Bolm. Zool., Univ. S. Paulo
3:121-142, 1978

FUNCTIONAL ANATOMY OF *DONAX HANLEYANUS* PHILIPPI 1847 (DONACIDAE – BIVALVIA)

Walter Narchi
Department of Zoology
University of São Paulo, Brazil

ABSTRACT

Donax hanleyanus Philippi 1847 occurs throughout the southern half of the Brazilian littoral. The main organ systems were studied in the living animal, particular attention being paid to the ciliary feeding and cleasing mechanisms in the mantle cavity. The anatomy, functioning of the stomach and the ciliary sorting mechanisms are described. The stomach unlike that of almost all species of *Donax* and like the majority of the Tellinacea belongs to type V, as defined by Purchon, and could be regarded as advanced for the Donacidae.

A general comparison has been made between the known species of *Donax* and some features of *Iphigenia brasiliensis* Lamarck 1818, also a donacid.

INTRODUCTION

Very little is known of donacid bivalves from the Brazilian littoral. Except for the publications of Narchi (1972; 1974) on *Iphigenia brasiliensis* and some ecological and adaptative features on *Donax hanleyanus*, all references to them are brief descriptions of the shell and cheklists drawn up from systematic surveys.

Beach clams of the genus *Donax* inhabit intertidal sandy shores in most parts of the world. *Donax hanleyanus* Philippi 1847 is one of four species occuring throughout the Brazilian littoral. Its known range includes Espirito Santo State and the southern Atlantic shoreline down to Uruguay (Rios, 1975). According to Penchaszadeh & Olivier (1975) the species occur in the littoral of Argentina.

The species is fairly common in São Paulo, Parana and Santa Catarina States where it is used as food by the coastal population (Gofferjé, 1950), and is known as "naninî" It is known by the name "beguara" (Ihering, 1897) in the Iguape region, but not in S. Sebastião (Morrison, 1971). Magnanini and Coimbra Filho (1964) recorded the name 'semambi", earlier used by Ihering (1968) for *Mesodesma mactroides.*

The shell is extremely variable in shape, size, color and sculpture. These animals are interesting chiefly because they maintain great populations in the relatively unstable environment of exposed wave-swept beaches.

There are many references to *Donax* in the literature through most of the published research concerns a few specific topics c.g. tidal migrations (Mori 1938, 1950; Turner & Belding, 1957; Trueman, Brand & Davies, 1966; Ansell & Trevallion, 1969; Irwin, 1973), life history (Wade, 1968), anatomy (Wade, 1967a, Pohlo, 1967; Moueza 1976; Moueza & Frenkiel 1974, 1976) and ecology (Coe, 1955; Loesch, 1957; Wade, 1967; Degiovanni & Moueza, 1972; Moueza 1972; Irwin, 1973; Penchaszadeh & Olivier, 1975) of some species of *Donax*. Hitherto no research dealing with aspects of the functional morphology of *D. hanleyanus* has been undertaken.

Wade (1967, 1967a, 1968 and 1969) made an extensive study of *D. denticulatus* and *D. striatus,* both from the Atlantic littoral. Pohlo (1967) studied some aspects of the biology and discussed the adaptations that allow *D. gouldi* to occupy the surf zone. Penchaszadeh & Olivier (1975) made an ecological study of *Donax hanleyanus* in Villa Gesell, Argentina. It would be of interest, therefore, to make a study of the functional morphology of *D. hanleyanus* and to compare this species with other donacids.

Living specimens were obtained from Itaguá beach, Ubatuba, on the coast of São Paulo State, Brazil.

Specimens were relaxed in isotonic magnesium sulphate. Ciliary currents were studied using fine carborundum, carmine suspensions or suspensions of Aquadag. Sections of 6 μm to 8 μm were made of tissues fixed in Bouin's fluid and stained with Ehrlich's haematoxylin and eosin. Heidenhain's Azan or Mallory's triple stain.

The sand samples from Itaguá beach were air dried and subjected to grade analysis by mechanically shaking 50 gr. portions in the "Rop-Tap Testing Sieve Shaker and Tyle Timer L.125"

I would like to thank Professor R. Tucker Abbott, Delaware Museum of Natural History, Greenville, Delaware, for his kindness in confirming the identity of specimens of *D. hanleyanus* Philippi, 1847.

ECOLOGICAL NOTES

Donax hanleyanus inhabits wave-swept sandy beaches (Fig. 1) and it is one of the most widespread and common intertidal clams in São Paulo. These bivalves are constantly flushed out of the sand by the pouding surf. Their ability to overcome the stresses of the environment is based on rapid burrowing: *D. hanleyanus,* like *D. denticulatus* (Wade, 1967), may completely bury itself in under 2 seconds.

The beach clams are adapted to life on exposed shores and they do not occur on protected beaches or in shallow bays. The clams require an environment in which

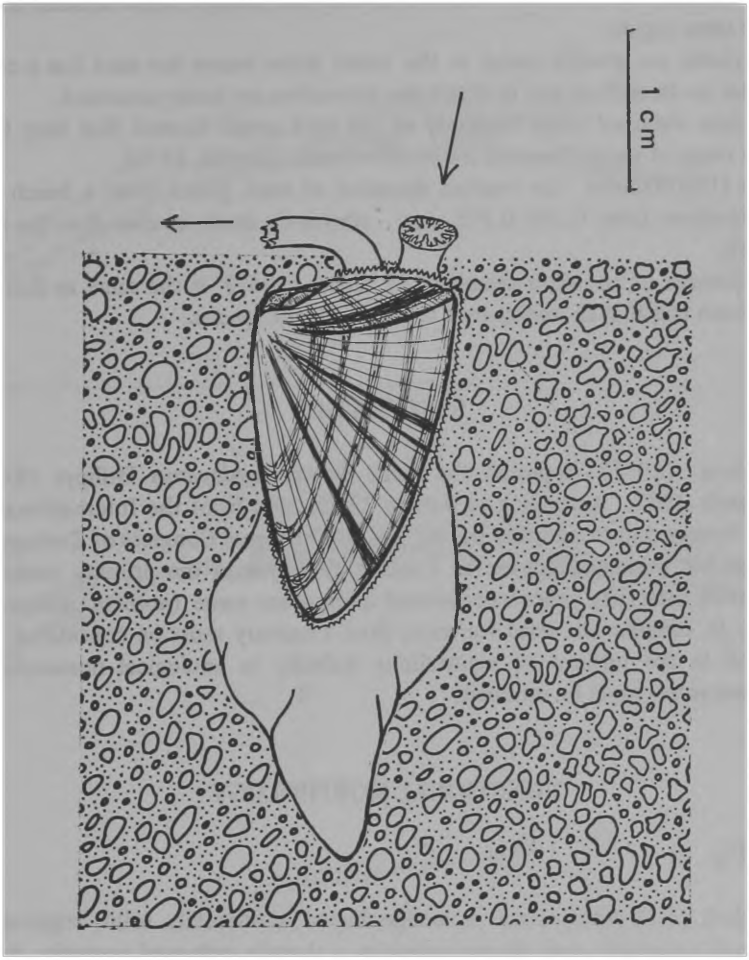


Figure 1 – ***Donax hanleyanus.*** **External view of the left side. Living specimen with ornamentated shell in the sand.**

there is a fair amount of wave action to keep the sand aerated and clean, to keep organic detritus in suspension and to permit tidal migration (Mori, 1938; 1950).

Itaguá beach shows a considerable surf beating on the shore but is relatively less exposed than other beaches in the Ubatura area. The slope of the beach is very steep in the place where the animals were collected. I observed that the ebbing tide leaves the clams high on the beach, as observed by Edgren (1959). At the lowest tide I found many clams in the sand, as much as 5 m above the low tide line. For Loesch (1957) this fact represents occasional individuals trapped into the sand.

Wade (1967) observed that when the surf beats on the shore, smaller clams being less efficient in their ability to anchor firmly in the sand and then to burrow quickly, tend to be flushed out more often and washed further up the beach than large specimens.

I have not observed this in the Ubatuba littoral and always found animals of different sizes in the same region.

The clams are always found in the lower shore where the sand has a continuous film of water on its surface and in which the interstices are water-saturated.

The data obtained from the study of the sand grains showed that they fall within the narrow range of mean diameter 0.074-0.147 mm (Narchi, 1974).

