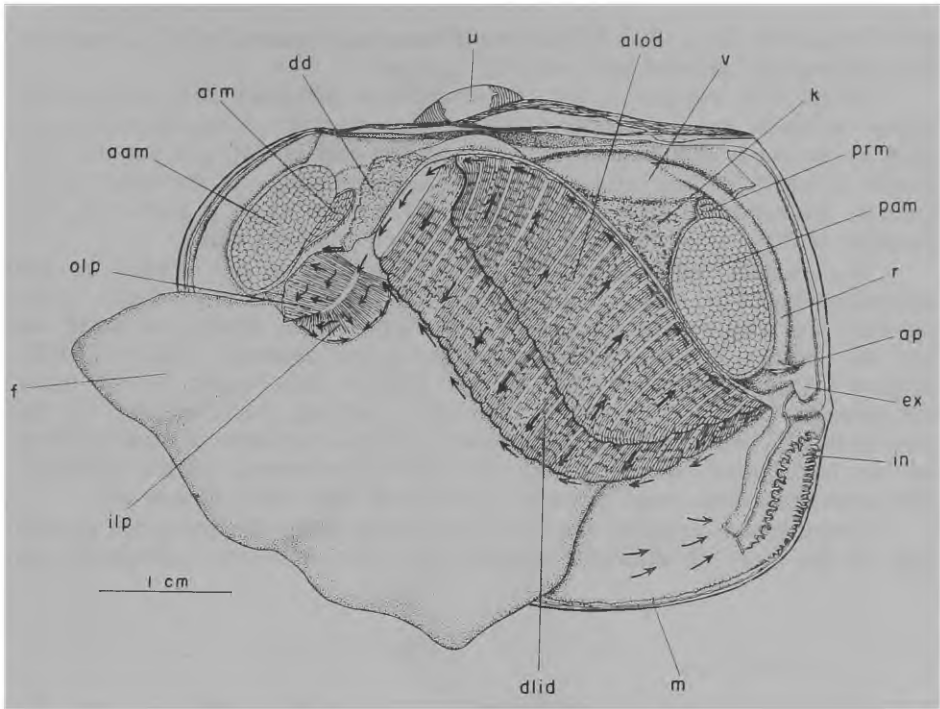


Fig. 6 — *Anodontites trapezeus*. Viewed from the left side after removal of the left shell valve and mantle lobe. Arrows show direction of ciliary currents. aam, anterior adductor muscle; alod, ascending lamella of outer demibranch; ap, anal papilla; arm, anterior retractor muscle of the foot; dd, digestive diverticula; dlid, descending lamella of inner demibranch; ex, exhalant siphon; f, foot; ilp, inner labial palp; in, inhalant siphon; k, kidney; m, mantle; olp, outer labial palp; pam, posterior adductor muscle; prm, posterior retractor muscle of the foot; r, rectum; u, umbo; v, ventricle.

A. trapezeus and *A. trapesialis* belong to the D type described by Atkins (1937), in which the only groove is situated on the free border of the inner demibranch. The outer demibranch (od) is always less deep than the inner (id), mostly at the anterior region.

In *A. trapezeus*, the ctenidia are formed by shallow folds (Figs. 9B and 10B) formed by an average of 22 filaments, ranging from a minimum of 16 to a maximum of 28, both in the outer and inner demibranch. At the anterior and posterior regions of the ctenidia, this number is slightly smaller. The filament width is $50\ \mu$, approximately, and that of the interfilamentary spaces is $20\ \mu$, and the interfilamentary anastomosis are $150\ \mu$ apart.

The *A. trapesialis* ctenidia are also formed by shallow folds (Fig. 11), formed by an average of 21 filaments, with extreme number of 16 and 26 respectively. At both anterior and posterior regions of the ctenidia, the number of filaments per fold ranges from 10 up to 16. The width of

the filament is 50μ , that of the interfilamentary spaces is 15μ , and the interfilamentary anastomosis are 135μ apart.

On the free borders of the demibranchs a curvature of the filaments occurs without any interruption of the lateral cilia. The lateral-frontal cilia of the outer demibranch in *A. trapezeus* end at 740μ from the free border of each filament and at 800μ in *A. trapesialis*. In the outer demibranch, the lateral-frontal cilia in *A. trapezeus* end at 50μ and in *A. trapesialis* at 80μ from the free border of each filament while.

The frontal currents of the outer demibranch are dorsal in the ascending lamella (alod) as well as in the descending one (dlod). Apparently no modification occurs in the frontal cilia, which are small on the free border, and do not give origin to any current. Atkins (1937) observed that in *Anodonta* the frontal cilia at this region of the outer demibranch beat in the ventral direction, sending particles out of the demibranch. In the species under study, the cilia revealed a weak beating on the free border, there existing no directed movement of the particles, for sometimes they beat upward, sometimes they beat downward.

Longitudinal currents oralward are found along the marginal groove (g) of the inner demibranch between the bases of both demibranchs on

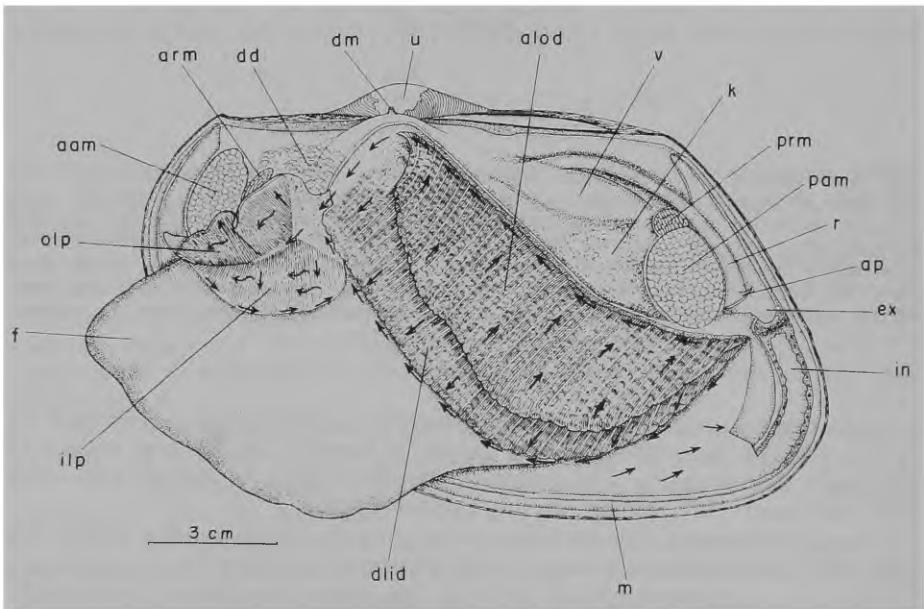


Fig. 7 — *Anodontites trapesialis*. Viewed from the left side after removal of the left shell valve and mantle lobe. Arrows show direction of ciliary currents. aam, anterior adductor muscle; alod, ascending lamella of outer demibranch; ap, anal papilla; arm, anterior retractor muscle of the foot; dd, digestive diverticula; dlid, descending lamella of inner demibranch; dm, dorsal muscle; ex, exhalant siphon; f, foot; ilp, inner labial palp; in, inhalant siphon; k, kidney; m, mantle; olp, outer labial palp; pam, posterior adductor muscle; prm, posterior retractor muscle of the foot; r, rectum; u, umbo; v, ventricle.

