

Functional morphology of *Heterodonax bimaculatus* (Linné, 1758) (Bivalvia: Psammobiidae)

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Abstract: *Heterodonax bimaculatus* (Linné, 1758) apparently is restricted to the coasts of temperate and tropical America. In southern Brazil, this species occurs infaunally in shallow bay areas on coarse sand substrata. A comparison is made between *H. bimaculatus* and other infaunal Psammobiidae wherein the most significant adaptations concern the organs of the mantle cavity.

The major structural features and ciliary currents are described. Special attention is paid to the ctenidia, labial palps and stomach, and its functional morphology is similar to *Gari* and *Asaphis*. The stomach of *Heterodonax bimaculatus* could not be defined as Type V as exists in all studied Psammobiidae. The major typhlosole does not send a flare into the right caecum but describes a loop very close to the mouth of it. Of all known species of Psammobiidae, only *H. bimaculatus* has a stomach of Type IV. The species can be regarded as being near the ancestral condition in the process of evolution in the Tellinacea and so is at the base of the Psammobiidae lineage.

The genus *Heterodonax* Mörch, 1853, occurs in the West Indies (Keen, 1969), along both coasts of temperate and tropical America (Coan, 1973) and both coasts of Africa (Boss, 1969; Cosel, 1989). *H. pacificus* (Conrad, 1837) was recorded by Coan (1973) and Keen (1971) from southern California to Panama. In the Atlantic, *H. bimaculatus* (Linné, 1758), the type species of the genus, ranges widely throughout the Caribbean (McLean, 1951; Warmke and Abbott, 1962; Keen, 1969, 1971; and Abbott, 1974); Rios (1985) recorded it from Venezuela. So similar is *H. pacificus* to *H. bimaculatus* that most authors consider them conspecific (Keen, 1971).

Heterodonax bimaculatus has been collected rarely along the coast of Brazil; the first record was at São Sebastião Channel, São Paulo, by Ihering (1897). Subsequent records are from Ilha de São Sebastião, São Paulo, by Lange de Morretes (1949) and Rio de Janeiro (Rios, 1985). Although this species commonly is found alive in southern California and northern Mexico, it has not been studied anatomically (Coan, 1973).

Studying the subfamily Tellininae in South African waters, Boss (1969) discussed two species incorrectly placed in the Tellininae: *Scissulina dispar* (Conrad, 1837) and *Heterodonax ludwigii* (Krauss, 1848). Boss (1969) recognized the latter as belonging to the Psammobiidae and gave a diagrammatic illustration of its anatomy.

Isolated references to *Heterodonax bimaculatus* are found mainly in systematics accounts. It is of interest, therefore, to study the functional morphology of this species and to compare it to other psammobiids already known.

MODE OF LIFE

Living specimens were obtained from Praia do Codó, Flamengo Creek, Ubatuba (23°27'S, 45°06'W) on the coast of São Paulo, Brazil. The animals occur in shallow bay areas on the sand substratum (Fig. 1). Like *Gari tellinella* (Lamarck, 1818) and *G. fervensis* (Gmelin, 1791) (Yonge, 1949), they usually inhabit coarse sands, to which they appear to be specially adapted. During high tide *Heterodonax bimaculatus* lives close to the surface in the wave-swept zone, being scoured out of the sand by wave action. The animals are rapid burrowers and have features typically found in organisms that inhabit unstable sediments (Stanley, 1970). The pointed foot emerges from the elongated anterior region of the shell and probes the sand quickly to gain a foothold. Erection of the shell is accomplished by a single burrowing sequence which pulls the animal directly downwards without the rocking movement described for other bivalves, e.g. *Mesodesma mactroides* Deshayes, 1854 (Narchi, 1981).

Heterodonax bimaculatus does not migrate seawards as the tide recedes, but instead they remain high on the beach where they bury deeply looking for moisture. In this condition, *H. bimaculatus* can bury up to ten times the length of its own shell.

Codó Beach has characteristically an upper, shoreward sandy zone and a lower, seaward clay sand zone; the latter becomes exposed only at the lowest tides. On the sand clay zone the water currents inside the bay transfer sand grains from the upper zone and form ripple sand bars.

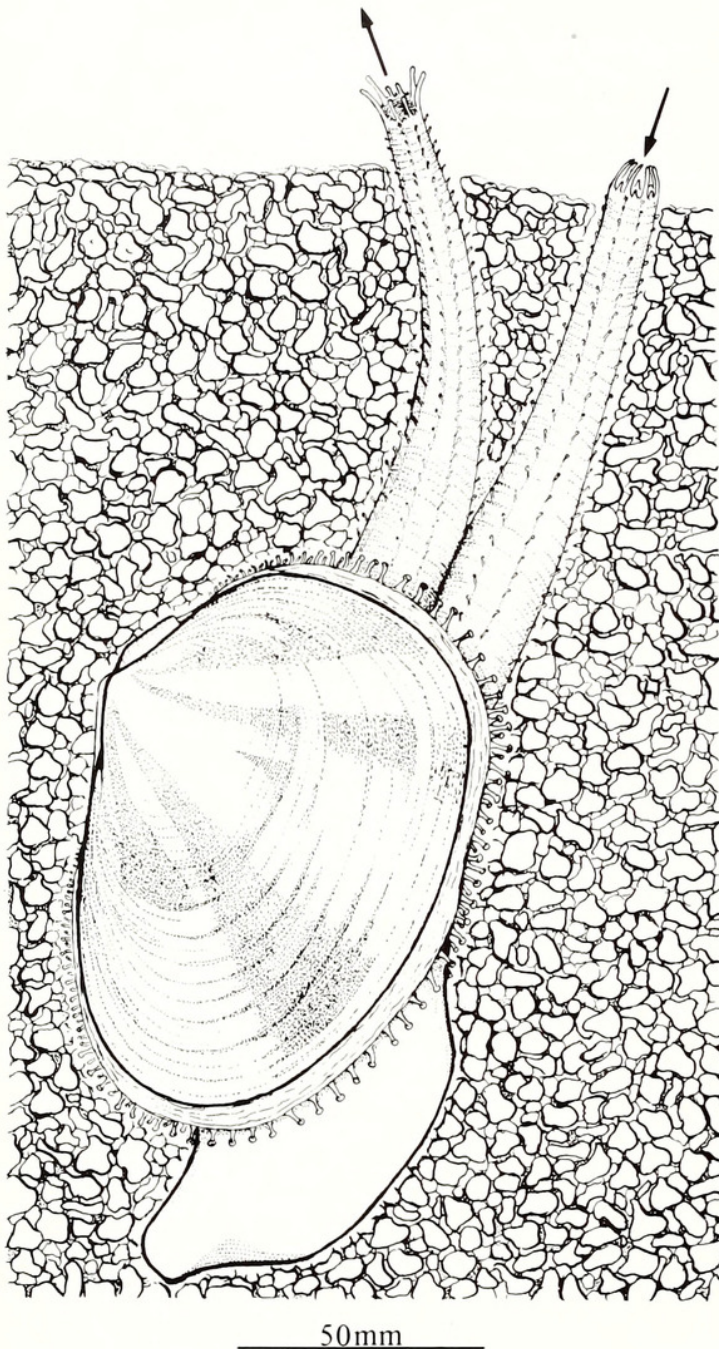


Fig. 1. *Heterodonax bimaculatus*. Animal in natural habitat; exhalent siphon not fully extended. The arrows show the direction of inhalent and exhalent currents.

Heterodonax bimaculatus was first found on this beach by sieving the sand of a ripple sand bar at low tide. Contrary to statements by Abbott (1974) and Rios (1985), *Heterodonax bimaculatus* was not found alive with *Donax* on exposed beaches, as described by Narchi (1978).

MATERIAL AND METHODS

Some behavioral attributes of *Heterodonax bimaculatus* were observed in the natural habitat on the beach at

low tide. Live specimens were also kept in aquaria with water and sediment, at room temperature of 21°C, at the Departamento de Zoologia, Universidade de São Paulo, Brazil.

Ciliary currents of feeding and other functional adaptations were observed in live specimens. Studies of the anatomical features and drawings are of living as well as of relaxed and preserved specimens. Magnesium sulphate was used as the relaxing agent. Ciliary currents were studied using carborundum, carmine suspension and graded sand particles. Histological sections (6 to 8 µm thick) were made of tissues fixed in a 10% formalin solution in distilled water and were stained with Ehrlich's haematoxylin and eosin.

