

Some Aspects of the Biology and Functional Morphology of *Trapezium* (*Neotrapezium*) *sublaevigatum* (Lamarck) (Bivalvia: Arcticacea)¹

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ABSTRACT: *Trapezium sublaevigatum* is a widely distributed nestler in rocky intertidal and sublittoral crevices in Hong Kong. It occurs on a range of beach types and in waters of different salinity; it is byssally attached and weakly heteromyarian in form. The quadrangular shell is often distorted. The basic structure of the shell and the morphology of the organs of the mantle cavity, visceral mass, and pericardium are broadly similar to a wide range of veneroid relatives. However, the species is weakly heteromyarian, which results from the assumption of the byssally attached, epifaunal mode of life. There is thus a reduction of the anterior face of the shell and an enlargement of the posterior face with corresponding modifications to the shell (notably hinge teeth and ligament) and to musculature. Similar, convergent adaptations are seen in members of the veneroid superfamilies Carditacea, Gaimardiacea, and Dreissenacea, with which *Trapezium* can be compared. Further study of other members of the (isomyarian) Arcticacea might help to establish how the heteromyarian form arose in *Trapezium*.

THE EPIFAUNAL BIVALVE colonizers of the rocky intertidal and sublittoral are variously adapted to their mode of life. Many are permanently byssally attached, whereas others are only temporarily attached as larvae prior to the adoption of, for example, a cemented life-style.

On exposed shores many genera are either heteromyarian in form, e.g., *Mytilus* and *Septifer* (Mytilacea) (White 1937, Yonge and Campbell 1968); laterally flattened, e.g., *Anomia* (Anomiacea) (Yonge 1977); or cemented, e.g., *Chama* (Chamidae) (Yonge 1967) and *Cleidothaerus* (Anomalodesmata) (Morton 1974). On less exposed, often estuarine boulder- or cobble-strewn beaches, bivalves with similar habits are found, e.g., the heteromyarian *Brachidontes* and *Xenostrobus* (Mytilacea) (Wilson 1967) and the cemented oysters *Ostrea*, *Crassostrea*, and *Saccostrea* (Ostreacea) (Yonge 1953). Similarly in the sublittoral, the byssally attached heteromyarian bivalves *Cardita* and *Beguina*

(Carditacea) (Yonge 1969) and the cemented *Spondylus* (Spondylidae), *Plicatula* (Plicatulidae) (Yonge 1973), and *Dimya* (Dimyidae) (Yonge 1975) occur.

Aside from the bivalves associated commensally with other organisms, such as the colonizers of compound ascidians, e.g., *Ryenella* (Mytilacea) and *Mytilimeria* (Anomalodesmata) (Yonge 1952), and the borers of soft rocks and shales, e.g., *Barnea* and *Pholas* (Pholadidae) (Purchon 1955b) and *Petricola* (Petricolidae) (Purchon 1955a), a third major category of epifaunal bivalves are the nestlers. Nestlers are usually small, secretive, byssally attached bivalves, which are hidden in crevices, in the holdfasts of algae or among masses of larger bivalves. Representatives from a wide range of families fall into this category, such as members of the Arcacea (*Barbatia*, *Arca*), Mytilacea (*Modiolus*), and Saxicavacea (*Hiatella*) (Yonge 1971), together with delegates from a range of families belonging to the vast, cosmopolitan, and highly successful order Veneroida. These include members of the Leptonacea (*Lasaea*) (Oldfield 1955), Gaimardiacea (*Neogaimardia*) (Morton 1979),

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Veneracea (*Venerupis*) (Ansell 1961), Petricolidae (*Claudiconcha*) (Morton 1978), and *Trapezium* (Arcticacea, Trapeziidae).

The arcticiid *Trapezium sublaevigatum* is closely allied to a wide range of infaunal animals which have not been adequately studied. The present study seeks information on *T. sublaevigatum* in order to supply information on the superfamily and also to compare the adaptations of *T. sublaevigatum* with those of other nestling bivalves about which more is known and which have a similar mode of life.

MATERIALS AND METHODS

The ciliary currents of dissected individuals were studied using carmine suspended in seawater. Specimens for sectioning were fixed in Bouin's fluid, sectioned at 6 μm , and stained in Ehrlich's hematoxylin, Heidenhain's hematoxylin, or Mallory's triple stain.

TAXONOMY

The veneroid superfamily Arcticacea Newton 1891 comprises nine families (Keen 1969) which have been little studied. In the Trapeziidae Lamy 1920 there are seven genera, of which only *Trapezium* Megerle von Mühlfeld 1811 and *Coralliophaga* de Blainville 1824 are extant. Both genera have subgenera and the species reported upon here is the type species for the subgenus *Neotrapezium* Habe 1951. This was originally described as *Cardita sublaevigata* Lamarck 1819; the corrected name for the species is *Trapezium* (*Neotrapezium*) *sublaevigatum* (Lamarck 1819).

Previous reviewers of the family include Reeve (1843), Lamy (1920), and Solem (1954). The latter author comprehensively described the known species and summarized data on the ecology of the family. Solem describes a total of nine extant species of *Trapezium* (6) and *Coralliophaga* (3) plus the somewhat dubious *Isorropodon perplexum* Sturany 1896 from 2420 m in the Mediterranean, which has not been reported since. The three species of *Trapezium* (*Trapezium*) and three species

of *Coralliophaga* are coral-associated nestlers; *Trapezium* (*Glossocardia*) *obesa* is a deepwater species while the two species of *Trapezium* (*Neotrapezium*) inhabit crevices of rocks or oysters in shallow, intertidal waters.