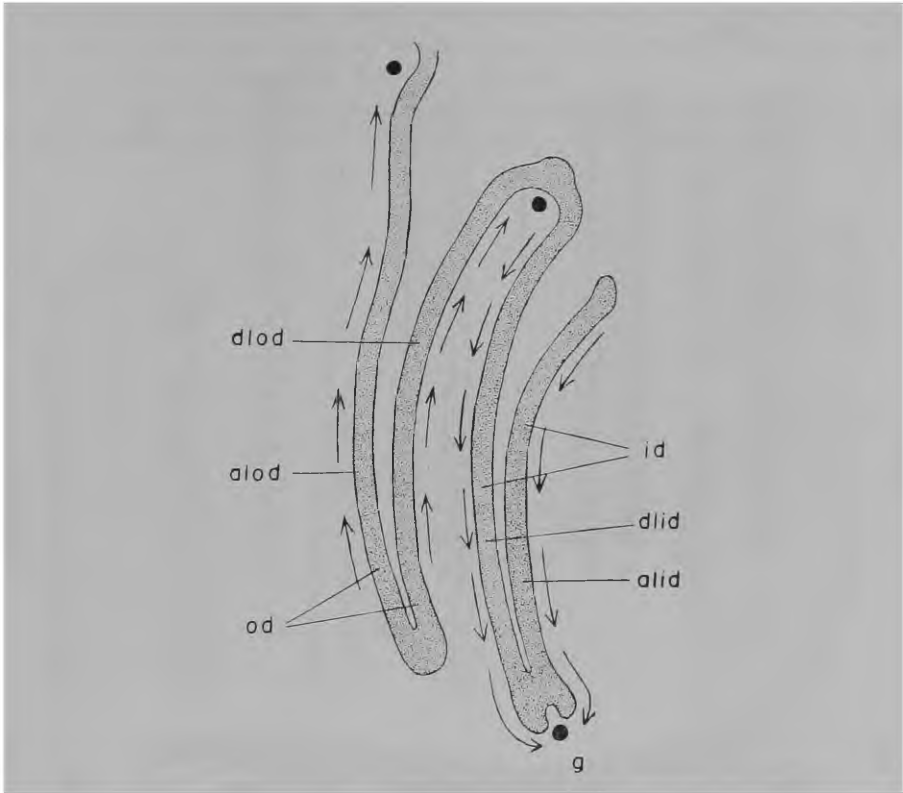


Fig. 8 — Diagrammatic vertical section through the ctenidium of *Anodontites trapezeus* and *Anodontites trapesialis* to show the direction of beat of the frontal cilia: alid, ascending lamella of inner demibranch; alod, ascending lamella of outer demibranch; dlid, descending lamella of inner demibranch; dlod, descending lamella of outer demibranch; g, marginal groove of inner demibranch; id, inner demibranch; od, outer demibranch; •, current with oral direction.

each side of the body and on the base of the outer demibranch and mantle insertion.

In the inner ctenidia, both in the ascending lamella (alid) and in the descending lamella (dlid), the frontal currents are ventralward.

The lateral-frontal cilia (lfc) 15.4μ long in *A. trapezeus* and 15μ long in *A. trapesialis* separate the filaments (Figs. 9A and 10). These cilia are situated on each side of the filament and beat outward in the interfilamentary spaces, causing the particles to be transported by the frontal cilia (fc). Due to the fact that the lateral-frontal cilia of a filament alternate with the cilia of the adjacent filament, a kind of railing between them is formed, what prevents the larger particles from passing into the interior of the demibranchs. Internally to the lateral-frontal cilia, there appear the lateral cilia (lc) which beat, causing strong currents of water. In accordance with what happens in *Unio* and *Anodonta* (Wallengreen, 1905), the lateral cilia of the ascending lamella in the outside

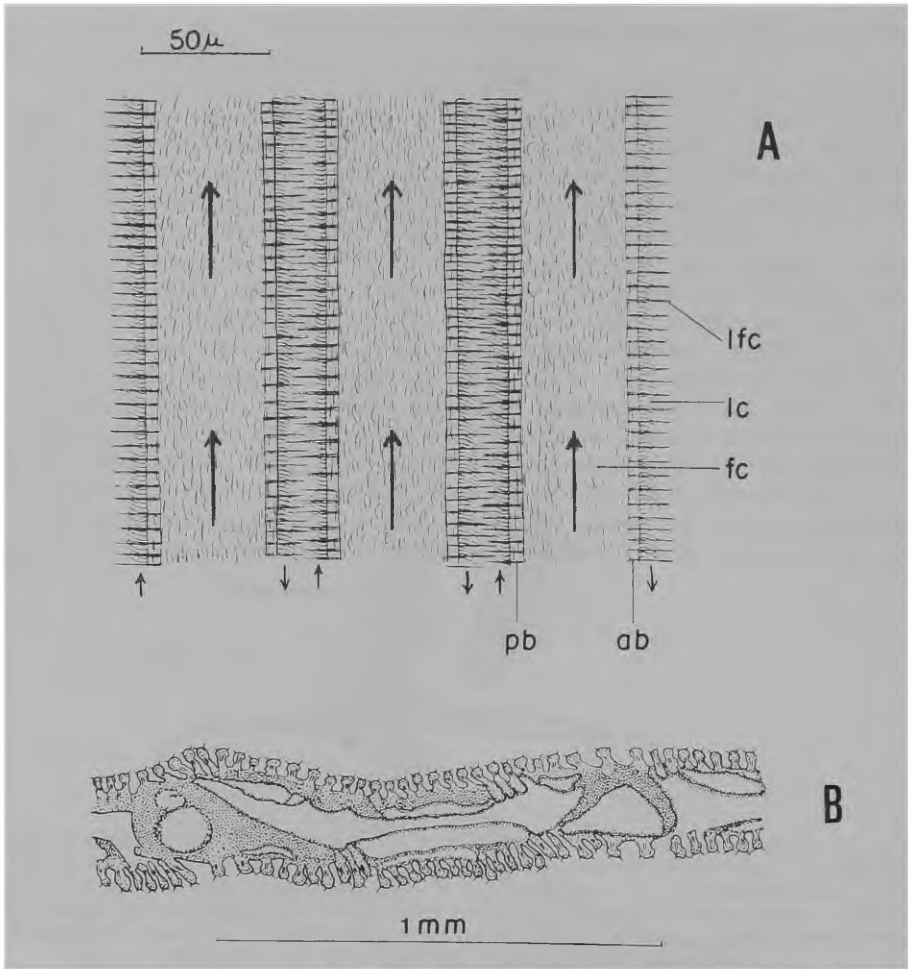


Fig. 9 — *Anodontites trapezeus*. A, Cilia on outer surface of outer demibranch. B, Transverse section through a portion of the outer demibranch showing the folds and the filaments disposition. Arrows indicate direction of ciliary currents. ab, anterior border of the filament; fc, frontal cilia; lc, lateral cilia; lfc, laterofrontal cilia; pb, posterior border of the filament.

demibranch beat downward on the anterior border of the filament (ab), and upward on the posterior border (pb). In the descending lamella of the outside demibranch, this beating is inverted, i.e. upward on the anterior border and downward in the posterior border. In both species studied the lateral cilia measure 7.7μ .

Covering the external surface of the filaments, there appear the frontal cilia (fc) beating regularly, driving the particles toward the oral currents. Their length is 3.2μ in *A. trapezeus* and 2.5μ in *A. trapesialis*.

At the apical region of the inner demibranch filaments, the frontal cilia are replaced by the terminal cilia (tc), larger than the first ones.

These cilia beat obliquely, driving the particles toward the anterior region through the marginal groove of the inner demibranch. They measure 7.7μ both in *A. trapezeus* and *A. trapesialis*.