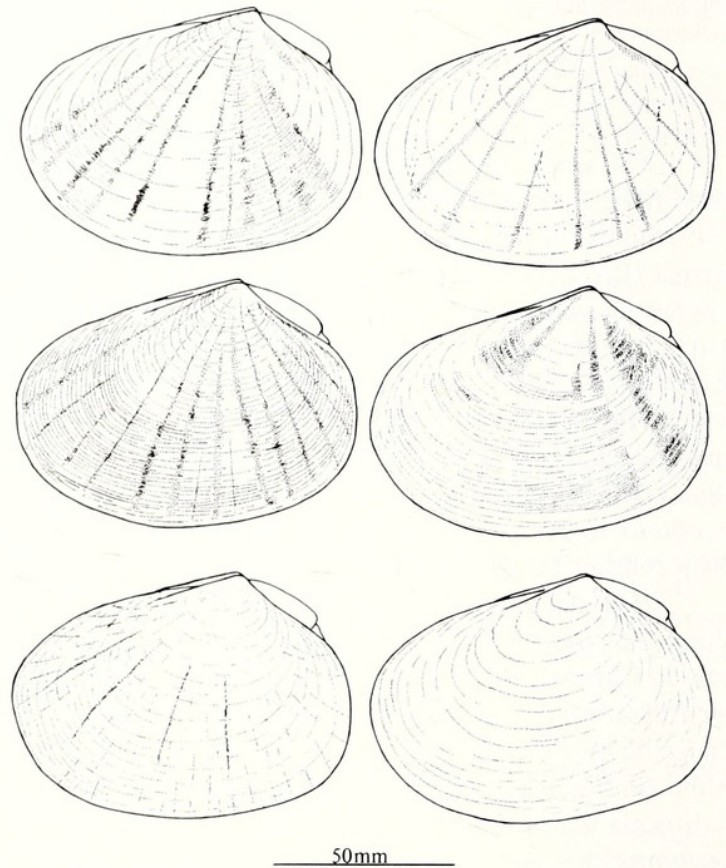


Fig. 2. *Heterodonax bimaculatus*. External view of left shell valves, showing different colour patterns.

SHELL

The shell is bluntly ovate, moderately inflated, inequilateral, thin, fragile, broadly rounded anteriorly and more or less truncate posteriorly. The outer surface of the valves is smoothish and sculptured with fine concentric growth lines (Fig. 2). The hinge plate is thick below the ligament and cardinal teeth and then it is followed by a thinner concave anterior portion. The hinge teeth are relatively large for the size of fully grown specimen. The right valve

has two well developed cardinal teeth, the posterior stronger and slightly bifid; the left valve has a large bifid anterior cardinal and a lamellar posterior cardinal (Fig. 3). There are no lateral teeth in either valve. The ligament is external, opisthodontic and rests on a nymph plate. The large "U" shaped pallial sinus, extending from the base of the posterior adductor muscle scar, is broadly rounded anteriorly, irregularly and arcuately extends toward the ventral pallial line which it may or may not meet depending on the specimen. Cruciform muscle scars are not easily discerned.

The valves occur in a variety of colors. They can be white, blue, purple, red, orange, or nearly any combination of these. The color pattern can consist of rays of purple coloration or irregular clouding or flecking. The periostracum is colorless and translucent, but in a few specimens it is yellowish. The shell of the largest animal studied measured 11.4 mm in length, 8.0 mm in height and 5.0 mm in width, and the smallest specimen found measured 4.1 mm in length, 3.0 mm in height and 1.4 mm in width.

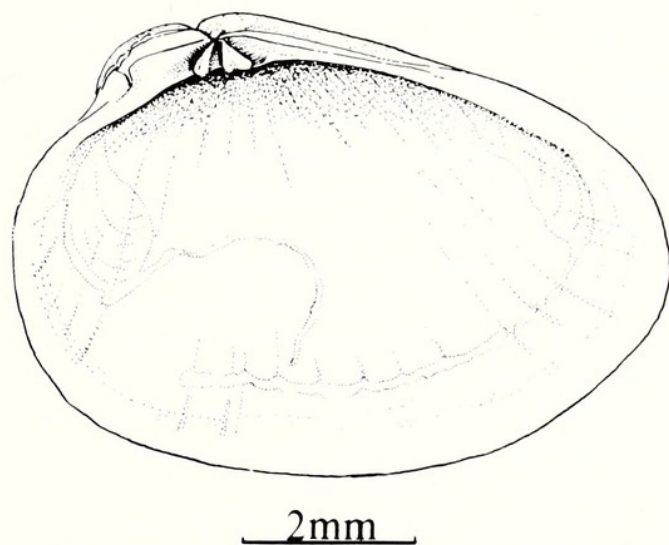


Fig. 3. *Heterodonax bimaculatus*. Internal view of the left valve, showing details of the teeth, ligament, pallial sinus, pallial line and adductor muscle scars. Specimen where the connection of the pallial sinus with the pallial line is absent.

SIPHONS

The siphons are separate and well developed. Their detailed structure is shown in figure 4. The external surface of the exhalent and inhalent siphons bears eight and six longitudinal rows of minute simple and colorless tentacles respectively, underlain by internal, milk-white nerve cords. Both the tentacle rows and the nerve cords are more developed and conspicuous on the ventral and dorsal surfaces than on the lateral surface of the exhalent siphon. The minute tentacles correspond to the sense organs described by Rawitz (1892, cited by Yonge, 1949) for *Gari* and

Solecurtus. The sense organs are concerned with tactile stimuli or the detection of more delicate water movements.

The orifice of the exhalent siphon is fringed with eight, long, knobbed tentacles, each of which is situated at the distal end of one of the longitudinal rows. The tentacle pairs at dorsal and ventral margin are nearer and more developed than the others. Between the tentacles there are small papillae.

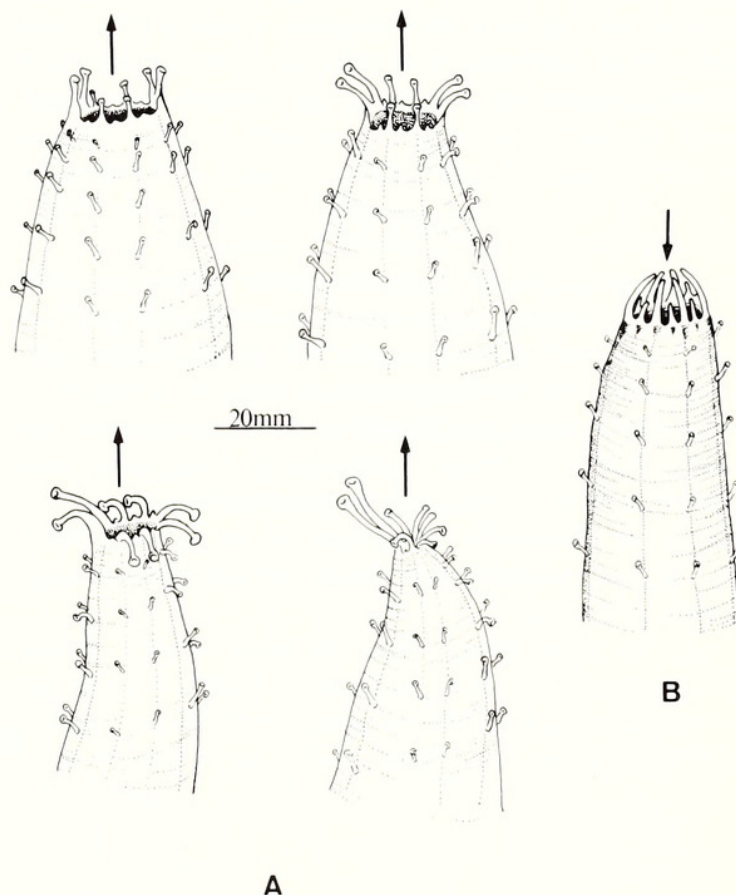


Fig. 4. *Heterodonax bimaculatus*. A, appearance of fully extended exhalent siphons, showing movements of the tentacles around their orifices. B, detail of the distal end of the inhalent siphon.

The orifice of the inhalent siphon is fringed with twelve tentacles, six of them more developed and situated at the end of the longitudinal rows. The tips of the tentacles are flattened and at its basal region there is a milk-white spot.

Completely buried clams extend their siphons as long as their own shell length. The inhalent siphon extends straight through the substratum keeping its opening a little above the sediment surface. Surrounding suspended material and dense particles lifted from the bottom reach the pallial cavity by the inhalent current. The tentacles can be directed inward to the siphonal aperture creating a feeble barrier against the entrance of large particles; when in clean water they bend outwards.