BIOLOGY

Solem (1954) considers *Trapezium sublaevigatum* to be a continental or large island species because, although it is widely distributed in the Indo-Pacific, it has only rarely been recorded from offshore islands. Solem's review of the literature pertaining to the ecology of this species establishes that it is byssally attached within the crevices of rocks or oysters in the intertidal zone. Nothing is known of the adaptations of *T. sublaevigatum* (or of any other trapeziid) to its particular mode of life.

Trapezium sublaevigatum is widely distributed in Hong Kong and is common in the many small bays characteristic of the coastline. It is a nestler that is usually attached by a stout byssus to the undersurface of stones and boulders of the lower shore. Where it nestles in crevices there is often a resulting distortion of the shell. The habitat always has a freshwater input and is sheltered from strong wave action. The species is commonly found attached to cultivated oysters in Deep Bay, where salinity can be very low and the sediment load high (Wong 1975); it also occurs on experimental panels as a member of the fouling community. The specimens reported here were collected mainly from sublittoral boulders at the mouth of the bay at Hoi Sing Wan, near the village of Wu Kwai Sha, Tolo harbor, or from sublittoral dead coral heads, similarly collected from Tolo harbor.

FUNCTIONAL MORPHOLOGY

The Shell and Ligament

The shell of *Trapezium sublaevigatum* (Figure 1A) is approximately quadrangular

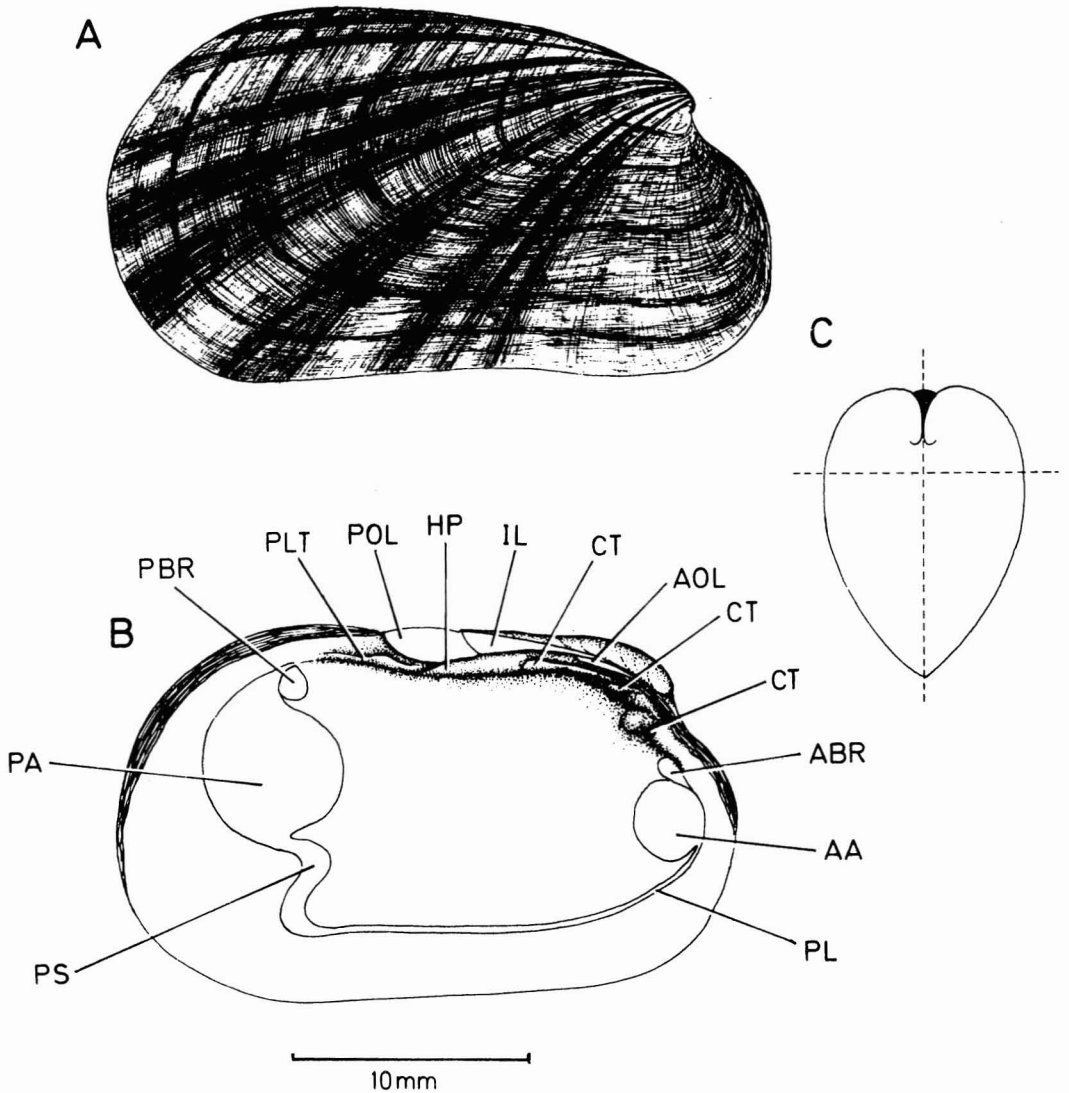


FIGURE 1. *Trapezium sublaevigatum*. A, exterior view of the right shell valve; B, interior view of the left shell valve; C, end-on view showing the widest region of the shell.