Wade (1967) found the median diameter of sand grains from a beach colonised by *D. denticulatus* from 0.150-0.375 mm; obviously much coarser than the sand from Itaguá beach.

The pattern of zonation described by Wade (1967) is the same as that observed at Itaguá beach and that *D. hanleyanus* is the dominant species.

SYSTEMATICS

Morrison (1971) replaced the name *Donax hanleyanus* Philippi 1847, by *D. hilairea* Guerin 1832. According to Article 23, Section b, of the International Code of Zoological Nomenclature adopted by the XV International Congress of Zoology (1964), a name that has remained unused as a senior synonym in the primary zoological literature for more than fifty years is considered a forgotten name (*nomem oblitum*).

Thus, *D. hilairea* not used for more than a century must be considered a *nomem oblitum* and in the interest of maintaining stability in zoological nomenclature, the name *D. hanleyanus* must be retained.

FUNCTIONAL MORPHOLOGY

The shell (Fig. 2)

The shell of *D. hanleyanus* is wedge-shaped, moderately solid, trigonal in outline, produced anteriorly and characterized by a sharply carinated posterior ridge. The entire surface is sculptured with radial riblets, those on the disk faint, flat and narrow, those on the posterior truncation thinner and much more distinct. Crowded miscroscopic concentric striae traverse the surface, being much more distinct in the intercostal spaces of the posterior slope than elsewhere. The ventral margin is crenulate.

The adductor muscle scars are distinct, the anterior narrowly pyriform, the posterior transversely oval. The pallial sinus is U-shaped; the pallial line being close to the shell margin posteriorly and more remote anteriorly. The color is dull white or sometimes buff with concentric bands and stripes of gray, lavender or pale purple; usually presenting a single or double ray of ground color diverging, sharply from the beak, the ray broadening to the base.

On the hinge plate there is an oval ligamental fosset under the beak. The cardinal teeth of the left valve are subequal, divergent and united above, the socket separating them being triangular. The lateral teeth are prominent, the anterior one long. On the right valve the central cardinal is stout, the anterior one minor.

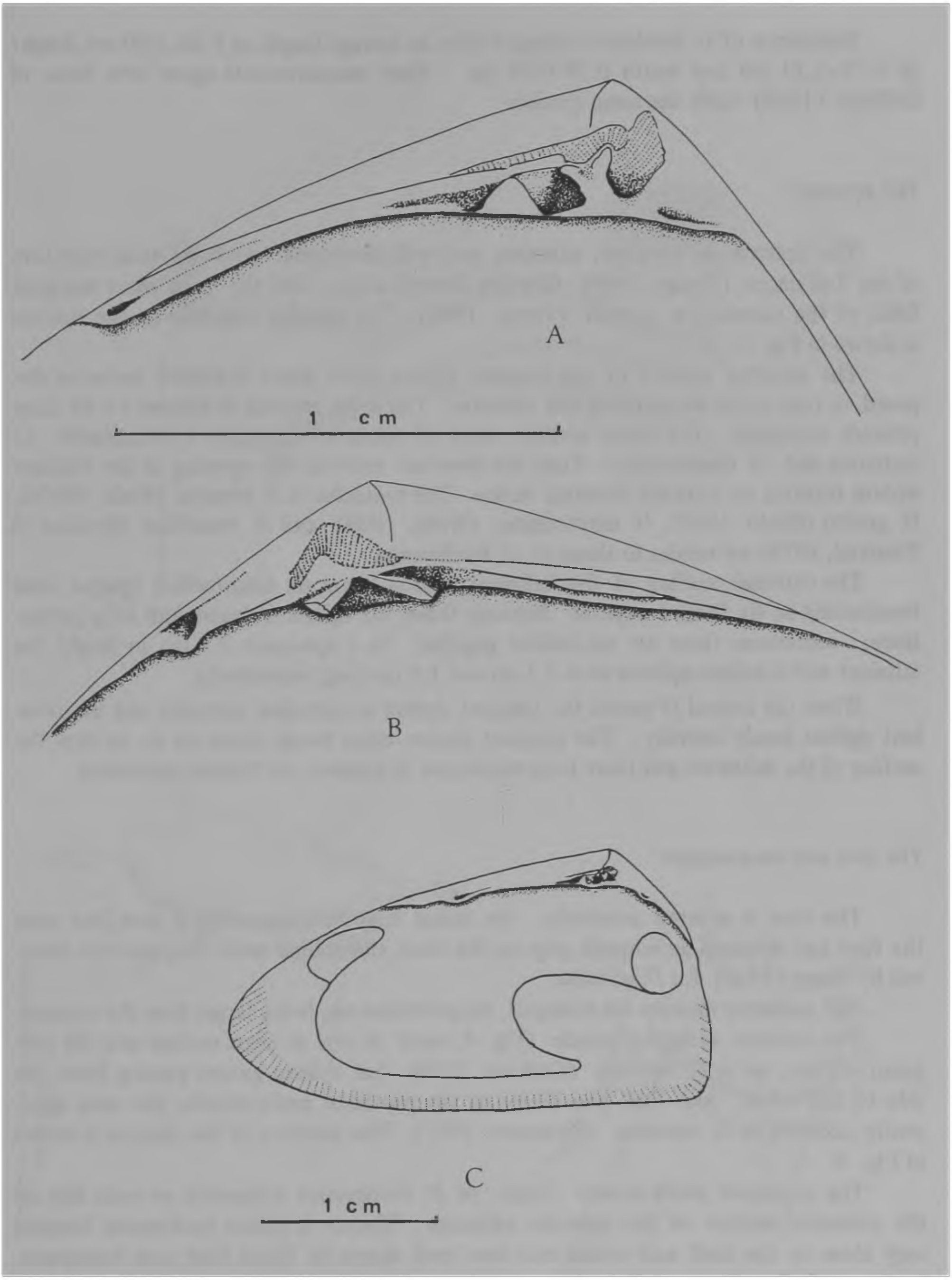


Figure 2 – ***Donax hanleyanus*****. Internal view of the hinge teeth. A, Right valve; B, Left valve. C, Right valve showing the pallial sinus and the adductor muscles scars.**

Specimens of *D. hanleyanus* ranged from an average length of 1.20-3.90 cm, height of 0.78-2.39 cm and width 0.38-0.89 cm. Such measurements agree with those of Gofferjé (1950) upon the same species.

The siphons

The siphons are separate, extensile and well developed. As in all other members of the Tellinacea (Yonge, 1949) they are formed solely from the fused inner marginal folds of the mantle i. e. type A (Yonge, 1948). The detailed structure of the siphons is shown in Fig. 3.

The external surface of the inhalant siphon bears many branched tentacles disposed in four series surrounding the aperture. The most internal is formed by six large primary tentacles. The three smaller series of tentacles comprise 6 secondaries, 12 tertiaries and 24 quaternaries. They are directed towards the opening of the inhalant siphon forming an intricate straining device. The tentacles of *D. striatus* (Wade, 1967a), *D. gouldi* (Pohlo, 1967), *D. denticulatus* (Wade, 1969) *and D. trunculus* (Mouëza & Frenkiel, 1974) are similar to those of *D. hanleyanus.*

The external surface of the exhalant siphon bears six longitudinal opaque lines terminating in six fringed papillae. Between these, the siphon is ringed with frilly projections; sometimes there are six smaller papillae. In a specimen 2.7 cm in lenght the inhalant and exhalant siphons were 2.2 cm and 1.5 cm long respectively.

When the animal is buried the inhalant siphon is extended vertically and the exhalant siphon bends laterally. The inhalant siphon never bends down on to, or over the surface of the substrate and there is no movement to explore the bottom sediments.

The foot and musculature

The foot is pointed anteriorly; the initial stages of burrowing is slow, but once the foot has obtained an adquate grip on the sand, the animal soon disappears as observed by Yong (1949) for *D. vittatus.*

The adductor muscles are subequal, the posterior one being larger than the anterior.

The anterior adductor muscle (Fig. 4, aam) is oval in cross section and the posterior surface, as in *D. vittatus* (Graham, 1934) has a deep groove passing from one side to the other; into this, pass fibres of the protactor pedis muscle, the same apparently occuring in *D. cuneatus* (Pelseneer, 1911). The position of the muscles is shown in Fig. 4.