The exhalent siphon curves dorsally as it extrudes from the substrate; its opening is maintained out of the bottom surface and far from the inhalent. When observed in the laboratory, living specimens protracted both siphons, the exhalent twice or more distance of the inhalent. This condition is maintained even in well relaxed and preserved specimens.

The behaviour of the inhalent siphon during feeding was used, along with other features, by Pohlo (1969) and Reid and Reid (1969) as a criterion for classification of feeding types in bivalves. Later, both Reid (1971) and Pohlo (1982) dedicated more attention to this problem and proposed a more useful criterion for categorizing feeding types.

MANTLE

The two mantle lobes are completely separated, leaving a large pedal gape that extends from the anterior adductor to the cruciform muscle. The middle fold is moderately developed and bears only one row of cylindrical, cup shaped tip tentacles, similar to the ones described by Narchi (1978) for *Donax hanleyanus* Philippi, 1847. The middle folds along with the protraction of the foot and the siphons are extended well beyond the limits of the shell exposing an external surface covered by a thin layer of periostracum.

The inner surface of the mantle is ciliated and its ciliary currents are shown in figure 5. Over a wide dorsal area of the mantle surface the ciliary currents are antero-ventrally directed; they carry particles to an anterior con-

vergent area immediately beneath the external labial palp; that area also receives particles from the anterior part of the anterior adductor muscle. Rejection currents are directed ventrally, but a major, powerful rejection tract is situated near the ventral margin, running posteriorly from a point near the anterior adductor muscle to the base of the inhalent siphon.

MUSCULATURE AND FOOT

The adductor muscles and pedal musculature are shown in figure 6. The anterior adductor muscle (aam) is elongated and more developed than the posterior adductor (pam), that is transversely oval. The foot is axe-shaped without a flattened sole. There is no aperture of the duct of the byssus gland as Graham (1934a) described for *Gari tellinella*. The foot of *Heterodonax bimaculatus* emerges from the elongated anterior region of the shell to probe the sand and quickly burrow into the substrate, in a similar fashion to that of *Donax hanleyanus* (Narchi, 1978) and of *Mesodesma mactroides* (Narchi, 1981).

The well developed protractor muscles (pm) are attached to the shell juxtaposed to the postero-ventral surface of the anterior adductor muscle. From its insertion on the shell, the protractors pass backwards, twist abruptly as they enter the foot, and spread fanwise to form the outermost muscular layer of the foot.

The two posterior retractor muscles (prm) are inserted on the shell antero-dorsally to the posterior adductor muscle. They pass towards the midline where their bundles of fibers cross each other and split again; the ones coming from the right pass deeply into the left side of the foot, and vice versa, lying internal to the layer formed by the protractor muscle.

The two anterior retractor muscles (arm) are inserted on the shell postero-dorsally to the anterior adductor muscle. Thence they pass ventrally converging so as to form a thick median bundle; without crossing each other, the right and left muscles pass deeply into the foot where they form its innermost muscular layer.

In addition to these muscles, the visceral and ventral parts of the foot present transversely-directed fibres which form a large number of strands crossing from one side to the other. These isolated bundles were considered (Graham, 1934a) to form the true intrinsic pedal muscles.

Despite careful searching no pedal elevator muscles were found in the specimens studied.

The cruciform muscle, characteristic of all Tellinacea (Ihering, 1900), lies at the ventral side of the base of the inhalent siphon. Its morphological features and functions were discussed by Graham (1934), Yonge (1949), Moïeza and Frenkiel (1974, 1976, 1977).

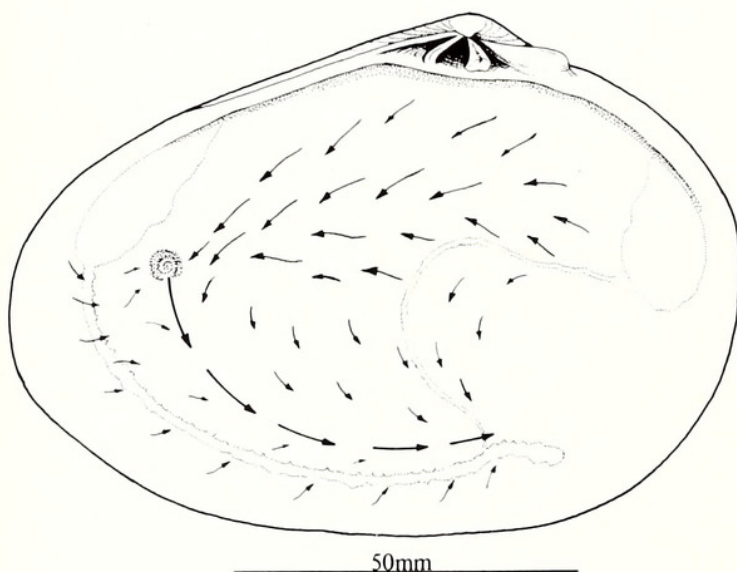


Fig. 5. *Heterodonax bimaculatus*. Inner surface of right mantle lobe, showing ciliary cleansing currents; the arrows show the minor currents and the main rejection tract.

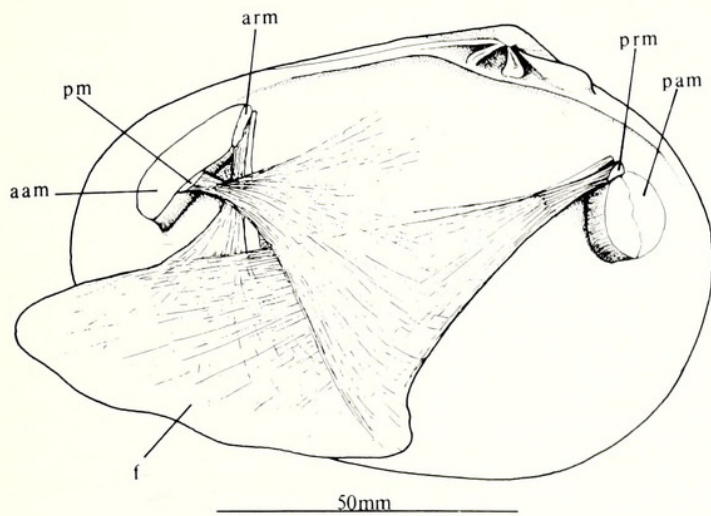


Fig. 6. *Heterodonax bimaculatus*. Diagrammatic representation of the musculature, as seen from the left side (aam, anterior adductor muscle; arm, anterior retractor muscle; f, foot; pm, protractor muscle; pam, posterior adductor muscle; prm, posterior retractor muscle).

CTENIDIA

The arrangement of the organs in the mantle cavity after removal of the left valve and mantle lobe is shown in figure 7. The form of the ctenidia and the general course of the ciliary currents are shown diagrammatically in figure 8. The inner demibranch hangs much lower than the outer and

the ascending lamella of the latter rises considerably above the level of the gill-axis, forming a supra-axial extension as Ridewood (1903) described for the Psammobiidae. The inner demibranch is wider than the outer, particularly anteriorly as in *Asaphis dichotoma* (Anton, 1839) [= *A. violacens* (Forsskål, 1775)] (Narchi, 1980).

The ctenidia of *Heterodonax bimaculatus* (Figs. 7, 8, 9) are heterorhabdic with a groove along the free ventral margin of the inner demibranch only. They seem to be like the type C (1a) described by Atkins (1937a).

The posterior half of the infra-axial extension and the posterior end of the supra-axial extension of the outer demibranch are shallowly plicate while the rest of the demibranch is smooth. There is no interruption of the cilia at the free edge of the outer demibranch, the appearance is that of a simple bending of the filaments.

On the ascending lamella of the outer demibranch ciliary currents on the smooth area and on the crests and in the troughs between the plicae convey particles toward the free margin. Material is driven around the free margin and toward the gill axis on the descending lamella. Some particles are transferred onto the descending lamella of the inner demibranch.