AA, anterior adductor muscle scar; ABR, anterior byssal retractor muscle; AOL, anterior outer ligament layer; CT, cardinal tooth; HP, hinge plate; IL, inner ligament layer; PA, posterior adductor muscle scar; PBR, posterior byssal retractor muscle; PL, pallial line; PLT, posterior lateral tooth; POL, posterior outer ligament layer; PS, pallial sinus.

in appearance. There is no radial or concentric sculpture, though there are often distinct growth rings. The shell is delicately radially patterned, typically with nine dark-brown stripes. The shell is equivalve and markedly inequilateral, a condition resulting from the assumption of a weakly hetero-

myarian form with the anterior slope of the shell reduced relative to the posterior. Thus, the umbones are located close to the anterior end of the shell. In transverse section (Figure 1C) the greatest shell width is located dorsal to the midpoint of the dorsoventral axis of the shell. Other epifaunal heteromyarian

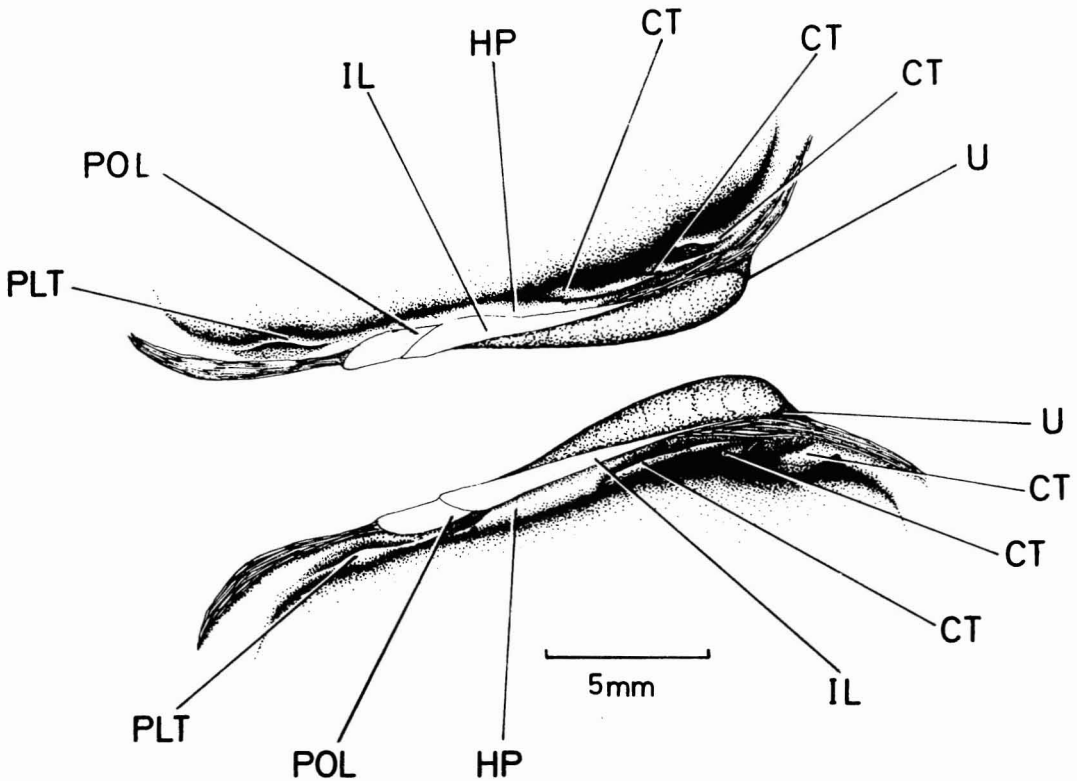


FIGURE 2. *Trapezium sublaevigatum*. The hinge plate of the right (above) and the left (below) shell valves.
 CT, cardinal tooth; HP, hinge plate; IL, inter ligament layer; PLT, posterior lateral tooth; POL, posterior outer ligament layer; U, umbo.

bivalves, e.g., members of the Mytilacea and Dreissenacea, are much wider ventrally. There is no byssal notch.

Internally (Figure 1B), the effect of the heteromyarian form upon the shell is more apparent. The posterior adductor (PA) and posterior byssal retractor muscles (PBR) are relatively larger than their anterior equivalents (AA and ABR). The pallial line (PL) is thick and has a shallow pallial sinus (PS). The hinge plate (Figures 1, 2, HP) is narrow, with a number of hinge teeth that can be interpreted as comprising either two (the posterior of which is bicuspid) or three cardinal teeth (CT) and a single posterior lateral tooth (PLT) located behind the ligament. The assumption of the heteromyarian form with the concomitant enhanced development of the posterior slope of the shell has also resulted in the elongation of the teeth and the separation of the lateral from

the cardinal teeth. Similarly, the absence of anterior lateral teeth can be accounted for by the reduction of the anterior slope of the shell.

The ligament (Figure 2) is opisthodontic and external. It comprises a posterior outer ligament layer (POL) overlying the inner ligament layer (IL). This in turn overlies a small anterior outer ligament layer that is often obscured by erosion of this region of the shell.

The Siphons

The siphons of *Trapezium sublaevigatum* (Figure 3) are relatively short and are retracted into a short pallial sinus. They are formed by fusion of the inner folds only and are thus of type A (Yonge 1948, 1957).