The protactor pedis muscle (app) of *D. hanleyanus* is inserted on each side on the posterior surface of the anterior adductor. Thence it passes backwards, keeping very close to the shell and twists into two level sheets of fibres that turn backwards. Pohlo (1967) observed that the anterior protactor muscle of *D. gouldi* is split into three bands at the site of its insertion near the anterior adductor. The fibres from the external side spread out fanwise so as to cover a great part of the postero-dorsal region of the body. The fibres from the internal side spread out postero-ventrally.

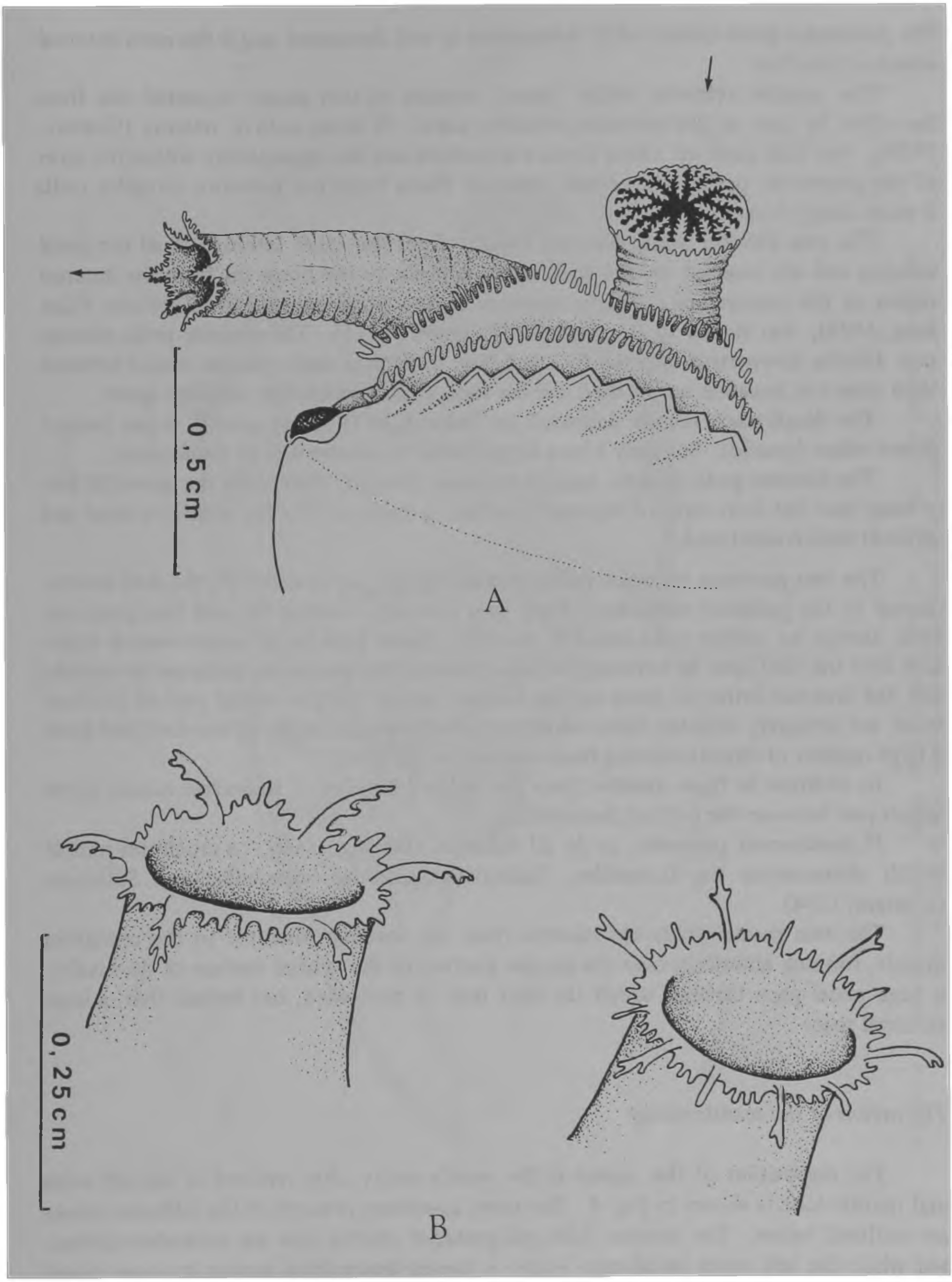


Figure 3 – *Donax hanleyanus.* **A** Appearance of siphons fully extended from between the shell valves. The inhalant siphon possesses branched tentacles around the inhalant aperture; **B** - The exhalant siphons of two individuals showing differences in structure.

The protractor pedis muscle of *D. hanleyanus* is well developed and is the most external muscle of the foot.

The anterior retractor pedis (arm) consists of two sheets separated one from the other, by part of the posterior retractor pedis. Of these, as in *D. vittatus* (Graham, 1934), one thin sheet of fibres is more superficial and lies immediately within the layer of the protractor pedis; the second sheet of fibres from the posterior retractor pedis is more deeply located in the foot.

The two elevator pedis muscles (epm) form the most internal of all the pedal muscles and are inserted on the shell valves anterior to the hinge far from the anterior region of the pericardium. This is contrary to the situation seen in *D. vittatus* (Graham, 1934), but similar to *D. cuneatus* (Pelseneer, 1911). The elevator pedis muscles pass directly downwards into the foot and fuse to form a single median muscle between their points of insertion on the shell and the foot, within which they separate again.

The demibranch muscle described by Pohlo (1967) for *D. gouldi,* is not present in any other donacids. Similarly I have been unable to observe it in *D. hanleyanus.*

The elevator pedis muscle, as in *D. vittatus* (Yonge, 1949) aids the animal in burrowing into the firm sand of exposed beaches, a mode of life for which its stout and smooth shell is also fitted.

The two posterior retractor pedis muscles (rpm) are inserted on the shell antero--dorsal to the posterior adductor. They pass ventrally towards the mid line, join, and then diverge to reform right and left muscles. These pass in an antero-ventral direction into the foot, and lie between the inner sheet of the protractor pedis on the outside and the anterior retractor pedis on the median aspect. In the ventral part of the foot there are obliquely directed fibres which extend the whole length of the foot and form a large number of strands crossing from one side to the other.

In addition to these muscles there are isolated bundles of transverse muscle fibres which pass between the coils of the intestine.

D. hanleyanus possesses, as do all tellinids (Ihering, 1900), a cruciform muscle which characterises the Donacidae, Tellinidae, Semelidae, Asaphidae and Solenidae (Graham, 1934).

The two mantle folds are separate from the anterior adductor to the cruciform muscle, forming anteriorly over the greater portion of the ventral surface of the bivalve, a large pedal gape through which the foot may be protruded, and behind that, a large siphonal space.

The organs of the mantle cavity

The disposition of the organs in the mantle cavity after removal of the left valve and mantle lobe is shown in Fig. 4. The more important features of the different organs are outlined below. The siphons, foot and posterior mantle lobe are somewhat contracted while the left outer labial palp (olp) is turned upwards to expose its inner ridged surface. The ctenidia were not touched and lie in the position they had when the animal was opened. The adductor muscles are sub-equal with the posterior muscle rounded in cross section.