Unlike the situation in *Asaphis dichotoma* (Narchi, 1980), there is an incipient oralward current along the ungrooved free edge of the outer demibranch. This is due to

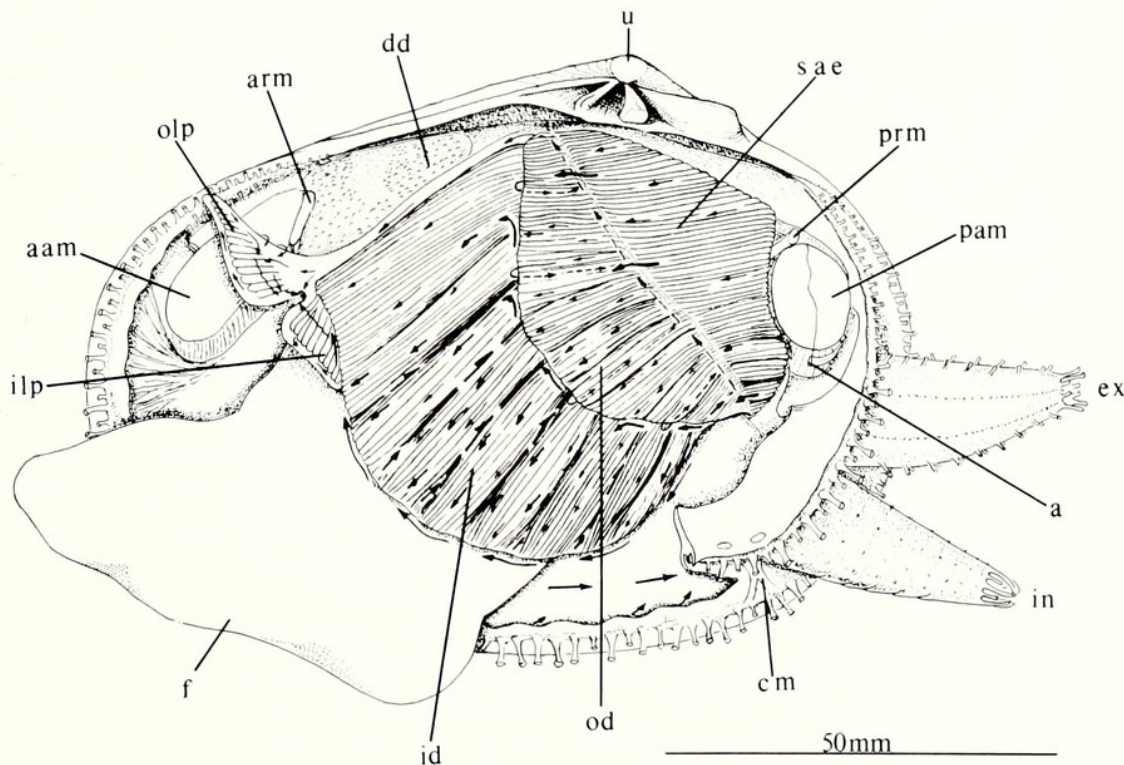


Fig. 7. *Heterodonax bimaculatus*. Animal viewed from the left side after removal of the left shell valve and mantle lobe (the siphons and foot are shown somewhat contracted). Arrows show the direction of ciliary currents (a, anus; aam, anterior adductor muscle; arm, anterior retractor muscle; cm, cruciform muscle; dd, digestive diverticula; ex, exhalant siphon; f, foot; id, inner demibranch; ilp, inner labial palp; in, inhalant siphon; od, outer demibranch; olp, outer labial palp; pam, posterior adductor muscle; prm, posterior retractor muscle; sae, supra-axial extension of outer demibranch; u, umbo).

the presence at the margin of coarse terminal cilia on the posterior half of the frontal surface of each filament; they beat toward the edge and forward, creating a slight longitudinal current or frequently sending particles off the demibranch onto the inner demibranch.

Except for a small smooth anterior portion, the rest of the inner demibranch is plicate. The frontal currents on the descending lamella are directed ventralward on the crest and sides of the plica and dorsalward on the troughs. They are only ventralward on the ascending lamella (Fig. 8). The presence of a dorsalward current makes these gills different from the Type C (1a) of Atkins (1937a) where all the currents are ventralward. Atkins (1937a) included *Gari fervensis* and *G. tellinella* of the Psammobiidae in her Type C (1a) gill ciliation. The number of filaments per plica ranges from 12 to a maximum of 14 at the inner demibranch and 7 to 8 in the outer demibranch.

On each side of the body there are two oralward currents, one in the ctenidial axis and the other in the groove along the free ventral margin of the inner demibranch. Two additional, incipient oralward currents exist; one at the free margin of the outer demibranch and the other at the point where the ascending lamella of the inner

demibranch fixes on the visceral mass.

The 70-116 μm wide filaments (Fig. 9) are separated by 100 μm long laterofrontal cilia (lfc). The lateral cilia (lc) produce a powerful respiratory and feeding current throughout the ctenidia and attain a length of 58 to 68 μm . The 12 μm long frontal cilia (fc) give place to increasingly longer (up to 200 μm) terminal cilia (tc) in the distal ends of the filaments which are placed around the food groove.

A simple row of 170 μm long, stout cilia (rc), is found on the anterior half of the frontal surface of the filaments on both lamellae of the inner demibranch. Each row extends from the free edge of the filament toward the ctenidial axis, attaining a varied length. In some specimens these cilia were present over the lower quarter to a half of the middle part of the inner demibranch, while in the anterior and posterior thirds of the latter they extended but a short distance from the free edge.

Sparse, long (190 μm) frontal cilia (rc_1) were observed at the inner demibranch of *Heterodonax bimaculatus*, similar to those recorded by Narchi (1972a) from the outer demibranch of the venerid *Tivela mactroides* (Born, 1778). The specialized large frontal cilia (rc, rc_1) were not observed on the outer demibranch of living specimens; in preserved specimens it was impossible to recognize them on either demibranch. Along the marginal groove of the inner demibranch a fan-shaped group of long (to 170 μm) guard cilia (gc) are clearly visible. Stout (70-110 μm), cirrus-like cilia (c) are present on the ends of the filaments bordering the marginal groove, mainly at the posterior part of both demibranchs. They beat obliquely forward. Generally there is only one at the tip of each filament.

LABIAL PALPS

The labial palps (Fig. 10A) have the same basic structure and muscular activity as those of *Gari tellinella* (Graham, 1934a) and *Asaphis dichotoma* (Narchi, 1980). The inner face of the labial palps of *Heterodonax bimaculatus* has almost invariably eight folds, whereas there are 12 in *G. tellinella* (Graham, 1934a).

The particles collected on the outer face of the palps are carried to the dorsal margin and then passed to the inner face. The internal, smooth, dorsal margin is relatively wide and its ciliary currents convey particles to the median region of the plicate area of the palp. The inner demibranch of the ctenidium projects deeply between the palps. Particles coming from the inner demibranch and ctenidial axis as well as those collected by the palps from the mantle and visceral epithelium pass to the inner folded surface of the palps.

The sorting mechanisms on the folded surface of the palps (Fig. 10B) carry particles in three major currents,

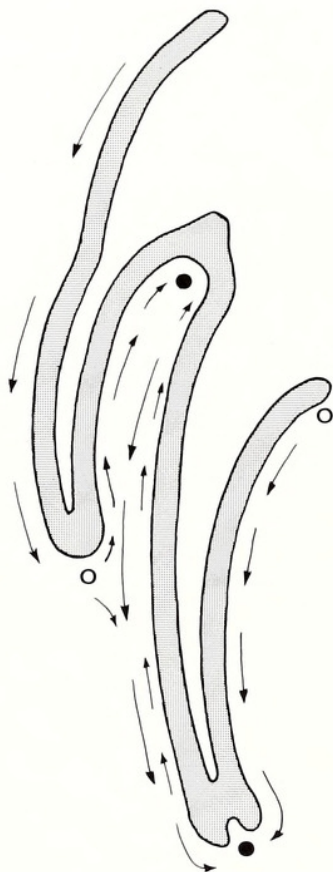


Fig. 8. *Heterodonax bimaculatus*. Diagrammatic transverse section showing the form and ciliary currents on one ctenidium. Arrows indicate the directions of major currents; solid circles, oralward currents and hollow circles, incipient oralward currents.