The wide inhalant siphon bears a crown of tentacles divided into four cycles. An inner cycle of typically 10 large tentacles is directed

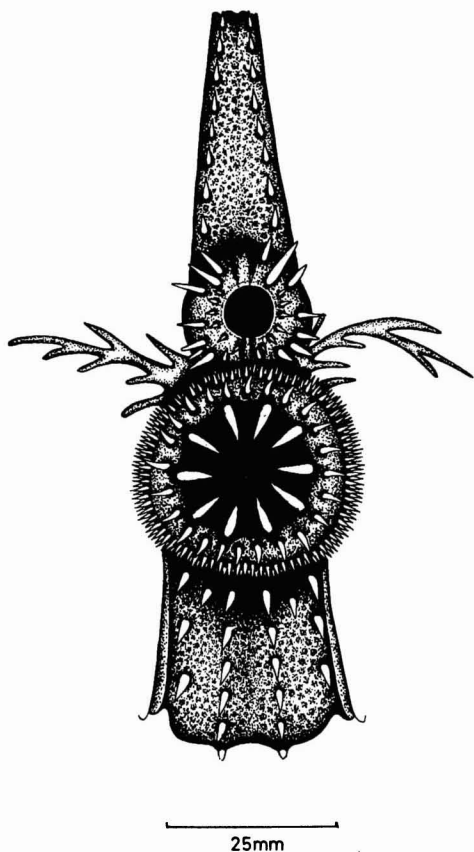


FIGURE 3. *Trapezium sublaevigatum*. The siphons as viewed posteriorly.

inward and forms a grid across the aperture. These are surrounded by approximately 20 smaller tentacles that are directed outward. Finally, two circles of very small tentacles, comprising some 70 and 130, respectively, line the margin of the siphon. The exhalant siphon does not bear a crown of tentacles and is in the form of a small cone, with the aperture distally. The external surface of both siphons has a number of papillae, which arise dorsal to the exhalant siphon as a single row of approximately eight on each lobe. Ventral to the inhalant siphon they arise as a double row on each lobe. There are three papillae in the outer row and seven in the inner. These rows of papillae extend around each siphon without apparent order, number, or grouping. The outer circlet of papillae on the exhalant siphon is, however, larger than the

inner row and is organized into groups. Between the siphons, on each side, one of the papillae is enlarged, forming a very long, branched tentacle. When the siphons are open, these tentacles are extended outward, but they fold across each other when the siphons are withdrawn.

The siphons, tentacles, papillae, and mantle tissue are delicately blotched with brown, yellow, and white pigment spots.

The Mantle

Dorsally the mantle secretes the ligament, the structure of which can be compared with that of *Hiatella* (Yonge 1971). Mantle fusions occur between the inhalant and exhalant siphons and for a distance of approximately half the length of the shell below the inhalant siphon. Beyond this there is a pedal gape. There is no fourth pallial aperture. A transverse section through the region of ventral mantle fusion (Figure 4) clearly shows that fusion involves the inner mantle folds only (FIMF) (type A of Yonge 1957).

Bands of muscle fibers, here termed *orbital muscles* (OR), extend across the fused tissue. The pallial muscles (PM) extend from the pallial line into the middle (MF) and outer folds (OF). The epithelium of the outer surface of the middle mantle fold (MF), abutting the periostracal groove, is densely pigmented. Similarly, the inner surface of the mantle stains densely in Ehrlich's and Heidenhain's hematoxylin and probably secretes mucus that is used in entrapping waste material destined to be expelled as pseudofeces via the major rejectory tracts (RT) of the mantle. The periostracum is secreted within the periostracal groove. This comprises two layers: an inner layer (IP) 10 μm thick is overlain by a much thicker (50–100 μm) outer layer (OP) that has a very ragged appearance. A similar two-layered periostracum is seen in *Dreissena polymorpha*, *Geloina erosa*, and *Claudiconcha japonica* (Morton 1969, 1976, 1978).