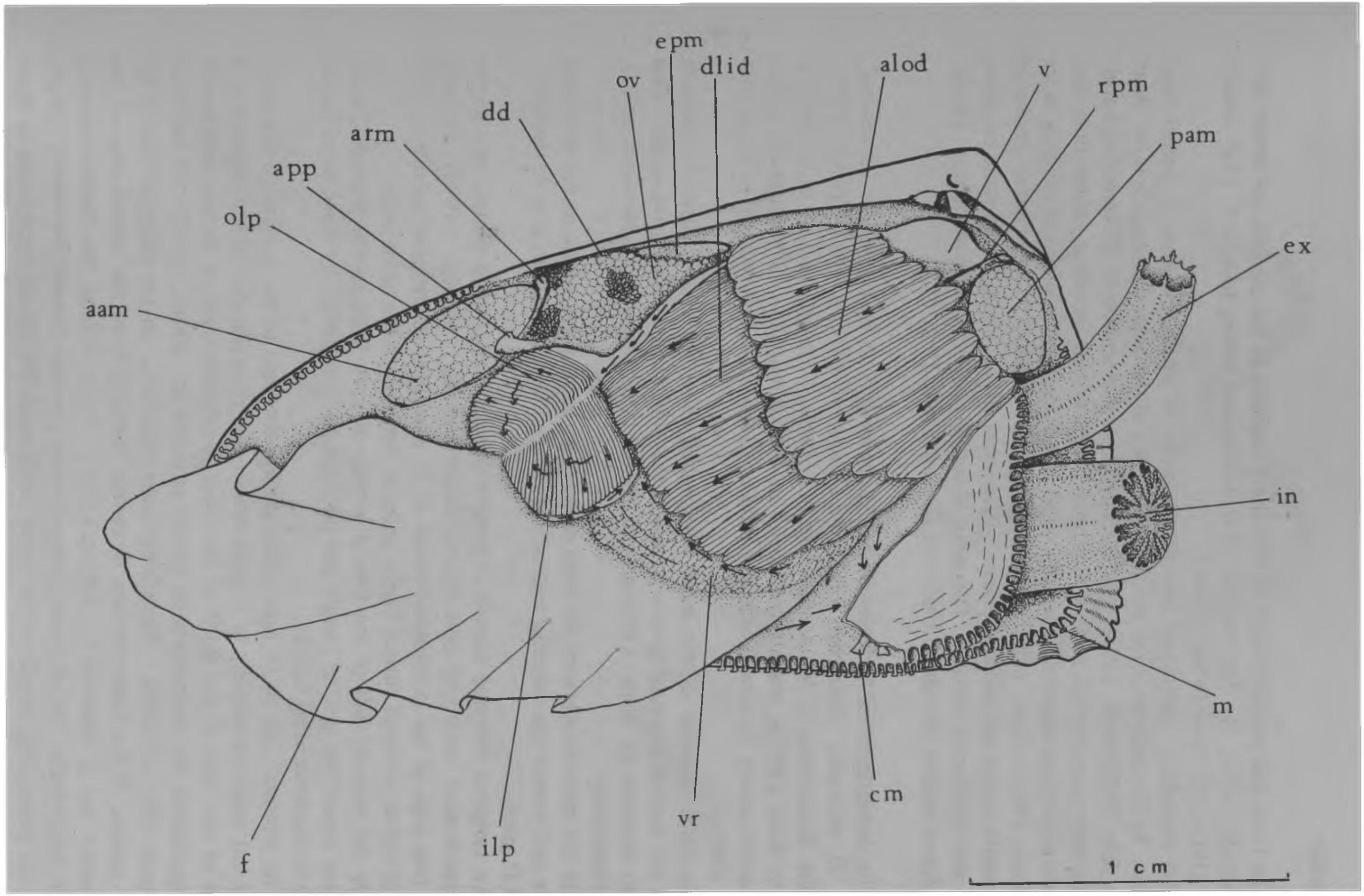


Figure 4 – ***Donax hanleyanus.*** **Matle cavity** viewed from the left side after removal of the left shell valve and mantle lobe. Arrows show direction of ciliary currents.

The ctenidia

The form and general course of the ciliary currents of the ctenidia are shown diagrammatically in Fig. 4. The ctenidia of *D. hanleyanus* belong to type C (1a) described by Atkins (1937) for *Donax vittatus.*

The ctenidium consists of two demibranchs of which the inner is deeper than the outer. In *D. hanleyanus* the descending lamella of the outer demibranch is not short as in *D. faba* (Ridewood, 1903); there is a supra-axial extension of the ascending lamella of the outer demibranch so that the total height of this lamella is greater than that of the corresponding descending lamella. The ascending lamella of *D. variabilis* is larger (Ridewood, 1903). Rice (1897) observed that flat lamellae occur in some species of *Donax* while others are broadly plicate. Pelseneer (1911) found, in the same lamellae, plicate and nonplicate regions. The same situation occurs in *D. denticulatus* (Wade, 1969), *Egeria radiata* (Purchon, 1963) and *D. hanleyanus* (Fig. 5).

The demibranchs of *D. hanleyanus* are homorhabdic as in *D. variabilis* (Ridewood, 1903), *D. trunculus* (Pelseneer, 1911) and *D. vittatus* (Atkins, 1937; Yonge, 1949). From the illustrations of the demibranchs of *D. serra, D. politus* and *D. trunculus* described by Rice (1897), these three species are also homorhabdic. The variability of the demibranchs cannot be related either to food or to the habitat preferences of the species (Wade, 1969).

On both lamellae of the inner demibranch there are ciliary currents, directed toward the ventral marginal groove in which the particles are transported orally. This was also observed by Wade (1967a) and Pohlo (1967) for *D. denticulatus* and *D. gouldi* respectively.

On the outer demibranch the main currents are toward the margin on the ascending lamellae and toward the ctenidial axis on the descending lamellae also as in *D. denticulatus* and *D. gouldi.*

An incipient oralward current is present along the ungrooved ventral edge of the outer demibranch caused by cilia beating antero-ventrally. Moueza (1976) observed at the free edge of the outer demibranch of *D. trunculus* an incipient groove. In the ctenidial axis an oralward current carries particles forwards to the labial palps.

On the anterior half of the frontal surface of each filament the frontal cilia are continuos around the ventral margin and particles are transported by these from the ascending to the descending lamella.

The terminal cilia in *D. hanleyanus* are not confined to the margins of the demibranchs but continue dorsally as a single row on the posterior side of the filament to a distance of one third of the depth of the inner demibranch as in *D. vittatus* and appear to be specialized for removing sand grains, as stated by Atkins (1937). In the outer demibranch they are scarce. These long stout cilia occur on the posterior side of the frontal surface of the filaments over a certain distance from the ventral edge of the demibranchs and as observed by Atkins (1937) for *D. vittatus* the distance varies in different individuals. On all lamellae they convey particles toward the ventral margin, and on the descending lamella of the outer demibranch the frontal currents are in opposite directions on the same filament, since the fine cilia on that lamella beat dorsally.