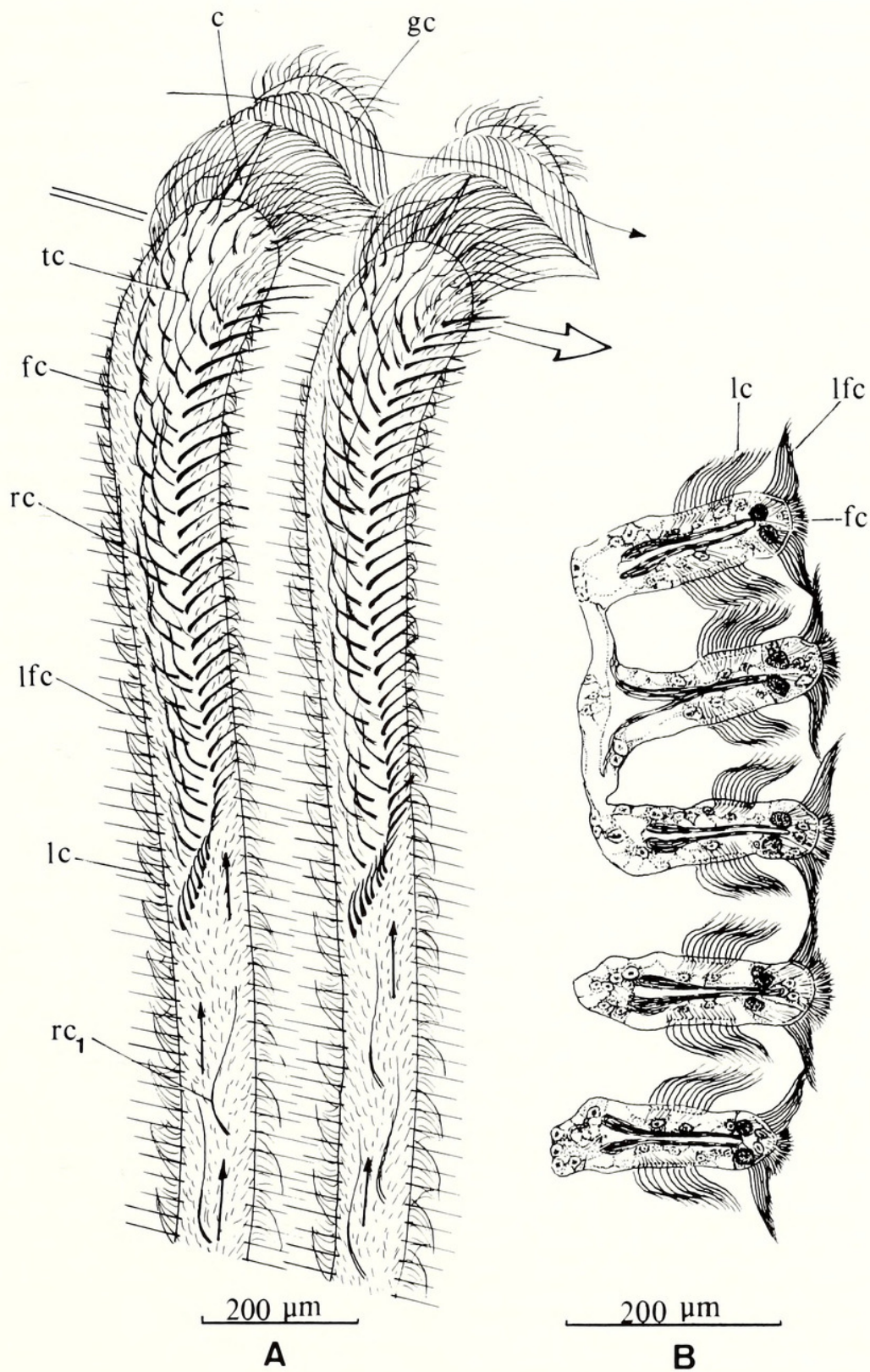


Fig. 9. *Heterodonax bimaculatus*. **A**, distal end of two living filaments of the inner demibranch, showing the arrangement of cilia. Short arrows indicate ventralward currents; long arrows, oralward currents. **B**, transverse section of some filaments, showing the arrangement of the different groups of cilia (*c*, cirrus-like cilia; *fc*, frontal cilia; *gc*, guard cilia; *lc*, lateral cilia; *lfc*, latero-frontal cilia; *rc*, long stout cilia; *rc₁*, long frontal cilia; *tc*, terminal cilia).

namely; a powerful current "a", on the aboral side of each plica; particles traveling dorsad on this current are caught by a tract of cilia and throw up to the crest of the plica. Here cilia convey fine particles from crest to crest in an oralward current "c" or throw large ones into the troughs between the folds. In the troughs, rejection currents "b" remove unwanted material onto the smooth ventral margin of the palp, where a vigorous rejection tract carries it to the distal end and on into the mantle cavity. Rejection currents "b" were more intensive on the proximal half of the palps; they were not observed all through the dorsal region of the organ.

These ciliary tracts in *Heterodonax bimaculatus* are

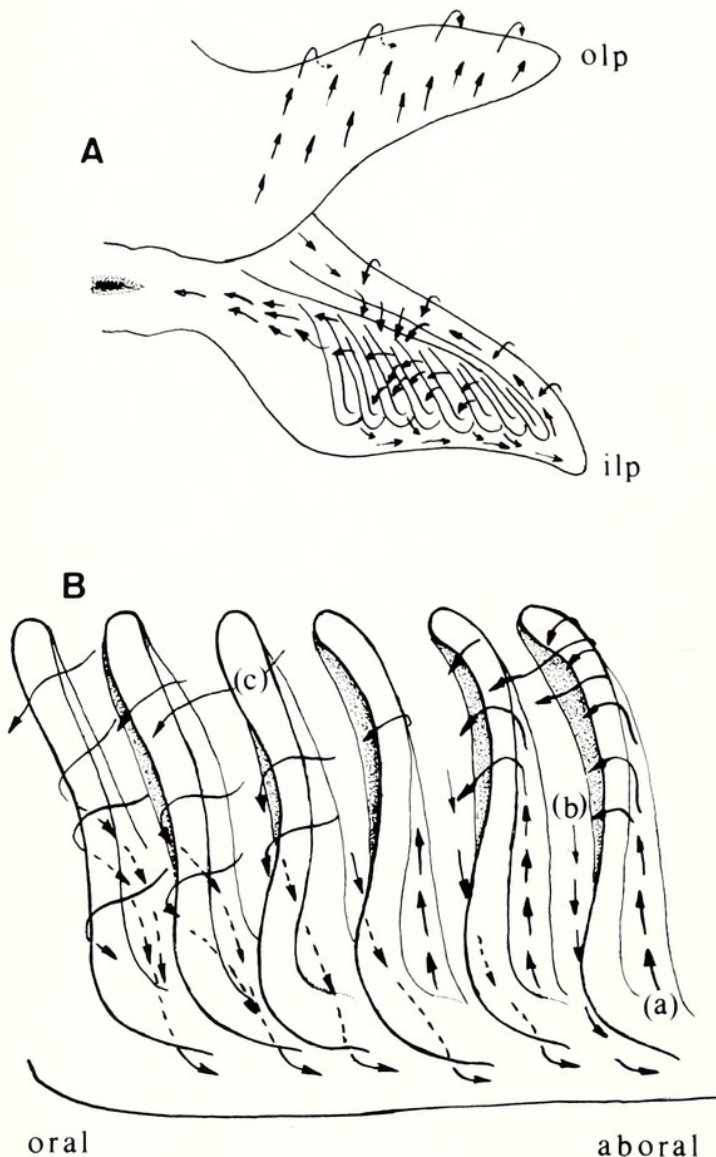


Fig. 10. *Heterodonax bimaculatus*. **A**, relationship between the inner and the outer labial palps, showing ciliary currents and acceptance tracts (ilp, inner labial palp; olp, outer labial palp). **B**, diagrammatic representation of the ciliary currents on the folds of the inner surface of the labial palp (a, dorsalward current on the aboral side of a plica; b, rejection current at the troughs between the folds; c, oralward current).

similar to those described by Narchi (1980) for *Asaphis dichotoma*, differing only by the absence in the first species of currents at the oral face of the folds.

The labial palps have an intense muscular activity of their own. They can roll up very easily or contract rhythmically without changing their shape. The inner palps often bend their tip to touch the visceral mass and capture particles on it. The outer labial palps do the same, touching the mantle epithelium.