It is difficult to see the relationship among the branchial type, the frontal currents, the "habitat" and the way of life (Atkins, 1937), but one

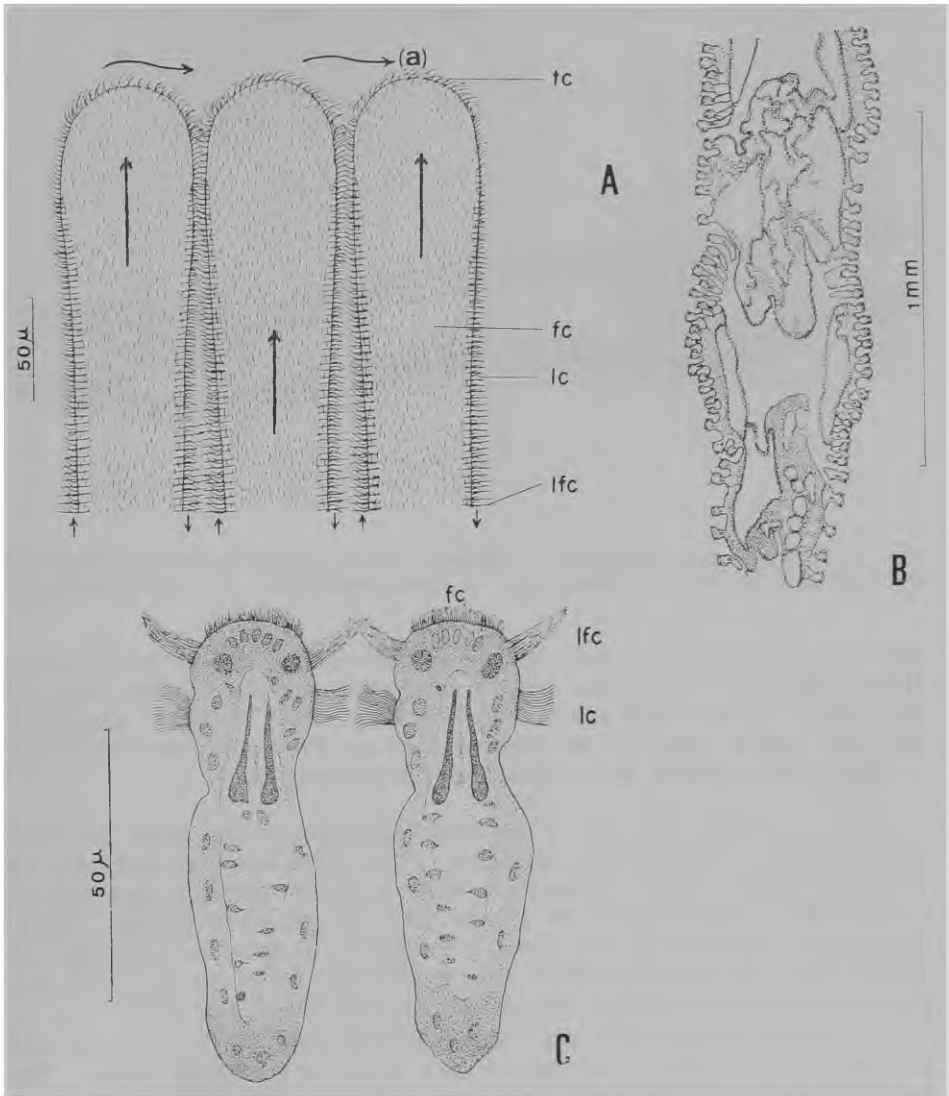


Fig. 10 — *Anodontites trapezeus*. A, Cilia on outer surface of inner demibranch. B, Transverse section of inner demibranch. C, Transverse section of two filaments of inner demibranch to show cilia. Arrows indicate direction of the ciliary currents, including oral one (a). fc, frontal cilia; lc, lateral cilia; lfc, laterofrontal cilia; tc, terminal cilia.

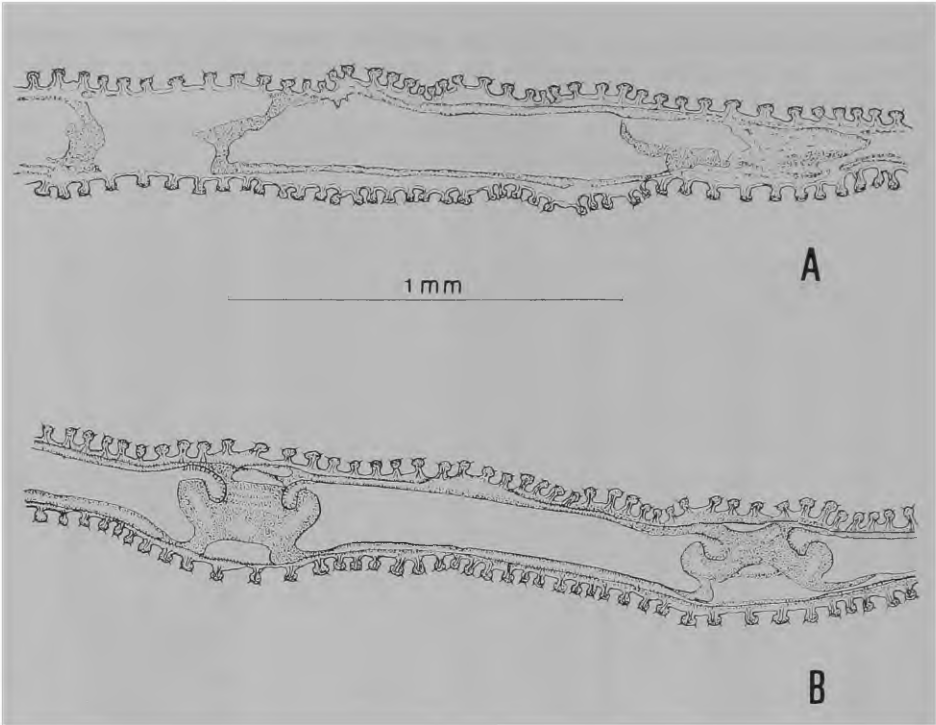


Fig. 11 — *Anodontites trapesialis*. Transverse section of the demibranchs showing the folds and the filaments disposition. A, outer demibranch; B, inner demibranch.

can draw the conclusion that the two species studied live in quiet waters. Hence they do not show any large frontal cilia, and the terminal ones do not have a great development and efficiency when they are compared with the species living in turbulent waters, as those observed by Narchi (1972a, 1974) *Donax hanleyanus* and *Tivela mactroides*.

C — LABIAL PALPS: The basic structure of the palps for both species studied is essentially the same. The palps are flat and have an elliptical shape, deeply plicated on their opposite surfaces and smooth on the sides turned toward the mantle and visceral mass (Thiele, 1886). They occur opposite to the inner demibranch in such a way that the folded faces are turned toward the demibranch. The palps in *A. trapezeus* are smaller and less elongated than those in *A. trapesialis*.

In both species there are areas without folds at the anterior and posterior regions and on the outside and inside of the labial palps. The posterior areas are connected, leaving an oral lateral groove between them, which extends up to the mouth, a fact also observed in *Unio* and *Anodonta* (Kellog, 1915). The schematic drawings in Fig. 12 show with as many details as possible the fold structures on the internal surfaces of the palps. The currents observed in the palps in *A. trapezeus* (Fig. 12A) were:

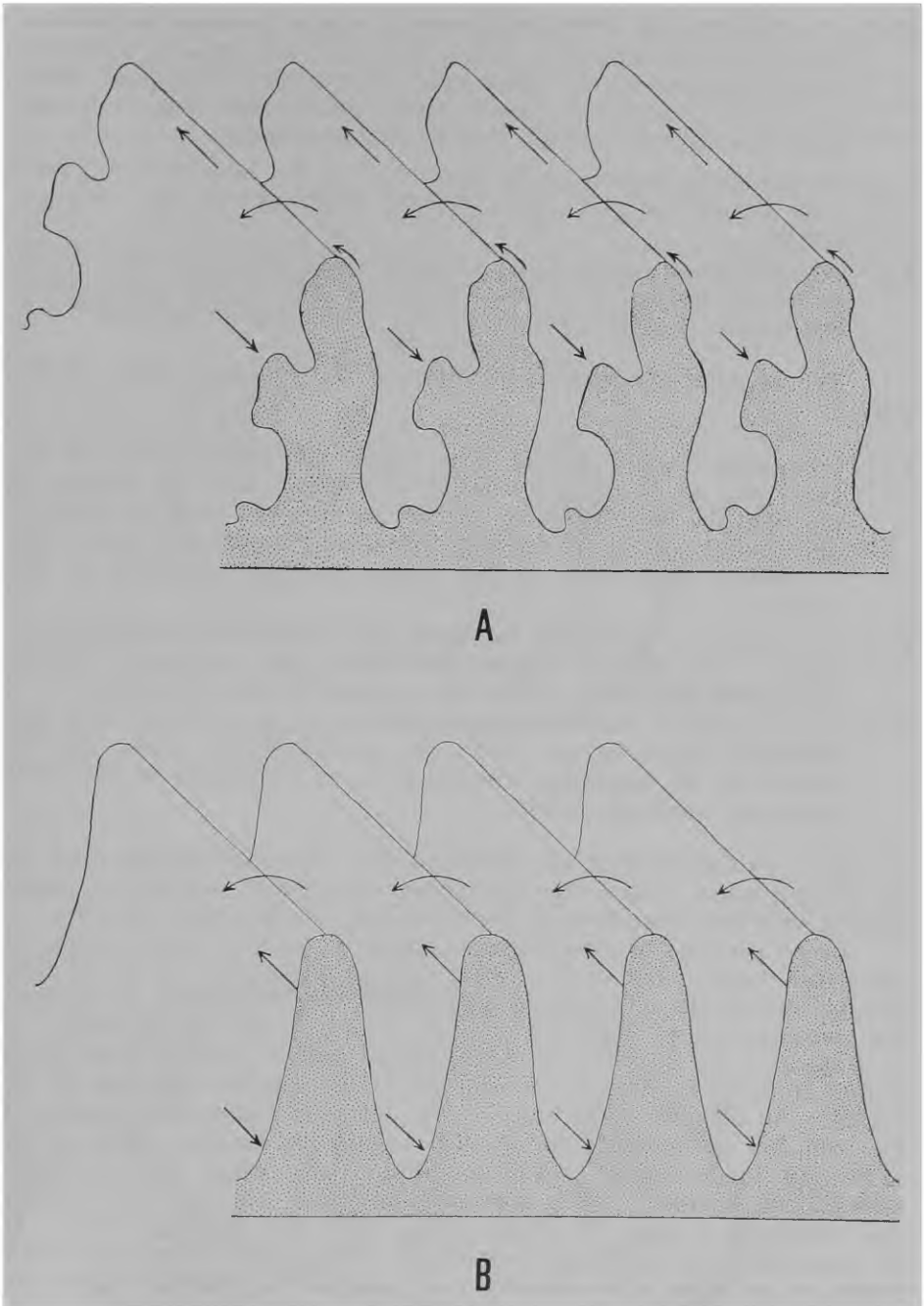


Fig. 12 — Diagrammatic representation of the ciliary mechanisms on the folded inner surface of the labial palps, to show the various ciliary tracts: A, *Anodontites trapezeus*; B, *Anodontites trapesialis*.

- 1 — a rejection current at the middle lateral region, proximal to the fold, where the cilia beat in a ventral direction, with drawing particles from the grooves on the anterior and ventral parts of the palp. Next to it, those particles are directed toward the border of the palp and from there to the rejection currents in the mantle;
- 2 — an acceptance current on the upper part of the folds, carrying particles toward the oral region, passing from apex to apex in great speed;
- 3 — a re-acceptance current in the subapical distal face of the fold, which is dorsally directed, as it was observed by Allen (1914) in *Lampsilis*, and another dorsally directed current on the apex of the folds.

The currents observed in the palps in *A. trapesialis* (Fig. 12 B) were:

- 1 — a rejection current on the floor region and on the sides of the lower part of the groove, between two folds. With the beating of the cilia, the particles in the groove are removed from the anterior and ventral regions of the palp, taken to the posterior region and transferred from there to the rejection currents existing in the mantle;
- 2 — an acceptance current on the upper part of the folds carrying particles to the anterior region, surrounding the consecutive apices, with great speed and sending the particles to the oral region;
- 3 — a re-acceptance dorsally-directed current on the proximal face and subapical region of the fold. The particles taken there, can be caught by the acceptance current n.º 2, as it happens in *Unio* and *Anodonta* (Kellogg, 1915).

D — ACCEPTANCE OF PARTICLES: The observations made in the present paper, concerning the particle acceptance, coincide in many aspects with those described by Narchi (1974), for the marine bivalves.

Large particles of carborundum, added to on the folded surface of the palps, tend to fall in the deeper part of the groove, to be at last, incorporated by the rejection current. They move afterwards, in the ventral direction, out of the grooves, to the ventral border of the palps. In *A. trapezeus*, the particles are taken to the middle region of the palps border from where they are transferred to the rejection currents of the mantle. An identical fact occurs at the posterior and ventral regions of the palp, but the particles are directed toward the anterior region of the same spot, in the middle part of the border, from where they are transferred to the mantle. This is a peculiar fact in *A. trapezeus*, but in *Unio* and *Anodonta* it does not occur (Allen, 1914 and Kellogg, 1915). In *A. trapesialis* they are directed out of the groove and toward the ventral border of the palps from where they are sent to the posterior region and incorporated to the mantle rejection current.

With the application of large quantities of carborundum, the folds separate through muscular action, a fact observed by other authors, making the particles to fall in the groove, from where they are rejected.

In both species, it was observed that when fine particles, in small quantities, are placed in the palps, two main currents appear. One, in which the particles are dorsally sent along the anterior-upper part of the apices of the folds and the other, where particles are directed toward the oral region, going from apex to apex, through the oral current situated on the fold tops.

The observation made by Allen (1914), Kellogg (1915), Ansell (1961) and Narchi (1974), asserting that besides the ciliary action, the particles are pushed toward the oral region through muscular activity of the folds, were confirmed by the present paper. In *A. trapezeus* and *A. trapesialis* it was observed that:

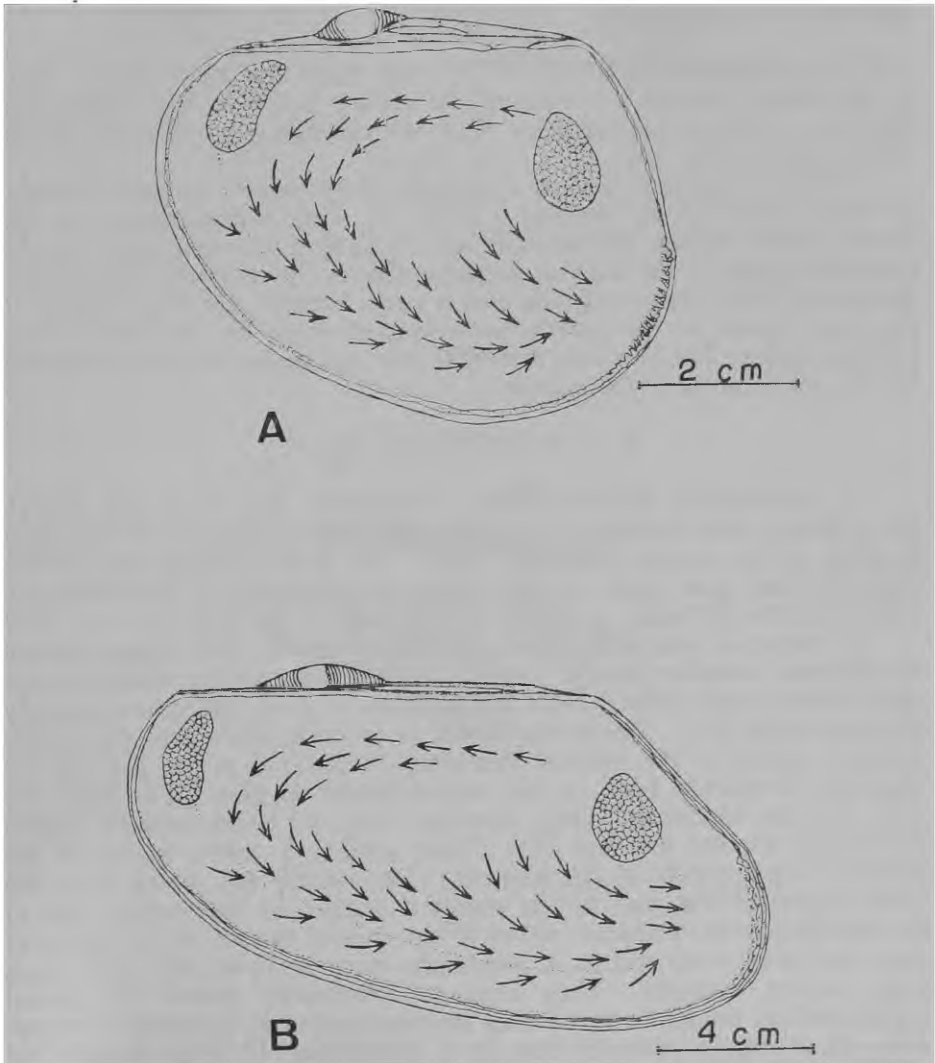


Fig. 13 — Inner surface of the right mantle lobe to show ciliary cleansing currents: A, *Anodontites trapezeus*; B, *Anodontites trapesialis*.

- 1 — when the folds are laid one upon the other, the orally directed currents are more accentuated.
- 2 — when the folds are upright, the acceptance and rejection currents predominate.
- 3 — when the folds are open, exposing more of the grooves, the rejection currents predominate.

The size of the palps must be considered also. Yonge (1949) mentions that the well developed palps appear in the species that live in muddy substrata, where a very fine material is found in the cavity of the mantle. This observation was partially confirmed for the species studied, specially in *A. trapesialis*.

E — CILIARY CURRENTS ON THE MANTLE SURFACE: Next to the ciliary currents of rejection, the ciliary action in the mantle was observed to direct the particles in a ventral direction, specially in the distal region (Fig. 13).

Both *A. trapezeus* and *A. trapesialis* show mantle currents identical to those described by Kellogg (1915) for *Unio complanatus*. In the dorsal mantle region, the particles are dragged antero-ventrally. In the posterior region of the anterior adductor muscle, the particles are directed downward where they accumulate in a large tract of rejection, parallel to the free border of the mantle posteriorly directed to the base of the inhalant siphon. The cilia that form that tract are larger than those existing on the other parts of the mantle.

8 — ALIMENTARY DUCT

a) GENERAL STRUCTURE: Dissections only were not enough for a perfect understanding of the digestive system, because of the great fragility of the various intestinal loops. The general topography of the digestive tract was made through serial sections, and its reconstruction seen from the left side, is shown in Fig. 14.

A. trapezeus and *A. trapesialis* have their mouths (mo) placed behind the anterior adductor muscle (aam), opening between the middle extensions of the labial palps. Both species show a short and dorso-ventrally flat esophagus (o). The stomach (st) is globular, placed in the middle anterior region of the visceral mass and shows the major part of the digestive diverticula (dd) in the ventral-lateral regions. The style sac (ss) and the middle gut (mg) continue from the basal-posterior region downward, toward the foot (f). Their conjoined cavity begins at the postero-ventral region of the stomach. The middle gut passes from the distal region of this duct to the posterior region, on the ventral side of the renalpericardial complex, where it has several turns. In *A. trapezeus* there are three loose and in *A. trapesialis* there are four very tight turns with varying diameter. They continue afterwards toward the dorsal region, behind the stomach, forming the hind gut (hg) which in *A. trapezeus* has a smaller diameter than in *A. trapesialis*. The gut crosses the pericardium, penetrates the ventricle (v), describes an arch over the posterior adductor muscle (pam) and ends at the anal papilla (ap).

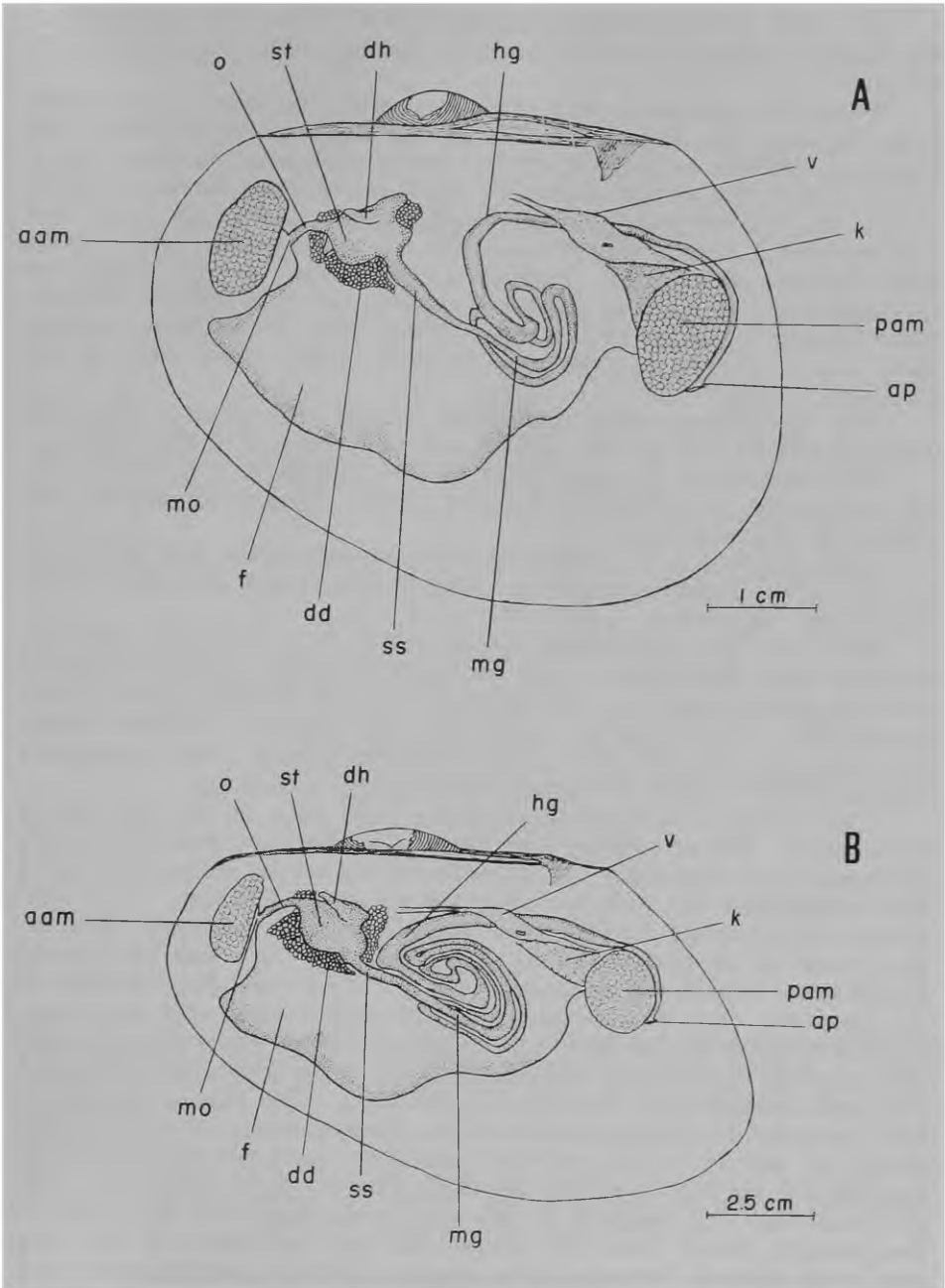


Fig. 14 — Drawing of the alimentary canal seen from the left side: A, *Anodontites trapezeus*; B, *Anodontites trapesialis*. aam, anterior adductor muscle; ap, anal papilla; dd, digestive diverticula; dh, dorsal hood; f, foot; hg, hind-gut; k, kidney; mg, mid-gut; mo, mouth; o, oesophagus; pam, posterior adductor muscle; ss, style sac; st, stomach; v, ventricle.

b) THE STOMACH DETAILED STRUCTURE: No studies about the internal anatomy of the stomach in Mycetopodidae have been done till now.