The Ctenidia and Labial Palps

The ctenidia comprise two subequal demibranchs; the inner demibranch (Figure 5,

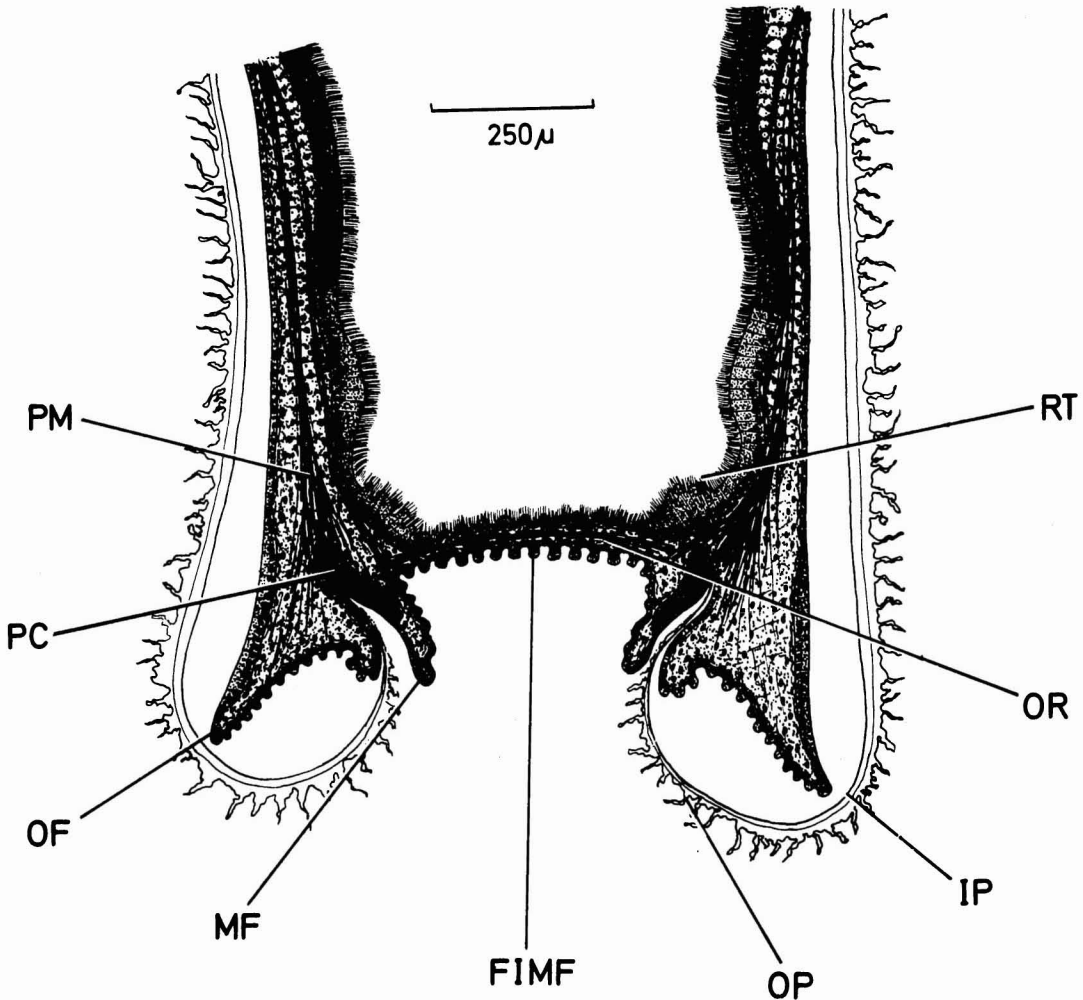


FIGURE 4. *Trapezium sublaevigatum*. A transverse section through the fused mantle margins, posterior to the pedal gape.

FIMF, fused inner mantle folds; IP, inner periostracal layer; MF, middle mantle fold; OF, outer mantle fold; OP, outer periostracal layer; OR, orbital muscles; PC, pigment cells; PM, pallial retractor muscle; RT, rejectory tract of mantle.

ID) is much longer than the outer (OD). The ctenidia are homorhabdic and plicate, with each plica comprising between 15 and 17 filaments. Posteriorly, the tips of both demibranchs extend into the inhalant siphon (IS), but anteriorly only the tips of the filaments of the inner demibranch extend between the labial palps (OLP and ILP). The ctenidia form the curve shown in Figure 5 and are directed in a posteroventral/anterodorsal plane. The ciliary currents they engender

(Figure 6) beat down toward the ventral margins of both demibranchs, but only the margin of the inner demibranch has a food groove. Particles arriving at the ventral margin of the outer demibranch are directed anteriorly but are typically removed by the cilia of the descending lamella of the inner demibranch before reaching the ctenidial-labial palp junction. An orally directed acceptance tract is also located in the ctenidial axis and is served by dorsally directed ciliary

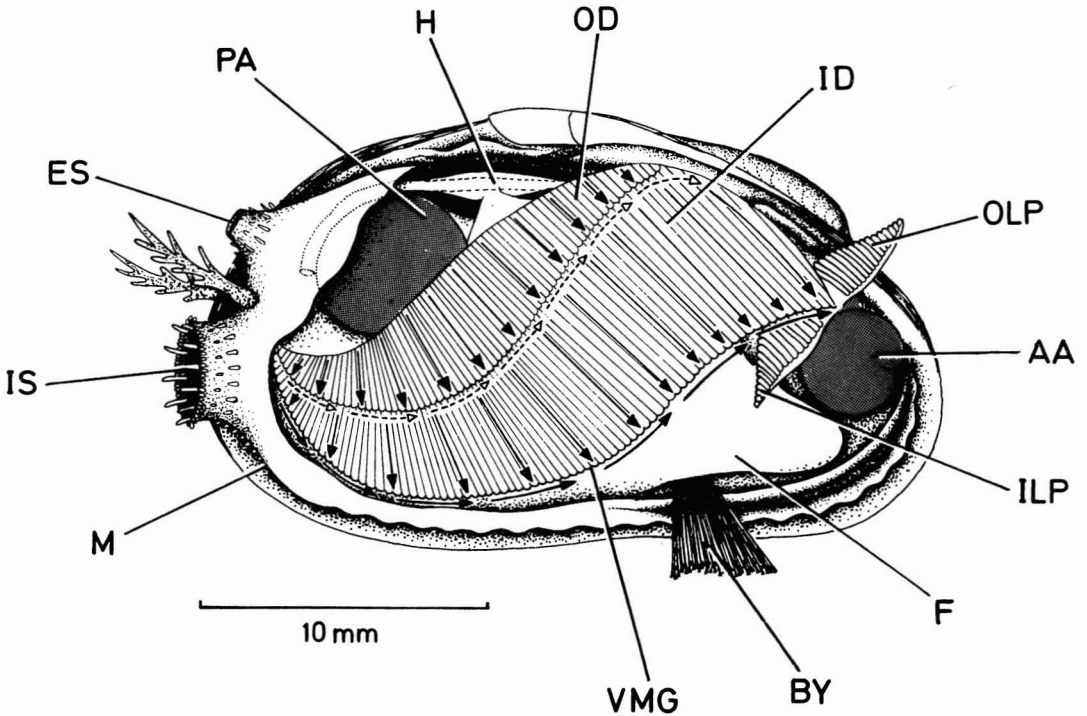


FIGURE 5. *Trapezium sublaevigatum*. The ciliary currents of the ctenidium and labial palps of the right side after removal of the right mantle lobe and shell valve.