ALIMENTARY CANAL

The inner demibranch of the ctenidia projects forward between the bases of the inner and outer labial palps. Anteriorly the palps are continuous with the smooth dorsal and ventral lips of the mouth, which have conspicuous muscular movements. Living, dissected specimens were observed to swallow pieces removed from their own ctenidia, muscles or mantle edge. Pieces of tissue as large as the diameter of the mouth were sucked up promptly. Arrival of material between the lips stimulates the mouth to expand and then to close pushing the material backward into the

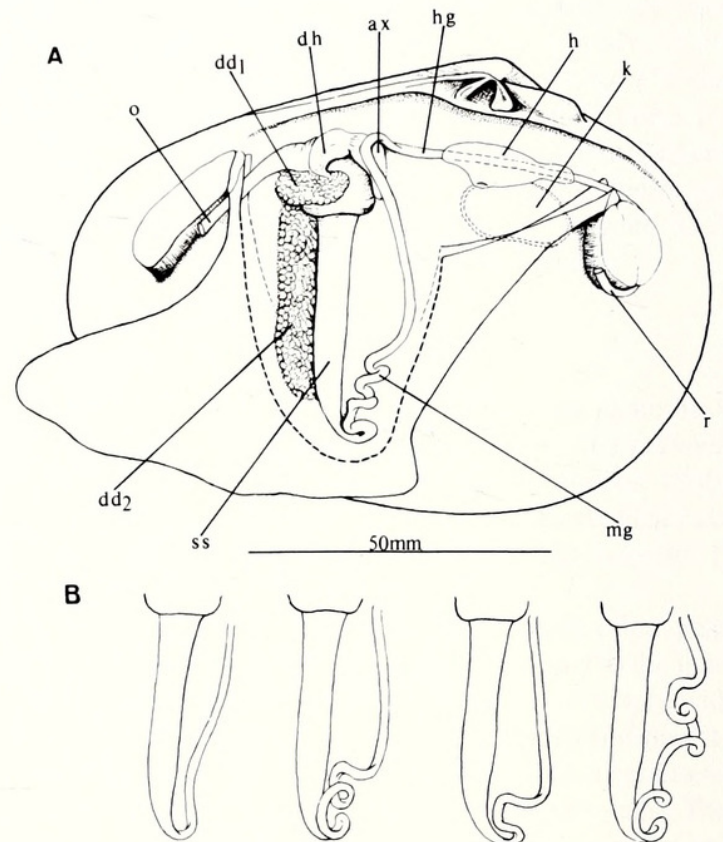


Fig. 11. *Heterodonax bimaculatus*. **A**, diagrammatic representation of the alimentary canal, as seen from the left side (ax, appendix; dd₁, digestive diverticula from the left pouch; dd₂, digestive diverticula from the right caecum; dh, dorsal hood; h, heart; hg, hindgut; k, kidney region; mg, midgut; o, oesophagus; r, rectum; ss, style-sac). **B**, four different midgut tracts found in different specimens.

expanding oesophagus. After this, the two anterior retractor muscles contract and pull the foot slightly back. The pressure exerted by the retractors and foot upon the oesophagus forces material into the stomach.

The oesophagus opens into the globular stomach in its anterior dorsal wall. The conjoined style-sac and intestine open into the postero-ventral region of the stomach and pass ventrally toward the foot (Fig. 11A). The midgut arises from the distal end of this wider tube, and ascends parallel to the style-sac and posterior side of the stomach toward the pericardial cavity. In *Gari tellinella*, Graham (1934a) illustrated the midgut separating from the style-sac near its distal end, bending back on itself and, exhibiting two or three closely packed coils, passing along the posterior part of the style-sac towards the hinder-end of the stomach.

Yonge (1949) observed in the Tellinacea that there is considerable variation in the degree of coiling, i.e. in the total length of the midgut. He observed that for *Donax vittatus* and *Gari tellinella* the midgut is quite short. Narchi (1978, 1980) observed the same in *D. hanleyanus* and *Asaphis dichotoma*. *Heterodonax bimaculatus* has a short midgut which exhibits considerable intraspecific variation (Fig. 11B): straight, or with one to four loose coils before it enters the pericardial cavity via its anterior wall. The hindgut passes through the pericardial cavity, traverses the ventricle and terminates in the anal papilla on the anterior face of the posterior adductor muscle.

STOMACH

The anatomy of the stomach of the genus *Heterodonax* (Fig. 12) is generally similar to that of other members of the Psammobiidae, but it is useful to describe and compare it with *Gari togata* (Deshayes, 1854) and *Asaphis deflorata* (Linné, 1758), adequately studied by Purchon (1960) and with *A. dichotoma* described by Narchi (1980).

The stomach lies dorsally and is surrounded laterally and ventrally by a thick layer of digestive diverticula and gonads. The oesophagus (o) enters the stomach antero-dorsally, its orifice into the stomach being marked ventrally by a transverse, lobed ridge (rm), which represents the swollen extremities of numerous, well defined longitudinal folds. The combined style-sac (ss) and midgut (mg) leave the postero-ventral wall of the stomach. The minor intestinal typhlosole (mt) terminates at the mouth of the midgut. The major typhlosole (ty) consists of two distinct parts. There is a stiff, raised semicircular elevation (e), which curves to the left over the floor of the stomach, the upper surface of which is lined by the gastric shield (gs) and shows no ciliary activity. Under the margin of this shelf, cilia beat strongly towards the orifice of the left caecum (lc); this ridge is not accompanied by an extension of the intestinal

groove and cannot be regarded as the major typhlosole as Purchon (1960) defined when describing the stomach of *Gari togata*. The major typhlosole properly arises in the mouth of the midgut and passes forward over the floor of the stomach, accompanied throughout its course by the intestinal groove (ig). Contrary to what was observed with *G. togata*, *Asaphis deflorata* (Purchon, 1960) and *A. dichotoma* (Narchi, 1980), the major typhlosole does not send a semi-circular tongue into the right caecum (rc). Near to the mouth of the right caecum the major typhlosole forms a semicircular loop, runs transversely across the anterior floor of the stomach, and enters the left caecum (lc). Due to this feature, the stomach of the *Heterodonax bimaculatus* could not be classified as Type V of Purchon (1960). There are five to six ducts of the digestive diverticula opening into the right caecum. At the left caecum there are only three, and one of these ducts receives a flare from the major typhlosole. The major typhlosole extends to the apex of the left caecum, turns back and terminates at the orifice of the left caecum after describing a loose and incomplete spiral of about one and a half turn.

The dorsal hood (dh) is large and well defined, the lower border of its orifice being protected by a very stiff, saddle-shaped sheath of the gastric shield. A broad ridge (r) enters the dorsal hood on the anterior side of its roof, while two parallel slender ridges (r_1 , r_2) lie on the posterior side of the roof. Between the ridges r and r_1 there is a ciliated area on which material is driven downward, to the apex of the dorsal hood.

The appendix (ax) is a large and well defined, distensible, conical chamber. It opens into the stomach by a large orifice surrounded by irregularly parallel folds that penetrate deeply into it. The majority of these folds convey particles from the mouth of the dorsal hood inward to the appendix; a few of them, running on the right wall of the stomach remove particles from the appendix onto the style-sac. No sand grains were found inside the appendix. The function of this organ was discussed by Yonge (1949), Purchon (1960) and Reid (1965).

The left pouch (lp) lies antero-ventrally to the opening of the dorsal hood; the posterior border of its mouth is protected by a stiff, saddle-shaped flare of the gastric shield. The left pouch passes backward under the dorsal hood. About nine ducts enter the left pouch from the digestive diverticula on the left side of the body. A sorting area of extremely fine striations (sa_6), divided into two bands, lies on the left anterior floor of the stomach and penetrates deeply into the left pouch. One band runs close to the wing of the gastric shield; at the distal end of the left pouch its striation invades the aperture of ducts of the digestive diverticula. The other band runs at the anterior wall of the left pouch where remaining ducts open. The ciliary currents on