From the comparison with other fresh-water bivalves a great similarity between the species studied of the Mycetopodidae family and Unionidae became evident. Gutheil (1912) published drawings and a concise description of the stomach of *Anodonta cellensis*, Graham (1949) studied the internal gastric structure in *Anodonta cygnea* and came to a conclusion in a general way that the stomach in *Anodonta cygnea* agrees with Gutheil's description. Purchon (1958) added several details on re-studying the stomach in *Anodonta cygnea*, and in *Hyridella australis*. More recently, Dinamani (1967) made a study about *Lamellidens corianus*. Both papers (Graham, 1949 and Purchon, 1958), refer only to the structural details.

The terminology used by Graham (1949), by Owen (1953), by Purchon (1958) and by Reid (1965) has been adopted in this paper.

The stomach of *A. trapezeus* (Fig. 15) and of *A. trapesialis* (Fig. 16) is type IV. as defined by Purchon (1958), whose comparative description is analysed below.

The esophagus (o) is relatively short, dorso-ventrally flat, and opens into the antero-dorsal region in the stomach (st), ending at a well defined transversal ridge (rm).

The style sac (ss) and the middle gut are separated only partially, and they leave the stomach at the postero-ventral region, going downward into the visceral mass and upward afterwards, to the proximities of the pericardium. The crystalline style turns in a clockwise direction (when it is observed from the front, from its anterior end), and it measures approximately the half of the total length of the animal.

There exists a well developed dorsal hood (dh) on the left side of the stomach. On its anterior wall there is a separating area (sa³) more developed in *A. trapesialis*. It is formed by transversal folds and grooves that extend from the ceiling of the stomach to the left side. In *A. trapezeus* the separating area is folded into two sections, one upon the other, as a result of the pressure of the posterior wall. This was observed in *Lamellidens corianus* by Dinamani (1967). There are three sections in *A. trapesialis*. The cilia on the crest of the folds in that area beat transversally, sending the particles into the hood. There exists a longitudinal current along the posterior and dorsal corner of the separating area which also sends material into the interior of the hood. The cilia in the grooves beat along them, sending particles to the rejection tract (rt) which passes along the anterior border of the separating area and discharges the unnecessary particles into the intestinal grooves (ig). There is a longitudinal ridge (r), ventrally to this tract, which begins at the ceiling of the stomach, comes down the lateral wall and terminates at the basal part of the stomach, between the esophagus and the separating area (sa³).

The minor typhlossole (mt) extends through a short distance and then turns upward, ending at the basal region, on the right side of the stomach. The major typhlossole (ty) follows the intestinal groove, passes over the stomach floor, turns gradually to the left and finally disappears into a wide opening (ddd¹) on the left wall of the stomach where in *A. trapezeus*

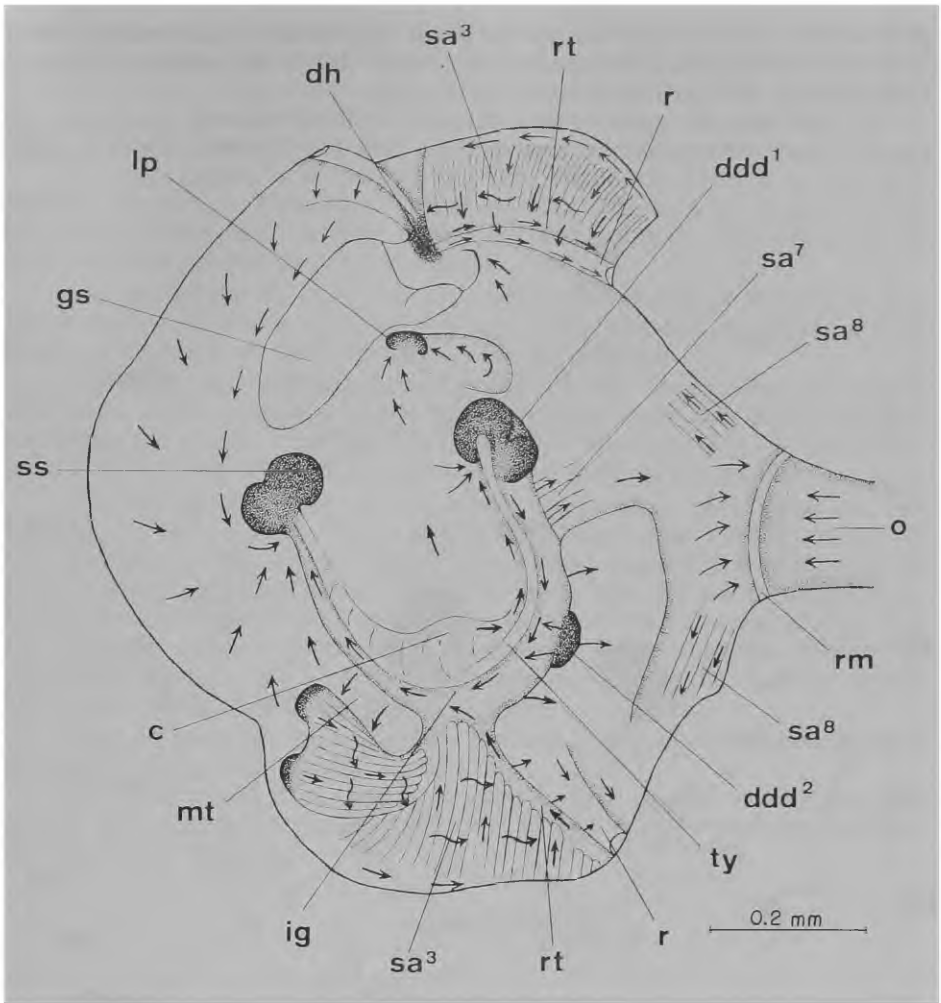


Fig. 15 — *Anodontites trapezeus*. Interior of stomach opened by middorsal incision from oesophagus to mid-gut. Arrows show direction of ciliary currents. c, conical protuberance on the floor of the stomach; ddd¹, orifice of the left duct of the digestive diverticula; ddd², orifice of the right duct of the digestive diverticula; dh, dorsal hood; gs, gastric shield; ig, intestinal groove; lp, left pouch; mt, minor typhlosole; o, oesophagus; r, longitudinal ridge; rm, transversal ridge; rt, rejection tract; sa³, sorting area in dorsal hood; sa⁷, sorting area lying just below the orifice of the oesophagus; sa⁸, sorting area in the anterior part of the stomach ceiling; ss, style sac; ty, major typhlosole.

six ducts open from the digestive diverticulum, two of them being directed toward the anterior region, three of them toward the posterior region and one to the inferior part of the body. In *A. trapesialis* four ducts come to this opening, two of them being directed toward the anterior region, one toward the inferior part of the body, and the last one toward the posterior

part of the body. The cilia in the major typhlossole beat sending particles into the digestive diverticulum and those cilia in the intestinal groove, beat sending the particles toward the outside.