AA, anterior adductor muscle; BY, byssus; ES, exhalant siphon; F, foot; H, heart; ID, inner demibranch; ILP, inner labial palp; IS, inhalant siphon; M, mantle; OD, outer demibranch; OLP, outer labial palp; PA, posterior adductor muscle; VMG, ventral marginal food groove.

tracts on the upper regions of the descending lamellae of both demibranchs. The ciliary currents of the ctenidia are thus of type C (Ib) (Atkins 1937) and compare with those of the venerid *Venus fasciata* (Ansell 1961). The edges of the ascending lamellae of both inner and outer demibranchs are connected to the visceral mass and mantle, respectively, by tissue fusions, as in *Dreissena polymorpha* and *Geloina erosa* (Morton 1969, 1976).

In transverse section (Figure 7) each filament is 20 μm in width and comprises two apical cells (with small nuclei) that have frontal cilia (FC) 5–6 μm long. These cells are bounded on each side by either one or two cells with large nuclei 6 μm in diameter and possessing eulaterofrontal cilia (EC) approximately 7.5–9 μm in length. Between these cells and the two cells that give rise to the lateral cilia (LC) (12–15 μm long) is a small, nonciliated cell (of unknown func-

tion) with a distal nucleus. Internal to the lateral ciliated cells are found a number of secretory cells (SC). Each filament is supported by chitinous rods (CR) joined by a transverse filament (TF).

Particles transported in the oral-directed current of the ctenidial axis pass onto the inner demibranch and together with particles from the ventral marginal food groove of the inner demibranch pass between the labial palps. On the surface of the labial palps (OLP and ILP), which are relatively large and triangular in shape, sorting currents occur (Figure 8). Details of the ciliary currents of the labial palps of *Trapezium sublaevigatum* are shown in Figure 9. Particles are passed toward the distal oral groove (DOG), over the crests of the ridged palps and thence to the mouth. Rejection of larger particles occurs in the depths of the grooves; these particles are transported toward the ventral

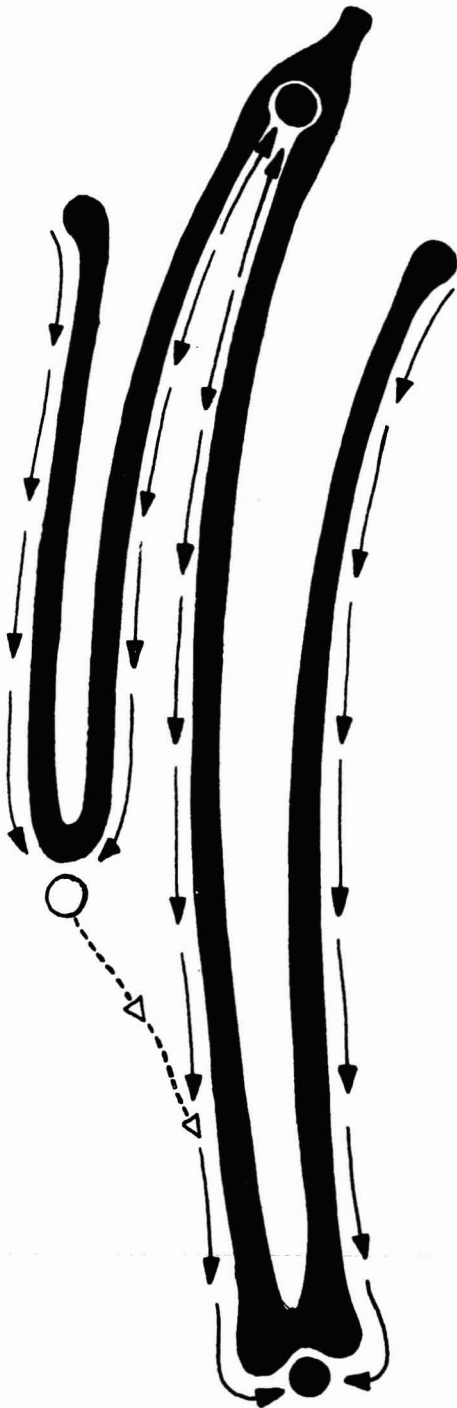


FIGURE 6. *Trapezium sublaevigatum*. A diagrammatic vertical section through the left ctenidium showing the ciliary currents.

● = oral-directed currents; ○ = rejectory currents.

edge and thence to the tip of the palp where they are rejected. Resorting currents occur on the ridge crests and on both oral and aboral faces of each ridge whereas upward-directed currents that take material out of the grooves occur on the aboral face of the ridges. Apposition or separation of the ridges enables material to be either totally accepted or rejected, respectively. Intermediate distances between these two extremes enable *Trapezium* to cope with a wide range of feeding circumstances in waters with a range of sediments that vary in both size and quantity.