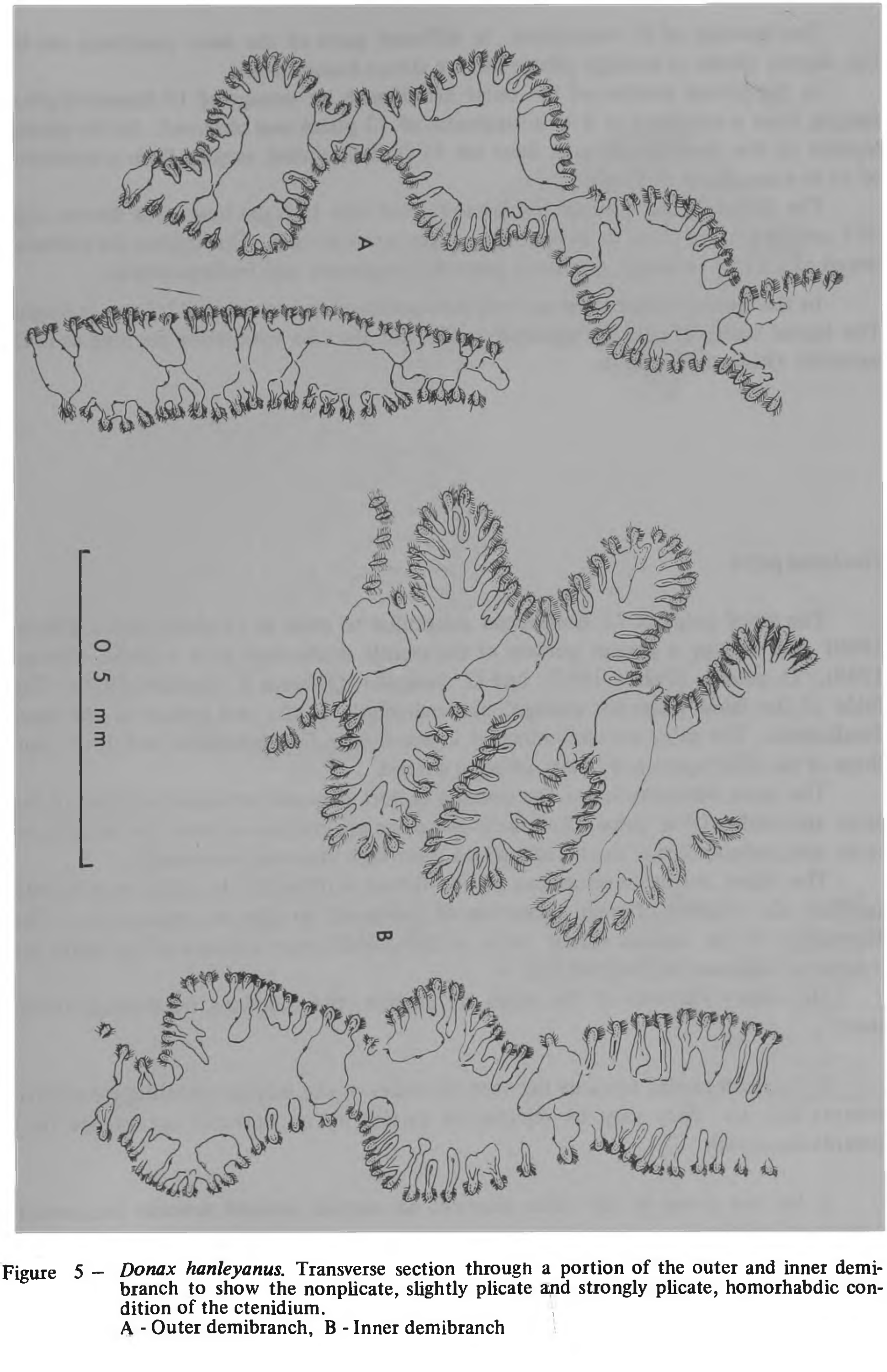


Figure 5 – ***Donax hanleyanus.*** Transverse section through a portion of the outer and inner demibranch to show the nonplicate, slightly plicate and strongly plicate, homorhabdic condition of the ctenidium.
A - Outer demibranch, B - Inner demibranch

The lamellae of *D. hanleyanus* in different parts of the same ctenidium can be flat, slightly plicate or strongly plicate but are always homorhabdic.

In the plicate portion of the outer demibranch an average of 10 filaments/plica, ranging from a minimum of 8 to a maximum of 12 plicae was observed. In the plicate portion of the inner demibranch there are 15 filaments/plica, ranging from a minimum of 12 to a maximum of 16 plica.

The filaments are bounded by latero-frontal cilia 13.6 µm long. The frontal cilia (0.7 µm long) give place to increasingly longer terminal cilia. Throughout the ctenidia, lateral cilia (11.8 µm long) produce a powerful respiratory and feeding current.

In the frontal region there are long stout cilia which may attain 22.7 µm in lenght. The lateral tracts of cilia are unusually wide and the cilia themselves are long as in *D. variabilis* (Ridewood, 1903).

The labial palps

The labial palps of *D. hanleyanus* are similar to those of *D. denticulatus* (Wade, 1969) and occupy a greater portion of the mantle cavity than in *D. vittatus* (Yonge, 1949), *D. gouldi* (Pohlo, 1967) and *D. trunculus* (Moueza & Frenkiel, 1976). The folds of the labial palps are arranged perpendicularly to the oral groove of the inner demibranch. The palps are semi-orbicular in shape as in *D. denticulatus* and differ from those of the other species of *Donax* hitherto studied.

The inner demibranchs of the ctenidia project forwards between the bases of the inner and outher labial palps. Anteriorly the palps are continuous with the smooth anterior and posterior lips of the mouth, which show slow muscular movements.

The ciliary sorting mechanisms on the folded surfaces of the palps were investigated by the addition of small quantities of powdered carmine or carborundum. The disposition of the various ciliary tracts of the folded inner surfaces of the palps are represented diagrammatically inf Fig. 6.

The ciliary currents of the palps are simples; the following tracts being recognized:

1. Particles carried towards the ventral border of the palp are eventually conveyed towards the tip. They may be rejected or carried by an oralward acceptance tract towards the mouth.

2. On the crests of the folds particles are carried forward towards the mouth, forming an oralward acceptance tract.

3. A re-sorting current, conveying particles dorsalwards, is present on the upper surface of the distal shelf of the fold.

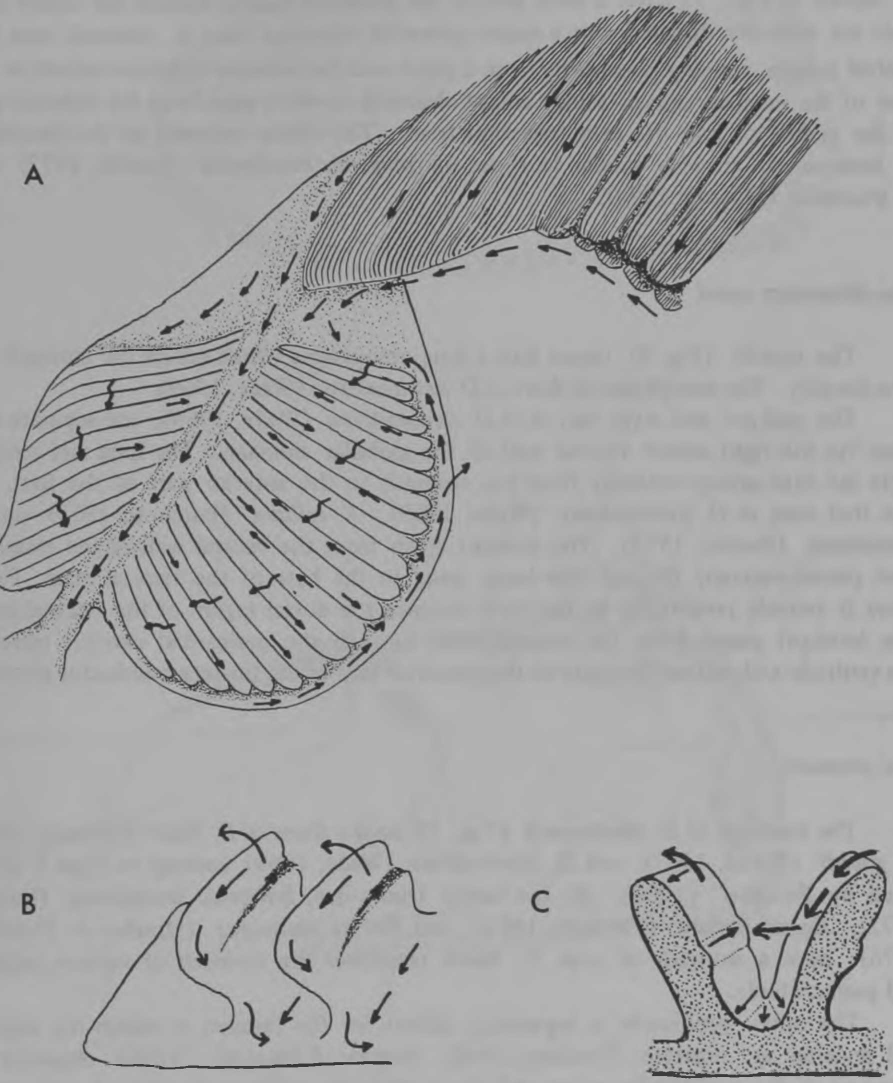


Figure 6 – *Donax hanleyanus.* A - Association of ctenidium and palp, showing detail of palp ciliation. B,C Diagrammatic representation of the ciliary mechanisms of the labial palps. The anterior end to the left.

The ciliary currents on the mantle

The surface of the mantle is covered with short cilia whose currents they engender are shown in Fig. 7. Over a wide area of the posterior mantle surface the ciliary currents are ventrally directed, 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 inhalant siphon. Minor ciliary cleansing currents pass from the anterior part of the mantle to join the main rejection tract. The ciliary currents on the mantle of *D. hanleyanus* are very similar to those of *Iphigenia brasiliensis* (Narchi, 1972) and *D. trunculus* (Mouëza, 1976).

The alimentary canal

The mouth (Fig. 8) opens into a long oesophagus which enters the stomach antero-dorsally. The oesophagus is short in *D. denticulatus* (Wade, 1969).