At the anterior part of the stomach ceiling, there is a system of parallel folds that constitute a separating area (sa⁸), where the cilia send

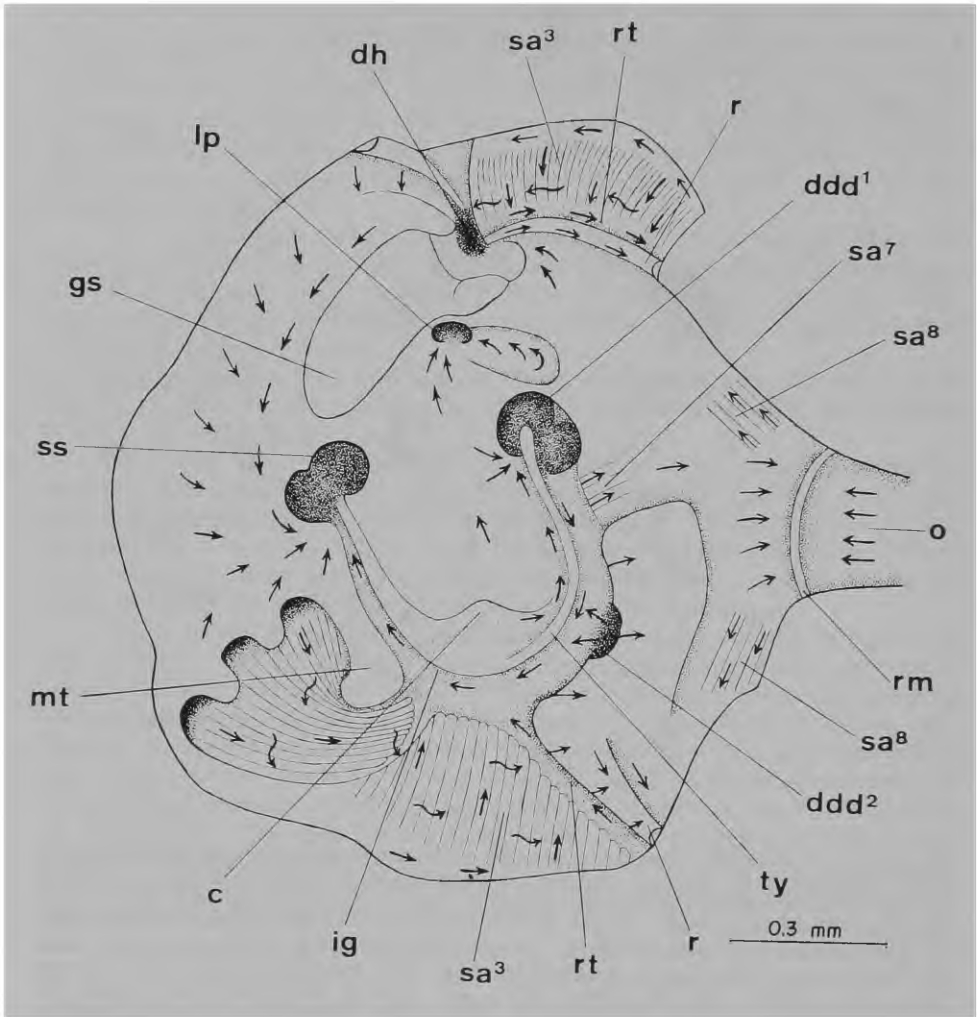


Fig. 16 — *Anodontites trapesialis*. Interior of stomach opened by middorsal incision from oesophagus to mid-gut. Arrows show direction of ciliary currents. c, conical protuberance on the floor of the stomach; ddd¹, orifice of the left duct of the digestive diverticula; ddd², orifice of the right duct of the digestive diverticula; dh, dorsal hood; gs, gastric shield; ig, intestinal groove; lp, left pouch; mt, minor typhlossole; o, oesophagus; r, longitudinal ridge; rm, transversal ridge; rt, rejection tract; sa³, sorting area in dorsal hood; sa⁷, sorting area lying just below the orifice of the oesophagus; sa⁸, sorting area in the anterior part of the stomach ceiling; ss, style sac; ty, major typhlossole.

particles toward the dorsal hood. Below the hood opening, there is a small left pouch (lp) where three ducts open from the digestive diverticulum, both in *A. trapezeus* and *A. trapesialis*, one of the ducts being dorsal and narrower, one lateral duct being directed toward the anterior region and another lateral duct directed toward the posterior region.

On the opposite wall, in front of the left pouch, there is a long but shallow concavity. Dinamani (1967) regards this area as a part of the left pouch, criticizing Purchon (1958) for not doing it. My observations in the species studied confirm Dinamani.

The gastric shield (gs) does not reach the opening of the left pouch. It remains on the left wall of the stomach, below the opening of the dorsal hood, in direction of which it emits a short extension.

Anteriorly on the stomach floor, there exists a separating area (sa^r) with wide and irregular folds in which the cilia beat anteriorly, sending particles toward the esophageal orifice. The distribution area (sa) described by Purchon (1958) does not exist in the species studied.

Besides the ducts of the digestive diverticulum that open on the left side of the stomach (lp, ddd¹), a very large duct (ddd²) opens on the right side, at the anterior region of the floor, near the intestinal groove. In *A. trapezeus*, four digestive diverticula open into this duct, two of them being directed toward the anterior region of the body, and two toward the posterior region, while in *A. trapesialis*, three digestive diverticula open into the duct, one of them being directed toward the anterior region and two of them toward the posterior region.

A minor posterior duct found by Purchon (1958) in *Anodonta cygnea*, does not occur in the species studied here.

On the stomach floor there is a quite evident conical mound (c) that divides the interior of the stomach into two compartments, one anterior and the other posterior.

9 — PERICARDIUM

The pericardium in *A. trapezeus* and in *A. trapesialis* is identical to the pericardium in *Anodonta cellensis* described by James (1904) and Krug (1922). It is placed on the middle dorsal line of the body. It surrounds the heart and part of the terminal gut which crosses the ventricle. It is ventrally limited by the kidney and by the venous sinus and distally by the posterior adductor muscle. The heart shows an elongated ventricle, posteriorly expanded and flanked by two flattened auricles which are lodged in the ventral part of the pericardium. The auricular-ventricular valves are situated ventro-laterally in the middle region of the ventricle. The aorta is directed toward the anterior region of the animal and posteriorly to the adductor muscle; it turns toward the anterior region, passing along the right side of the stomach. At this point, it branches into the pedal and visceral arteries. The posterior aorta emerges from the distal part of the ventricle and continues to the upper part of the posterior adductor muscle, where it branches off. Aortic bulbs do not appear in these species.

The pericardial glands appear and are more developed at the anterior region of the pericardium, around the two renal-pericardial orifices.

10 — EXCRETORY SYSTEM

The kidney is placed above the ctenidia, in the external and anterior part of the posterior retracting muscle of the foot, extending forward to the middle region of the animal body. They are superiorly delimited by the pericardium and posteriorly by the posterior adductor muscle.

Just as it occurs in *Anodonta cellensis* (Fernau, 1914, 1914a), the kidney in *A. trapezeus* and in *A. trapesialis* has the form of a pair of lying U shaped ducts, the vertexes of which are turned toward the posterior region. The lower branch of each, opens into the anterior region of the pericardium, through the renal-pericardial duct, and extends backward to the proximities of the posterior adductor muscle. Beyond this point, it turns upward, giving origin to the upper branch of the duct, the renal duct.

The external renal apertures are placed on each side of the body, between the ascendant and descendant lamellae in the inside demibranchia, in its proximal anterior part, a little above the genital orifices.

Semi-solid, yellow substances were sometimes found during the dissections of the animals. They were part of the excreted material.

11 — NERVOUS SYSTEMS

The nervous system of the species studied is identical to the one in *Anodonta cellensis* minutely described by Splittstösser (1913). It is formed by three pairs of ganglion-cells: cerebral, pedal and visceral, attached to each other by a pair of cerebral-visceral and a pair of cerebral-pedal connectives.

The cerebral ganglion-cells are placed at the anterior region, on each side of the body, between the base of the labial palps and the esophagus, behind the anterior adductor muscle. They are attached by a supra-esophageal commissure and emit one pair of paleal nerves which innervate the mantle and the anterior region of the body.

The pedal ganglion-cells are fused together, giving origin to a roundish ganglion, placed in the proximal part of the foot just below the digestive diverticula on the middle region of the stomach. Ventrally to the ganglion-cells, two major nerves are emitted and are directed toward the lateral parts of the foot.