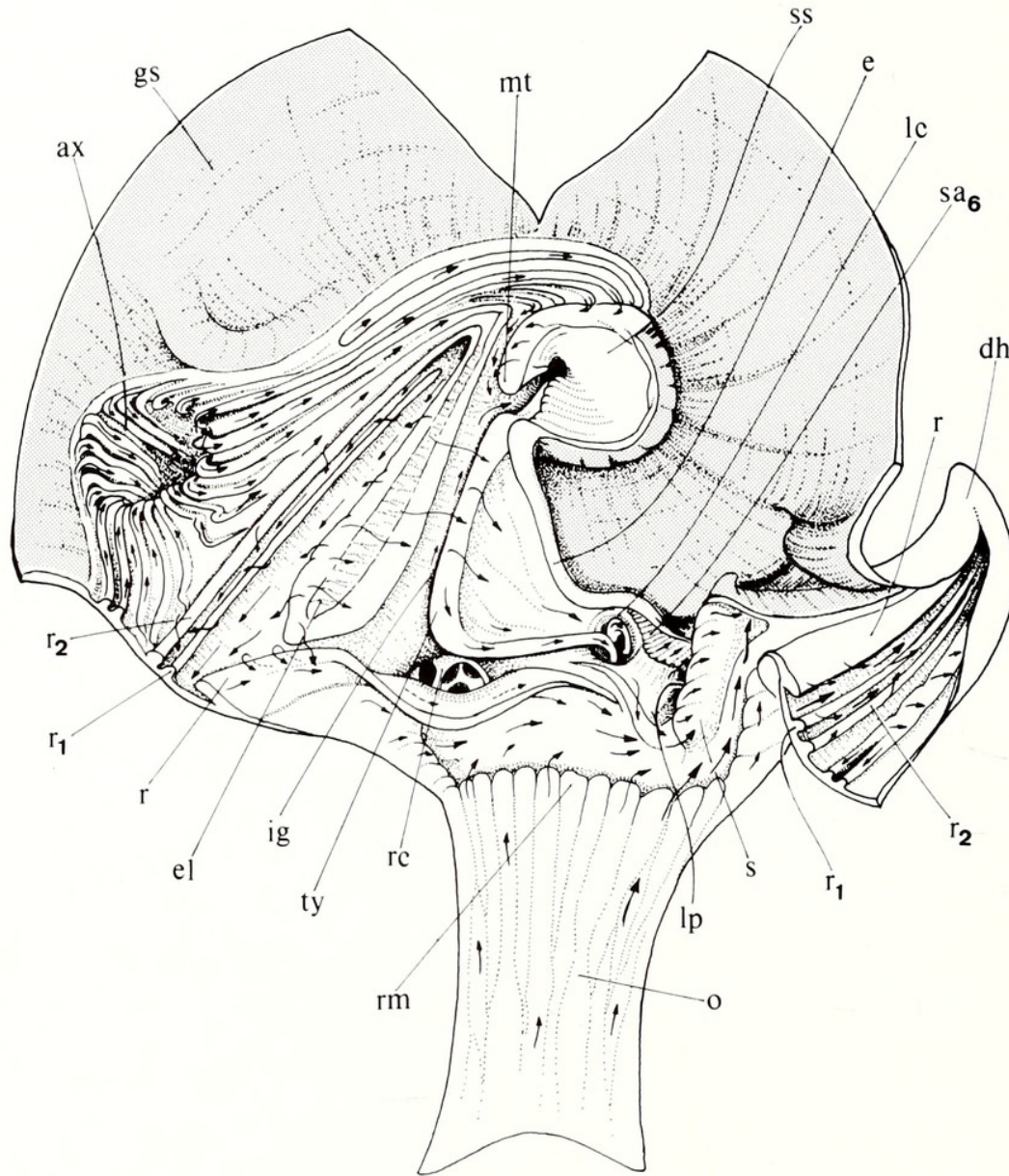


Fig. 12. *Heterodonax bimaculatus*. Interior of the stomach after its opening by an incision in the dorsal wall (ax, appendix; dh, dorsal hood; e, raised semicircular elevation; el, long forwardly projecting tongue; gs, gastric shield; ig, intestinal groove; lc, left caecum; lp, left pouch; mg, midgut; mt, minor typhlosole; o, oesophagus; r, broad ridge; r₁, r₂, ridges on the posterior wall of the dorsal hood; rc, right caecum; rm, rim to the oesophageal orifice; s, swelling of the left anterior wall of the stomach; ss, style-sac).

these two regions of sac always convey particles dorsalward; at the apertures of the ducts, cilia beat outward.

A broad swelling (s) on the left anterior wall of the stomach isolates the apertures of the left pouch and dorsal hood; its ciliary currents remove particles from the mouth of the left pouch into the dorsal hood. Together with the broad ridge "r" it forms an efficient barrier against the free passage of material coming from the oesophagus to the cavity of the stomach. Reaching the ridge "r", isolated particles from the oesophagus are driven to the left, then into the dorsal hood via a ciliary tract on the dorsal side of the

broad swelling (s).

The parallel ridges "r₁" and "r₂" emerging from the dorsal hood pass downward over the roof and right wall of the stomach ending up near the opening of the midgut. A "U"-shaped ventral tongue (el), similar to those described in *Gari togata*, *Asaphis deflorata* (Purchon, 1960) and *A. dichotoma* (Narchi, 1980), lies to the right and ventrally to ridges "r₁" and "r₂". The particles on its dorsal margin are driven to the gutter between "el" and "r₁" and then to the dorsal hood. Elsewhere, the cilia on the tongue pass particles to the intestinal groove (ig) or over the major typhlo-

sole and then either to the right or left caecum.

The crystalline style projects into the stomach and is brown in colour. In living dissected animals with stomach, appendix and dorsal hood empty, the crystalline style could be seen through the stomach wall.

A few seconds after adding carmine suspension to the pallial organs, a red mucous strand reached the stomach. Rotation of the style causes the material to be carried downward, toward the floor of the stomach. The crystalline style rotates in a clockwise direction when viewed from the anterior end, and the observed speed varied from 13 to 16 r.p.m. at 20°C and attained 26 r.p.m. at 21.5°C. Five minutes later, the red particles were driven by cilia from the floor and right wall of the stomach to the dorsal hood. Next, the appendix started to become red, giving clear evidence that it received particles from the dorsal hood. Thirty minutes after the beginning of the experiment, the foregut was stained red.

An extremely viscous mass with amorphous material was observed within the stomach of living dissected specimens and in fixed animals. The viscous mass that filled the stomach extended to all corners of this organ and few mineral grains (up to 0.2 mm) and entire diatoms (0.08 mm) were found.

DISCUSSION AND CONCLUSIONS

Heterodonax bimaculatus is an intertidal species living shallowly buried in sand or gravelly sand, in protected bays. A similar habitat is occupied by *H. ludwigii* (Boss, 1969) and *H. pacificus* (Keen, 1971; Coan, 1973). Broekhuysen and Taylor (1959 cited by Boss, 1969) obtained *H. ludwigii* in a sand bar in the estuary at Kosi Bay. According to Boss (1969), this latter species has "a preference for estuarine conditions with a considerable amount of suspended matter". At Codó Beach, the circulating water inside Flamengo Creek often keeps a large amount of fine organic matter in suspension.

As in the species of *Gari*, representative of the British seas (Yonge, 1949), *Heterodonax bimaculatus* seems to be specially adapted to the sandy or sandy gravel substrata, because it occurs only intertidally on Codó Beach. Its presence on the ripple sand bars formed on the sublittoral zone could be accidental. Specimens buried on the border between the sand beach and clay sand zone, or those less efficient in their ability to burrow quickly in the sand zone, could be scoured out of their natural habitat and transported into the sublittoral.

Heterodonax bimaculatus presents some features typically found in clams that inhabit unstable sediments. As with *Donax hanleyanus* (Narchi, 1978) and *Mesodesma mactroides* (Narchi, 1981), it has a wedge-shaped smooth

shell and a well developed and active foot. The elevator pedis muscle, characteristic of these high speed burrowing bivalves and correlated with the habit of burrowing in firm sand (Yonge, 1949; Narchi, 1978), is lacking in *H. bimaculatus*.

Atkins (1937a) classified *Gari tellinella* as a deposit feeder; Yonge (1949) observed the inhalent siphon of this species and *G. fervensis* opening widely for the passive intake of loose surface deposit and suspended material. Conflicting statements concerning the nature of feeding in the Tellinacea received exhaustive consideration by Pohlo (1969, 1982), Reid and Reid (1969) and Reid (1971).

According to the criteria for feeding types in bivalves, *Heterodonax bimaculatus* is a suspension feeder, more precisely a non-selective suspension feeder in Pohlo's (1982) classification. The clam possesses large ctenidia relative to the labial palps, which are small and characteristically with few folds; the outer demibranchs are not reflected although they are provided with a wide supra-axial extension; ctenidia type C (Ia) (Atkins, 1937a) (slightly modified) with a well-developed marginal groove on the inner demibranch; a waste canal (Kellogg, 1915) absent; a vertical orientation in the burrow and only finger-like non straining tentacles around the inhalent aperture.