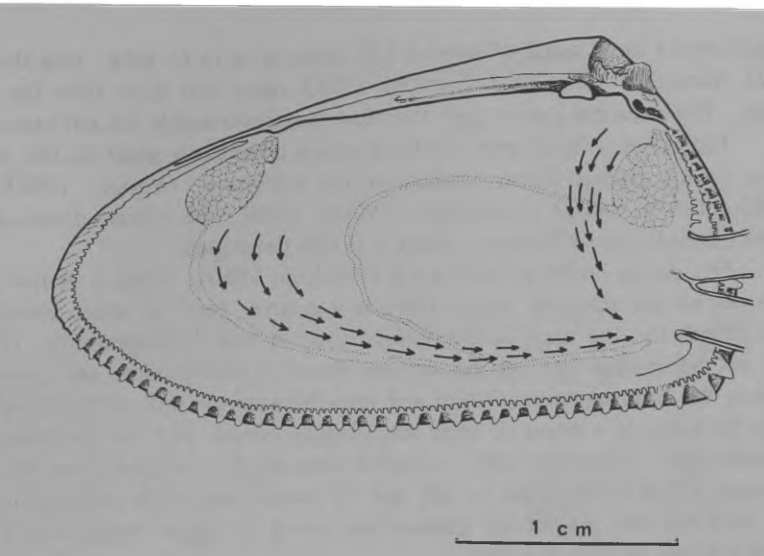
The mid-gut and style sac, as in *D. denticulatus* (Wade, 1969), are separate and open via the right antero ventral wall of the globular stomach. The long and straight style sac runs antero-ventrally from the stomach to the anterior part of the foot, unlike that seen in *D. denticulatus* (Wade, 1969), *E. radiata* (Purchon, 1963) and *I. brasiliensis* (Narchi, 1972). The mid-gut arises from the ventral wall of the stomach, then passes ventrally through one loose spiral to the base of the visceral mass. From there it ascends posteriorly to the style sac into the dorsal region of the visceral mass. The hind-gut passes from the visceral mass through the pericardial cavity, traverses the ventricle and ends at the anus on the posterior face of the posterior adductor muscle.

The stomach

The stomach of *D. hanleyanus* (Fig. 9) unlike those of *D. faba* (Purchon, 1960), *D. gouldi* (Pohlo, 1967) and *D. denticulatus* (Wade, 1969), belongs to type V as defined by Purchon (1960). In the family Donacidae, *Iphigenia brasiliensis* (Narchi, 1972), *Egeria radiata* (Purchon, 1963) and *Donax trunculus* (Mouëza & Frenkiel, 1976) have a stomach of type V, which resembles the stomach of various tellinids and psammobiids.

The minor typhlosole is apparently absent for the families in which the mid-gut and style-sac are separate (Purchon, 1960). Mouëza &Frenkiel (1976) observed the presence of the typhlosolis major and the typhlosolis minor in *D. trunculus, D. semistriatus* and *D. vittatus.*

The major typhlosole (ty) is well developed, arises in the aperture of the mid-gut (mg) and continues forward over the floor of the stomach, accompanied throughout its course by the intestinal groove (ig). Contrary to other species of *Donax*, and similarly the observed in *D. trunculus* (Mouëza & Frenkiel, 1976), it enters the right caecum (rc); into which open two ducts from the digestive diverticula. From the right caecum it traverses the anterior floor of the stomach to enter the left caecum (lc) in which



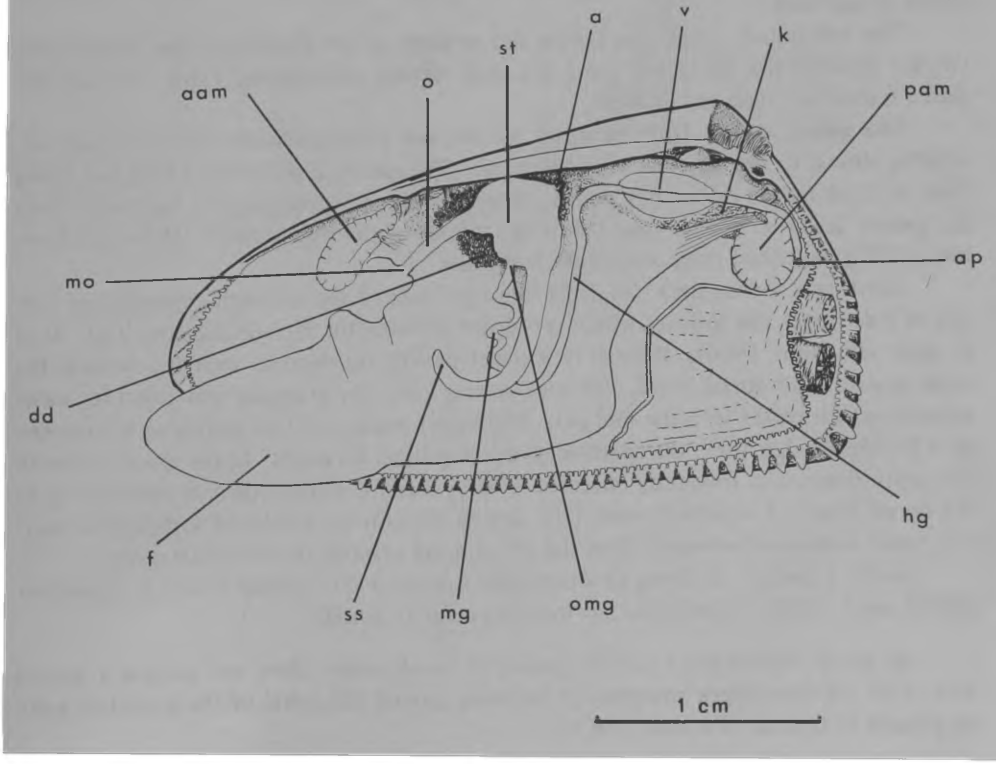


Figure 7 – ***Donax hanleyanus.*** Inner surface of the right mantle lobe to show the ciliary cleansing currents.

Figure 8 – ***Donax hanleyanus.*** The structure of the alimentary canal as seen from the left side.

it performs a loose spiral of some 1 1/2 turns, as in to *D. faba.* Into the left caecum as in *D. trunculus* (Mouëza & Frenkiel, 1976) open four ducts from the digestive diverticula. The intestinal groove (ig) therefore originates within the left caecum.

The postero-dorsal part of the stomach possesses a small sac-like appendix, equatable to the postero-dorsal caecum of the Tellinacea (Yonge, 1949). In *D. gouldi* (Pohlo, 1967) and *D. denticulatus* (Wade, 1969), the postero-dorsal appendix is also small but in *D. faba* (Purchon, 1960) it is well developed.

The dorsal hood, as in *D. faba* (Purchon, 1960), forms a shallow pocket on the left side of the stomach, where there is a groove (at) in which ciliary currents pass downwards to the apex of the dorsal hood. A well developed ridge (r) arises to the left of the median line on the anterior floor of the stomach and passes up the right wall of the stomach, over its roof and into the anterior wall of the dorsal hood. It projects forwards as a series of large and irregular pleats (fo) on the stomach wall on its anterior side. As in *D. faba,* material entering the stomach from the oesophagus is directed either to the right or left and its carried backwards into the dorsal hood over the roof and left side of the stomach and along the upper border of the thick roll forming the roof of the left pouch.

On the posterior wall of the dorsal hood cilia beat downwards and backwards out of the dorsal hood.

The left pouch (lp) lies below and in front of the opening to the dorsal hood. On the floor of the left pouch there is a long, slender sorting area (sa_6) of finely disposed transverse ridges and grooves.

The gastric shield (gs) occupies the left and posterior walls of the stomach, extending almost to the aperture of the style-sac. The gastric shield sends a long and strong flare into the mouth of the left pouch. A well developed tooth projects backwards from the gastric shield in front of and below the mouth of the dorsal hood. Mouëza & Frenkiel (1976) described three teeth in *D. trunculus.*

There is a sorting area (sa_3) on the right side of the stomach consisting of a series of fine ridges and grooves which run down towards the intestinal groove (ig). As in *D. faba* (Purchon, 1960), there is no currnet passing transversely over the crests of the folds towards the dorsal hood, this area serving only for trapping and rejecting waste material which passes into the mid-gut. The upper margin of this sorting area is marked by a U-shaped ridge (ur), the aperture of which project forwards. In the groove between the arms there is a forwardly directed ciliary current which conveys material up to the dorsal hood. A rejection tract (rt) lies on the anterior border of sorting area (sa_3) and passes material downwards from the dorsal hood towards the intestinal groove.