The lips of the mouth are fleshy (Figure 8, LI), and the mouth is located close to the posterodorsal surface of the anterior adductor muscle. The outer surface of the lips has rejection tracts that take material either toward the palps (where they meet with and add to the rejection tract located on the ventral edge of the palp) or toward the mantle (where they add to the posteriorly directed rejection tract of this structure).

The Ciliary Currents of the Mantle and Visceral Mass

The ciliary currents of the mantle (Figure 10) are rejectory. Particles falling upon the general mantle surface are directed posteroventrally and contribute to a major posteriorly directed rejectory tract that has its origin close to the position of the mouth, i.e., the posterodorsal edge of the anterior adductor muscle. The rejectory tracts of each lobe eventually join; this union commences with the fusion of the two mantle lobes posterior to the pedal gape. Pseudofeces traveling along this tract are rejected from the inhalant siphon by the rapid adduction of the shell valves. The main rejection tracts of each lobe are also supplied by the inwardly directed tracts of the pedal gape.

The ciliary currents of the visceral mass (Figure 11, VM) are similarly rejectory in nature. Particles that fall onto the dorsal region of the visceral mass below the point where the ascending lamella of the inner demibranch attaches to it are directed posteroventrally and contribute to a major rejection tract that has its origin close to the

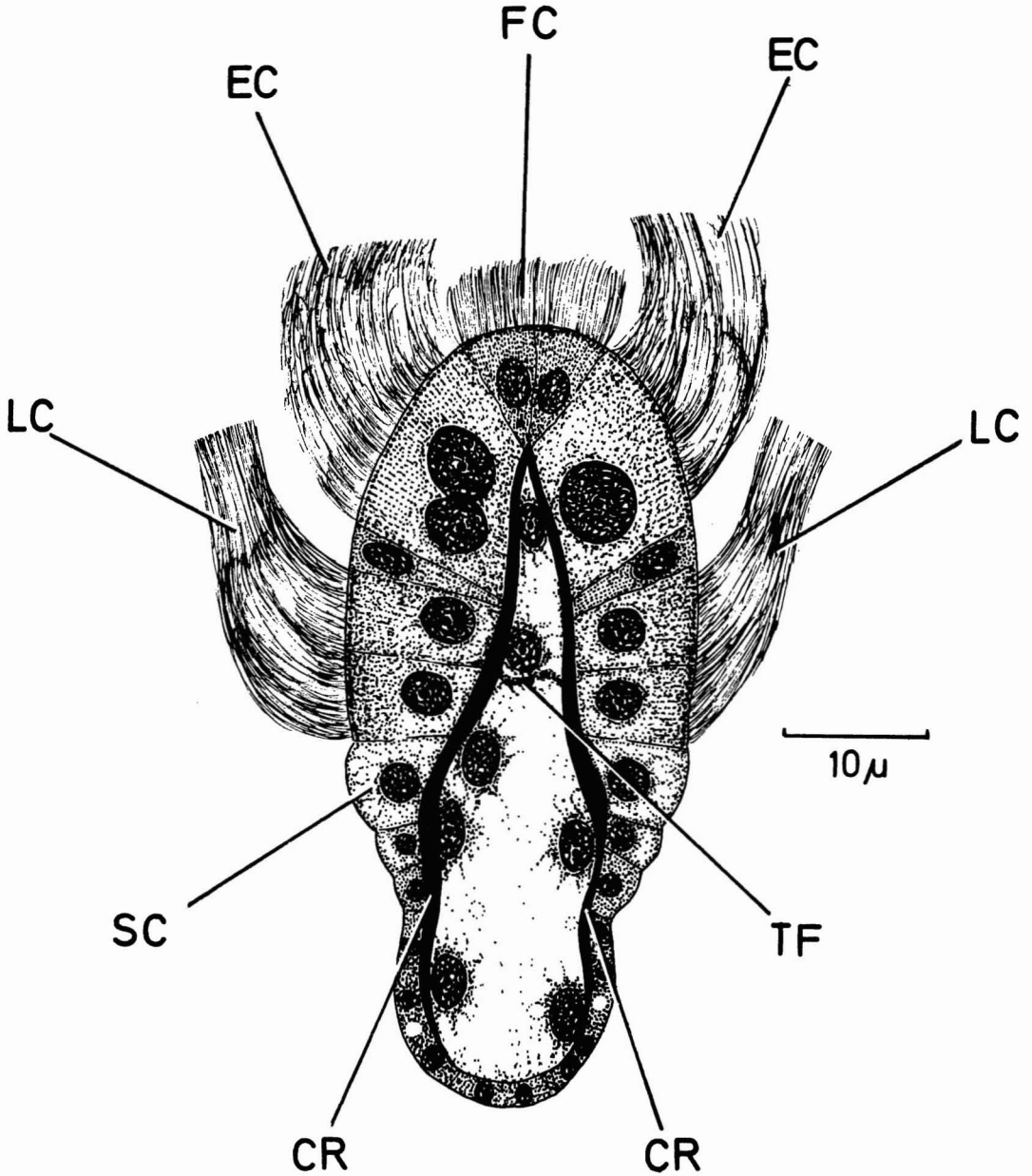


FIGURE 7. *Trapezium sublaevigatum*. A transverse section through a single ctenidial filament.