The visceral ganglion-cells are also merged, and are placed in the anterior-ventral region of the posterior adductor muscle. From the anterior region of these ganglia a pair of branchial nerves is originated of which the larger ones are directed toward the gills. From its lateral and superior regions, other branchial nerves part, to innervate several organs of the visceral mass, the posterior adductor muscle, the mantle and the siphonal process.

Connecting the cerebral ganglion-cells to the visceral ganglion-cells, there appear two nervous connectives involving the upper region of the visceral mass, like a belt. These connectives are well visible in the trans-

versal sections, specially at the region of the kidney. Two minor nervous cords lying oblique, toward the posterior region, connect the cerebral ganglion-cells to the pedal ones.

12 — REPRODUCTION SYSTEM

The gonads in *A. trapezeus* and in *A. trapesialis* are placed in the visceral mass, between the loops of the alimentary duct. The genital duct ends in two openings placed in the anterior proximal region of the inside demibranchia, between their ascendant and descendant lamellae. Each genital opening shows a papilla turned to the posterior region, just below the renal aperture. As soon as they are liberated, the sexual products pass into the cavity of the inner demibranch and are moved afterwards by an intense local ciliation.

The reproductive cycle in *A. trapezeus* apparently begins in July, extending for the two subsequent months.

Hermaphroditism is a common character in the *Anodontites* genus (Bonetto, 1951). *A. trapezeus* shows spermatozoids 3.2μ long, with pyriform heads, found in clusters of hundreds of individuals, forming spheres up to 30μ in diameter, similar to the colonies of *Volvox*. The spermatozoid heads are turned into the sphere and the tails are radially disposed outside the sphere, beating synchronously as described by Coe (1931) in *Ostrea lurida*. The name "spermballs" was given to these clusters of spermatozoids. They were observed by Edgar (1965) in *Anodontoides ferussacianus*.

Forthcoming surveys about the sexual cycle of this species may reveal in fact the presence of a functional hermaphroditism, a consecutive sexuality, rythmical consecutive sexuality, alternate sexuality or even the existence of a unisexuality, according to Coe's classification (1943).

Bonetto (1951) found larvae (lasidium) of *A. trapesialis* in July and August, though 80% of the animals observed by this time, were not yet completely developed. Dissections of this species performed here in different epochs of the year confirmed these data. A large number of animals were observed here with the inner demibranchia filled with eggs by the end of March and of fishes parasitized by *Anodontites* larvae were found in July.

The fact that the inside demibranchia works as a marsupium is quite common among the limnic bivalves in South America but quite rare in the animals from other parts of the world and which use the outside demibranchia. Several species have the outside demibranchia functioning as a marsupium, or even the outside and the inside concomitantly (Bloomer, 1931, 1932, 1934, 1935, 1939).

On the other hand, the internal insemination is quite common among the fresh water bivalves (Franzén, 1955) with retention of the eggs within the mother organism during the embrionic development.

The amount of eggs that were found in the inside demibranchia of a 10.4 cm long specimen of *A. trapesialis* was that of 3.200.000. Bonetto and Ezcurra (1962) found 3.500.000 eggs in a 9 cm. long animal.

A. trapesialis is hermaphrodite with its 2.4 μ long, pyriform-head spermatozooids clustered in spheres having a diameter ranging from 20 μ to 23 μ . The egg-cells measure, in average, 60 μ in diameter.

The lasidium in *A. trapesialis* preferentially parasites small fishes, fixing themselves all over the body, specially in the fins. The description of the larval fixing processes (Bonetto and Ezcurra, 1962a) were confirmed in the present paper, as well as the unspecificity of the parasitism in its early phase of development.

13 — GENERAL CONCLUSIONS AND DISCUSSION

The limnic bivalves studied live in a very soft substratum very near the surface. They feed on material in suspension including the plankton and organic finely divided detritus, a fact already observed by Cocker *et al.* (1919-1920), for other fresh water bivalves. Considering the general structure of the inhalant siphon, gills, the labial palps and the alimentary duct, it was concluded that *A. trapezeus* and *A. trapesialis* are suspension feeders. According to Oven *apud* Ansell (1961), the greatest adjustments that occur in the bivalves which are suspension feeders are restricted to the fact that the animal digs deeply and loses its horizontal mobility. *A. trapezeus* and *A. trapesialis* live superficially and are practically sedentary, since they are not influenced by a very great stimulus such as a prolonged drought, reproduction season and so on.

An important structure for these animals related to the kind of feeding is, undoubtedly the inhalant siphon through which the water and particles are taken to the interior of the mantle cavity. The fact that *A. trapezeus* has little developed simple tentacles, and that *A. trapesialis* does not have them, leads us to the conclusion that these species have to live in still waters. They were found in relatively clear waters, in mud-sand bottoms, where the water movement does practically not exist and the particles in suspension are minuscule.

Along with the inhalant siphon, the mantle functions as a particle selector. Both species studied live in a substratum where very small particles predominate; thus, the necessity of small folds that occur in the mantle free border in *A. trapezeus* and the perfect juxtaposition of the lobes of this organ in *A. trapesialis* are observed, closing their external openings almost totally, so as to stop the entrance of particles into the mantle cavity.

The particles entering the paleal cavity are submitted to the ciliary action in the demibranches of the animal, and they are submitted to a same kind of transportation in both species. The branchial cilia in *A. trapezeus* and in *A. trapesialis* can be considered as small ones when they are compared with the marine bivalves which live in regions of turbulent waters, like those studied by Narchi (1974). Besides, cleaning cilia do not occur in the demibranchia of these animals, so characteristic in the marine species from exposed shores.

From the demibranchia, the particles are either sent to the labial palps or they are eliminated through the ciliary action of the mantle.

In the major labial palps there is an efficient separation of particles that prevents the access of unselected material into the digestive duct. Large palps are common mud diggers, in which a very fine material enters into the mantle cavity, through a suction action of the inhalant siphon (Yonge, 1949).

Living in the same "habitat", i.e., in still waters with very fine particles in suspension and having the same type of gills, one should expect that *A. trapezeus* and *A. trapesialis* have the same type of labial palps. Contrary to what occurs with species that live in "habitats" with larger particles in suspension, the animals studied have a greater complication in the ciliary currents found in the palps, being more efficient in selecting the particles, confirming Purchon's observations (1963) for other bivalves. *A. trapezeus* shows a greater complication in the acceptance currents of particles in the labial palps.

From the palps, the particles reach the mouth, enter the alimentary duct, where they will suffer a last selection. The stomach, according to Purchon's conception (1959), could be used for a new classification to the Bivalvia. The species studied show a Type IV stomach, which according to the above mentioned author, is the primitive type and from which the Type V would be originated through specialization. Both species show an absolutely identical stomach, with only one difference in the separating area sa^3 that is much smaller in *A. trapezeus*. This occurs possibly because of the presence of tentacles in the inhalant siphon and more complex palps which perform a more efficient separation of particles than in *A. trapesialis*. In this species, the area sa^3 , within the stomach, undertakes the separation of particles so that they can be used for the digestion and, for this reason, it is more developed than in *A. trapezeus*.

When Purchon (1958) studied the stomach in *Anodonta cygnea* and in *Hyridella australis*, he concluded that the internal structure of the stomach is one of a great uniformity in Unionacea. Dinamani (1967) confirmed the fact with the study of *Lamellidens corrianus*.

The similarity in the species we have dealt with is undeniable, and in a general way it was also observed that they agree with the above mentioned authors' descriptions. Therefore it seems that in all the Mycetopodidae the stomach shows a great uniformity.

The studies performed with the limnic species of the Unionacea and of the Mutelacea, show that their similarity is due to an adapting convergence. The fresh water bivalves show only some differential features, but in the whole, the species are practically identical. In spite, of being submitted to equal ecological factors, they have not adapting differential characters, but genetical ones. Future studies will be able specifically to evidence up to what point the adapting convergence acts upon the modification of the genetical characteristics.

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