Wade (1967a) studying *D. denticulatus* named this sorting area the "posterior sorting area"; Pohlo (1967) did not mention it for *D. gouldi.*

As in *D. denticulatus* and *D. gouldi, D. hanleyanus* does not possess a sorting area (sa) of fine ridges and grooves radiating around the spiral of the intestinal groove, present in *D. faba* (Purchon, 1960).

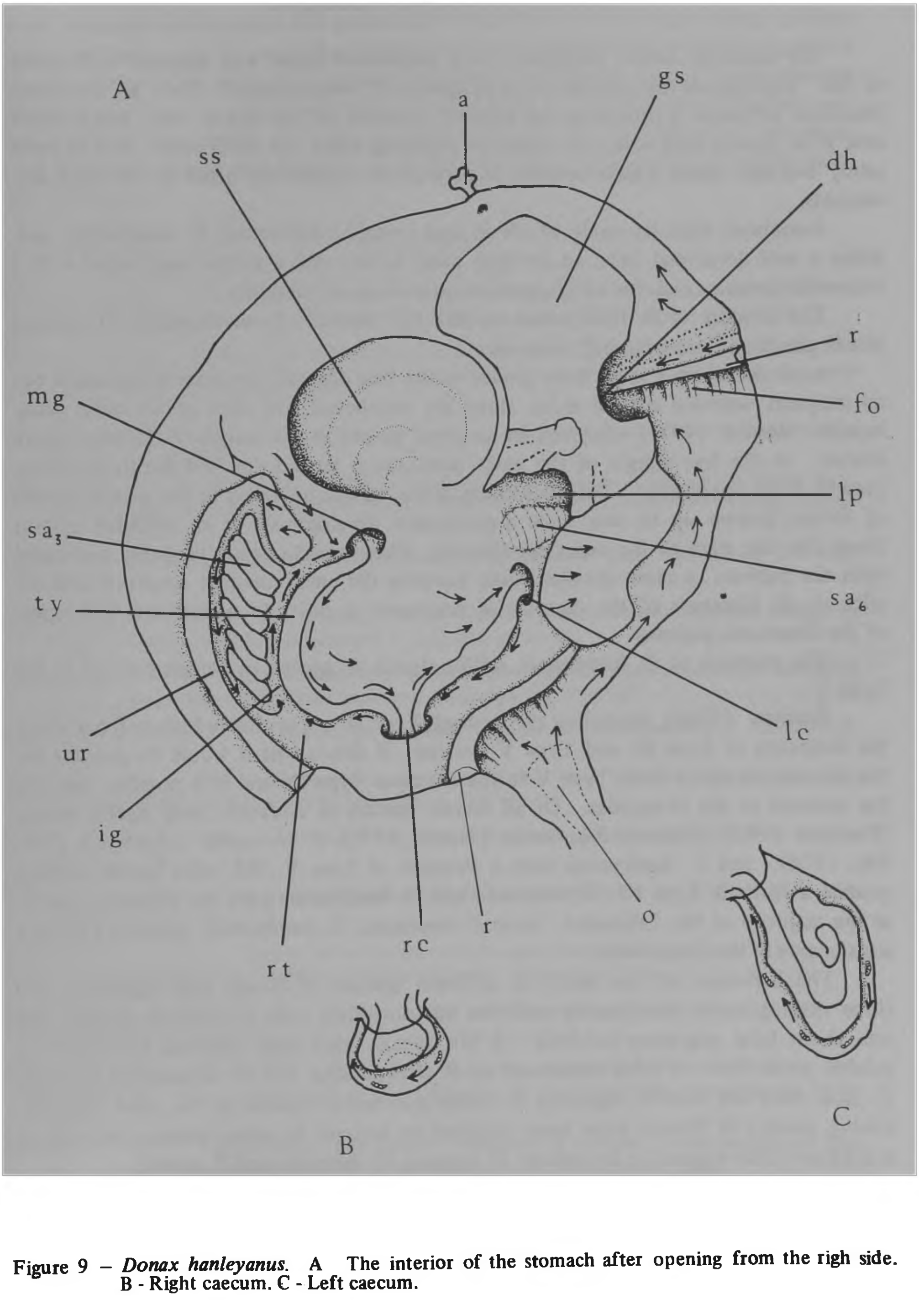


Figure 9 – *Donax hanleyanus.* A The interior of the stomach after opening from the righ side. B - Right caecum. C - Left caecum.

DISCUSSION AND CONCLUSIONS

The intertidal *Donax hanleyanus* is a suspension feeder well adapted to its mode of life. The siphons are very similar in all species of *Donax* studied. There are numerous branched tentacles surrounding the inhalant aperture of the siphon and which curve over it to form a sieve when the animal is pumping water. *D. hanleyanus* lives on open sandy beaches, where a large number of particles are constantly lifted by the wave movements.

Associated with its mode of life in firm littoral substractum, *D. hanleyanus* possesses a well developed foot, an elevator pedis muscle and a wedge-shaped-shell with a truncated posterior end, for a high speed of burrowing and mobility.

The ctenidia of *D. hanleyanus* are like the ones of *D. denticulatus, D. vittatus* and *D. gouldi,* differing from *D. trunculus.*

In *D. hanleyanus* there is no groove at the free edge of the outer demibranch but an incipient oralward current exists along the ungrooved free edge of the outer demibranch. Moueza (1976) observed an incipient groove at the margin of the outer demibranch; at the free margin of the inner demibranch he did not find the food groove, present in *D. hanleyanus.* The differences in the variations found in the several species of *Donax* known up to now show a progressive development of an oralward current along the free edge of the outer demibranch. These variations are probably correlated with the habitat; a more detailed study between the environmental condition and the cilia on all filaments of the ctenidia is necessary in order to understand this aspect of the functional anatomy.

The stomach of *D. hanleyanus,* unlike almost all species of *Donax* belongs to the Type V.

Purchon (1960) states that the stomach Type IV is a primitive feature from which the stomachs of Type III and Type V evolved. If this is true it would be possible for the stomach to revert from Type V to the ancestral Type IV and it is possible that this has occured in the Donacidae. Of all known species of donacids, only *Egeria radiata* (Purchon, 1963), *Iphigenia brasiliensis* (Narchi, 1972), *D. trunculus* (Moueza & Frenkiel, 1976), and *D. hanleyanus* have a stomach of Type V. All other known species, possess a stomach Type IV. *D. trunculus* and *D. hanleyanus* have the stomach type V, as the majority of the Tellinacea. As in *D. trunculus, D. hanleyanus* presents a distinct sorting area in the dorsal hood.

The literature on the study of different species of *Donax* falls markedly into three main groups: one dealing with the anatomy, one with population ecology and one about tidal migratory behavior. A few species have been reported to migrate or exhibit some form of tidal movement as *D. denticulatus* and *D. striatus;* in contrast, *D. faba* does not exhibit migration or other movements related to the tides. The following species of *Donax,* have been reported to migrate by some authors and not to exhibit any tidal migrations by others: *D. vittatus, D. variabilis* and *D. gouldi.*

D. hanleyanus presents some morphlogical devices which occur in species having only one or both modes of life.

Some particularities in the anatomy of *D. hanleyanus,* mainly the stomach Type V, present also in *D. trunculus,* could be an adaptation to the intertidal conditions, un unstable habitat which the animals occupy successfully. The stomach Type V, found in some donacids and mainly in the psamobiids which live in calm waters seems to show that *D. hanleyanus* and *D. trunculus* possibly are better adapted to live buried in regions where the shore is relatively less exposed. It seems that these species do not present tidal migration but may exhibit a preferred level on the beach. Probably, only the combined study of the habitat, the tidal migratory behavior and the anatomy, will show the correlation between the behavior and the anatomical adaptations of the animals to the environment.

REFERENCES

ANSELL, A.D. & A. TREVALLION 1969 Behavioral adaptations of intertidal mollusks from a tropical sand beach. *Journal of Experimental Marine Biology and Ecology, 4* (1): 9-35.

ATKINS, D. 1937 On the ciliary mechanisms and Interrelationships of lamellibranchs. Part III. Types of Lamellibranch Gills and their food currents. *Quarterly Journal of Microscopical Science* (N.S.), *79:* 375-421.