As in the donacids *Egeria radiata* (Purchon, 1963), *Iphigenia brasiliensis* (Narchi, 1972) and *Donax* itself (Yonge, 1949), the siphons of *Heterodonax bimaculatus* are relatively shorter and wider compared with most extant tellinaceans (particularly the deposit feeders Tellinidae, Scrobiculariidae and some Semelidae). In the species with shorter and wider siphons the inhalent current caused by the beating of the lateral cilia on the ctenidia is less concentrated and correspondingly less powerful (Yonge, 1949). *H. bimaculatus* is unable to tear off bottom material and suck it in actively as do the specialized deposit feeders, hence the clam deals with less pseudofaeces and these are expelled by the usual route, through the inhalent siphon, without the protection of a pair of folds that prevent the pseudofaeces from being washed forward by the very concentrated inhalent current.

In addition to the loss of ramified straining tentacles, the passive behaviour of the inhalent siphon which is kept well clear from the sediment surface seems to corroborate the suspension feeding habit of *Heterodonax bimaculatus*. Despite this, the clam may derive part of its nutritional requirements from loose surface deposits as well as from the dense deposited material. This latter is achieved passively when the inhalent aperture is kept widely open, or at slightly below, the sediment surface. At these times surrounding benthic organisms and sand grains may fall into the pallial cavity.

The presence of specialized large frontal cilia (rc,

rc₁) on the frontal surface of the filaments of the inner demibranchs is evidence that *Heterodonax bimaculatus* deals with large particles inside its pallial cavity. These stout frontal cilia are undoubtedly a specialization for removing unwanted material, such as sand grains from the lamellae (Atkins, 1937; Narchi, 1972). The bivalves described as possessing them are all sand dwellers, silty sand dwellers or borers in rock or wood (Atkins, 1937). These cilia in *H. bimaculatus* seem to be efficient in their function since only few and minute (up to 0.2 mm) mineral grains were found inside the stomach of one specimen examined for this purpose.

In *Heterodonax bimaculatus* the marginal groove on the inner demibranchs possesses fine guard cilia in common with *Gari tellinella* and *G. fervensis* (Yonge, 1949) and a wide variety of other Filibranchia and Eulamelli-branchia listed by Atkins (1937), most of which inhabiting silty or muddy substrata. According to this author, guard cilia are presumably efficient in dealing with the particles of a muddy soil, but not sufficiently robust when coarse material has to be dealt with.

At Codó Beach not only the layer subjacent to the superficial clean sand contains a large amount of silt but so does the circulating water, which may sporadically remove and transport mud particles from the sublittoral zone. Having both large frontal and guard cilia, *Heterodonax bimaculatus* is adapted to deal simultaneously with fine and coarse material present in its environment.

The observations made in the laboratory with the clam ingesting pieces of their own tissues, suggests that it is able to regulate the sorting mechanisms in the pallial cavity. Submitted to a dense inhalent current the animal can reject the excess of material. If the surrounding water is scanty in food material *Heterodonax bimaculatus* can retain and ingest even those large particles usually rejected. The small size of the palps and their reduced number of sorting folds could represent a simplification to facilitate an acceptance of large particles.

The large ctenidia of *Heterodonax bimaculatus* are responsible for the principal selection before material is passed to the palps; so, the palps could be maintained as small as possible with little contribution to the sorting devices inside the pallial cavity. The intense muscular activity of the palps, which roll up or bend at the sides to touch the visceral or mantle epithelium, contributes respectively to discharge the excess of material or to capture useful particles travelling ventralward on those epithelia.

Some species of the Psammobiidae were classified as deposit feeders by Hunt (1925) and Atkins (1937a), non-selective by Pohlo (1982) or even suspension feeders by Yonge (1949). According to Pohlo, the non-selective feeding type as observed in the family Solecurtidae and

Psammobiidae and in some species of the Donacidae, represents an intermediate stage of the evolution of the tellinaceans from a selective suspension feeding ancestral to a final stage represented by the specialized deposit feeders.

The alimentary canal of *Heterodonax bimaculatus* is similar to that of *Gari tellinella* (Graham, 1934a), and the stomach resembles that of the Tellinidae and Semelidae (Yonge, 1949) in relation to the presence of a straight style-sac with an associated intestinal groove and in the presence of an appendix. The internal anatomy of the stomach resembles that of *G. togata* and *Asaphis deflorata* studied by Purchon (1960) and *A. dichotoma* described by Narchi (1980), differing only in a few aspects.

The large and distensible appendix of *Heterodonax bimaculatus* differs from that of *Gari togata*, described by Purchon (1960) as a pear-shaped chamber opening into the stomach by a slender, smooth walled neck. Purchon (1960) and Narchi (1980) referred to the appendix of *Asaphis deflorata* and *A. dichotoma*, respectively, as a capacious sac, with the opening into the stomach guarded by two large flashy pads and flanked by two sorting areas (SA 11) of irregularly parallel folds, which do not penetrate into the appendix. Ciliary currents in that sorting area beat inward, passing material into the appendix; no outward ciliary currents were found by these authors. *H. bimaculatus* presents all around the mouth of the appendix only parallel folds penetrating deeply into the organ. Outward ciliary activity was detected on some of those parallel folds running on the right wall of the stomach.

As stated by Purchon (1960) and confirmed by Reid (1965), the real function of the appendix is for temporary storage of exceptionally large particles which have escaped rejection by the sorting mechanisms of the pallial cavity. In *Heterodonax bimaculatus*, very fine particles of carmine were found in the appendix. Its emptying is carried out by ciliary activity and it is possibly aided by muscular contraction of its walls, as proposed by Purchon (1960) for *Asaphis deflorata*.

In the stomach of *Heterodonax bimaculatus* there are not bead-like swellings in front of the broad ridge "r" which extends up to the right wall of the stomach into the dorsal hood, as well as any series of shallow blind pockets close to the mouth of the style-sac and midgut, present in *Gari* (Purchon, 1960).

Purchon (1960) stated that the type IV stomach is more primitive and possibly ancestral to type III and type V stomachs. Through a process of "juvenilization", i.e. by a reduction in size of individuals accompanied by a general simplification of parts of the organs, which if including a withdrawal of the tongues of the major typhlosole from association with the ducts of the digestive diverticula, stomach type V could revert to the ancestral type IV. According

to Purchon (1960), this theory could be advanced to account for the occurrence of a type IV stomach in the eulamellibranch families Sphaeriidae, Thyasiridae and in *Chama multisquamosa* (Chamidae). The type IV stomach of *Heterodonax bimaculatus* could represent a similar, and so far the only known, such reversion in the Psammobiidae.

In a revision of the basic form and adaptations of the Lucinacea, Allen (1958) admitted the occurrence of a simplification in the stomach of Thyasiridae and Lucinidae, accomplished by the loss of sorting areas and reduction of the number of apertures leading from the stomach to the digestive diverticula and an increase in the size of these apertures. This simplification occurred to facilitate the acceptance of large particles, since the animals live in an environment where the food supply is so low that all available particulated food has to be accepted. Thus the findings of Allen (1958) for the Lucinacea fit in well with the views expressed by Purchon (1960).

The simplicity of the stomach of *Heterodonax bimaculatus* expressed by the presence of only a few and poor sorting areas, in addition to the simplicity of the labial palps and the voracity exhibited in the laboratory, suggest a convergence with the Lucinacea. Purchon (1960) considered the paucity and the simplicity of the sorting areas of the stomach of *Gari togata* as being probably correlated with the unusually high viscosity of the stomach contents, which prevents individual particles from being brushed against the ciliary sorting area.

According to Pohlo (1982), the type IV stomach is also the ancestral condition from which the type V stomach evolved. This point of view is supported by the presence in the extant Donacidae (*Donax*), which he considered as retainers of more ancestral features of a type IV stomach. From a *Donax*-like stage with a selective mode of suspension feeding, evolution then proceeded to less selective suspension feeding as seen in some Donacidae and also in the Solecurtidae and Psammobiidae. The stomach also shows an advance to type V (Pohlo, 1982), a stage present in some of the Donacidae, e.g. *Donax trunculus* (Moïeza and Frenkiel, 1976), *Egeria radiata* (Purchon, 1963), *Iphigenia brasiliensis* (Narchi, 1972) and *D. hanleyanus* (Narchi, 1978). This stomach type then remains throughout the rest of the superfamily (Pohlo, 1982).

From Pohlo's (1982) point of view, *Heterodonax bimaculatus* can be regarded as being near the ancestral condition in the Tellinacea and so, at the base of the Psammobiidae lineage, since it has retained a type IV stomach and the majority of its anatomical features relate to a selective suspension feeding behaviour except in the absence of straining tentacles around the inhalent aperture.

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