COE, W.R. 1955 Ecology of the bean clam *Donax gouldi*, on the coast of Southern California. *Ecology, 36* (3): 512-514.

DEGIOVANNI, C. & M. MOUEZA, 1972 Contribution a l'étude de la biologie de *Donax trunculus* L (Mollusque, Lamellibranche), dans l'Algérois: Écologie en Baie de Bou-Ismail. *Tethys, 4* (3): 729-744.

EDGREN, R.A. 1959 Coquinas (*Donax variabilis*) on a Florida beach. *Ecology, 40* (3): 498-502.

GOFFERJÉ, C.N. 1950 Contribuição à zoogeografia da malacofauna do litoral do Estado do Paraná. *Archivos do Museu paranaense, 8:* 221-282, pl. 31-35.

GRAHAM, A. 1934 The structure and relationships of lamellibranchs possessing a cruciform muscle. *Proceedings of the Royal Society of Edinburgh, 54:* 158-187.

IHERING, H. von 1897 A ilha de São Sebastião. *Revista do Museu paulista, 2:* 129-216, pl. 1-2.

IHERING, H. von 1900 The musculus cruciform of the order Tellinacea. *Proceedings of the Academy of Natural Science of Philadelphia*, p. 480-481.

IHERING, R. von 1968 Dicionário dos animais do Brasil. Editora Universidade de Brasília, São Paulo, 790 pp., 12 pls.

IRWIN, T.H. 1973 The intertidal behavior of the bean clam, *Donax gouldii* Dall, 1921. *The Veliger, 15* (3): 206-212.

LOESCH, H.C. 1957 Studies of the ecology of two species of *Donax* on Mustang Island, Texas. *Publications of the Institute of Marine Science*, University of Texas, *4* (2): 201-227.

MAGNANINI, A. & A.F. COIMBRA FILHO 1964 Animais da praia. *Departamento de recursos naturais da Secretaria de Economia.* Rio de Janeiro, 64 pp.

MORI, S. 1938 Characteristic tidal rhythmic migration of a mussel, *Donax semignosus* Dunker, and the experimental analysis of its behavior at the flood tide. *Dobutsugaku Zasshi, 50* (1): 1-12.

MORI, S. 1950 Characteristic tidal rhythmic migration of a mussel, *Donax semignosus* Dunker, and the experimental analysis of its behavior (II). *Dobutsugaku Zasshi, 59* (4): 87-89.

MORRISON, J.P.E. 1971 Western Atlantic *Donax*. *Proceedings of the Biological Society of Washington, 83* (48): 545-568.

MOUEZA, M 1972 Contribution a l'étude de la biologie de *Donax trunculus* L. (Mollusque, Lamellibranche), dans l'Algérois: Éthologie en Baie de Bou-Ismail. *Tethys, 4* (3): 745-756.

MOUËZA, M. 1976 Contribution à l'étude de *Donax trunculus* (Mollusque Lamellibranche). Mécanisme de la nutrition. *Journal of Molluscan Studies, 42* (1): 17-30.

MOUËZA, M. & L. Frenkiel 1974 Contribution à l'étude des structures palléales des Tellinacea. Morphologie et structure du manteau de *Donax trunculus.* L. *Proceedings of the Malacological Society of London, 41* (1): 1-19.

MOUËZA, M. & L. FRENKIEL 1976 Contribution à l'étude de la biologie de *Donax trunculus* (Mollusque Lamellibranche). Morphologie fonctionelle - anatomie microscopique - histologie de l'appareil digestif. *Journal of Molluscan Studies, 42* (1): 1-16.

NARCHI, W. 1972 On the biology of *Iphigenia brasiliensis* Lamarck, 1818 Bivalvia, Donacidae. *Proceedings of the Malacological Society of London, 40* (2): 79-91.

NARCHI, W. 1974 Aspectos ecológicos e adaptativos de alguns bivalves do litoral paulista. *Papéis Avulsos de Zoologia.* S. Paulo, *27* (19): 235-262.

PELSENEER, P. 1911 Les lamellibranches de l'expédition du Siboga. Partie Anatomique. *Siboga-Expeditie, 53a:* 1-125, 26 pls.

PENCHASZADEH, P. E. & S.R. Olivier 1975 Ecología de una población de "Berbrerecho" (*Donax hanleyanus*) en Villa Gesell, Argentina. *Malacologia, 15* (1): 133-146.

POHLO, R.H. 1967 Aspects of the biology of *Donax gouldi* and a note on Evolution in Tellinacea (Bivalvia). *The Veliger, 9* (3): 330-337.

PURCHON, R.D. 1960 The stomach in the Eulamellibranchia; Stomach Types VI and V. *Proceedings of the Zoological Society of London, 135* (3): 431-489.

PURCHON, R.D. 1963 A note on the biology of *Egeria radiata Lam. (Bivalvia, Donacidae). Proceedings of the Malacological Society of London, 35* (6): 251-271.

RICE, E.L. 1897 Die systematische Verwertbarkeit der Kiemen bei den Lamellibranchiaten. *Jenaische Zeitschrift für Naturwissenschaft, 31:* 29-89, 2 pls.

RIDEWOOD, W.G. 1903 On the structure of the gills of the Lamellibranchia. *Philosophical Transaction of the Royal Society of London* (B), *195:* 147-284.

RIOS, E.C. 1975 Brazilian marine mollusks iconography. Fundação Universidade do Rio Grande. Centro de Ciências do Mar. Museu Oceanográfico, 331 pp., 91 pls.

STOOL, N.R. et all. 1964 International Code of Zoological nomenclature adopted by the XV International Congress of Zoology. Lond. The Internationl Trust for Zoological Nomenclature, xx + 176pp.

TRUEMAN, E.R., A.R. BRAND & P. DAVIS 1966 The dynamics of burrowing in some common littoral bivalves. *Journal of Experimental Biology, 44*(3):469-492.

TURNER, H.J. & D.L. BELDING 1957 The tidal migrations of *Donax variabilis* Say. *Limnology and Oceanography, 2* (2): 120-124.

WADE, B.A. 1967 Studies on the biology of the West Indian Beach clam, *Donax denticulatus* Linné. 1. Ecology. *Bulletin of Marine Science, 17* (1): 149-174.

WADE, B.A. 1967a On the taxonomy, morphology and ecology of the beach clam, *Donax striatus* Linné. *Bulletin of Marine Science, 17* (3): 723-740.

WADE, B.A. 1968 Studies on the biology of the West Indian Beach clam, *Donax denticulatus* Linné. 2. Life - history. *Bulletin of Marine Science, 18* (4): 876-901.

WADE, B.A. 1969 Studies on the biology of the West Indian Beach clam *Donax denticulatus* Linné. 3. Functional Morphology. *Bulletin of Marine Science, 19* (2): 306-322.

YONGE, C.M. 1948 Formation of siphons in Lamellibranchia. *Nature, 161:* 198-199.

YONGE, C.M. 1949 On the structure and adaptation of the Tellinacea, deposit feeding Eulamellibranchia. *Philosophical Transaction of the Royal Society of London, 234:* 29-76.

ABBREVIATIONS USED IN FIGURES

a	appendix
aam	anterior adductor muscle
alod	ascending lamella of outer demibranch
ap	anal papilla
app	anterior protractor pedis muscle
arm	anterior retractor pedis muscle
cm	cruciform muscle
dd	digestive diverticula
dh	dorsal hood
dlid	descending lamella of inner demibranch
epm	evelator pedis muscle
ex	exhalant siphon
f	foot
fo	folded region
gs	gastric shield
hg	hindgut
ig	intestinal groove
ilp	inner labial palp
in	inhalant siphon
k	kidney
lc	left caecum
lp	left pouch
m	mantle
mg	midgut
mo	mouth
o	oesophagus
olp	outer labial palp
omg	opening of midgut
ov	ovary
pam	posterior adductor muscle
r	ridge
rc	right caecum
rpm	posterior retractor pedis muscle
rt	main rejection tract

sa_3	principal sorting area of dorsal hood
sa_6	sorting area of left pouch
ss	style sac
st	stomach
ty	major typhlosole
ur	U-shaped ridge
v	ventricle
vr	visceral region