CR, chitinous rod; EC, eulaterofrontal cilia; FC, frontal cilia; LC, lateral cilia; SC, secretory cell; TF, transverse filament.

position of the mouth. Very few currents were discernible on the foot, though the major rejection tract of the visceral mass is also supplied from the upper edges of the foot, i.e., by material traveling in a postero-dorsal direction. The ciliary rejection tracts

of the mantle and visceral mass thus complement each other.

The Alimentary Canal

The esophagus enters the stomach antero-

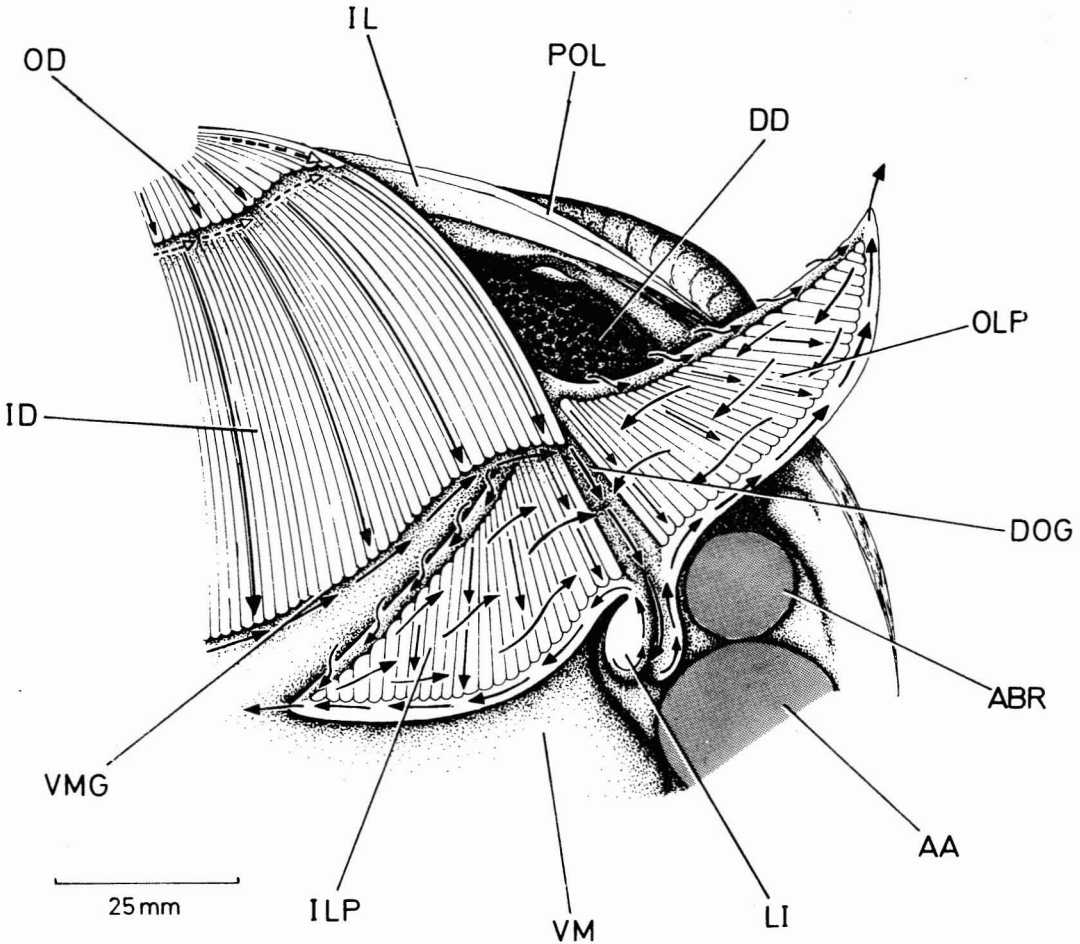


FIGURE 8. *Trapezium sublaevigatum*. The ciliary currents of the labial palps and anterior end of the ctenidium as seen from the right side.

AA, anterior adductor muscle; ABR, anterior byssal retractor muscle; DD, digestive diverticula; DOG, distal oral groove; ID, inner demibranch; IL, inner ligament layer; ILP, inner labial palp; LI, lip of mouth; OD, outer demibranch; OLP, outer labial palp; POL, posterior outer ligament layer; VM, visceral mass; VMG, ventral marginal food groove.

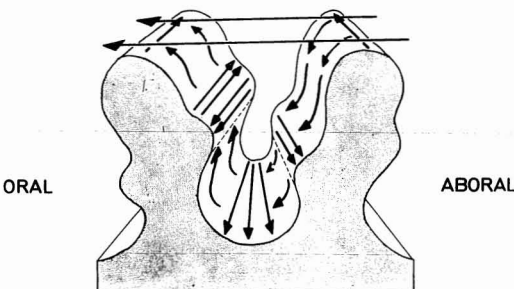


FIGURE 9. *Trapezium sublaevigatum*. A small portion of the ridged surface of the labial palps showing the various ciliary tracts.

ventrally and in transverse section (Figure 12A) comprises a dorsoventrally flattened tube 350 μm in diameter. The columnar epithelium of the tube is thrown into a large number of folds. The cells making up the epithelium of the esophagus vary in height from 30 to 70 μm ; they have nuclei 6 μm in diameter and cilia 10 μm long. Clusters of nonstaining, yellowish concretions are interspersed between the epithelial cells.

The stomach of *Trapezium sublaevigatum* has been described by Purchon (1960) and is of type V. It is thus similar to a wide range

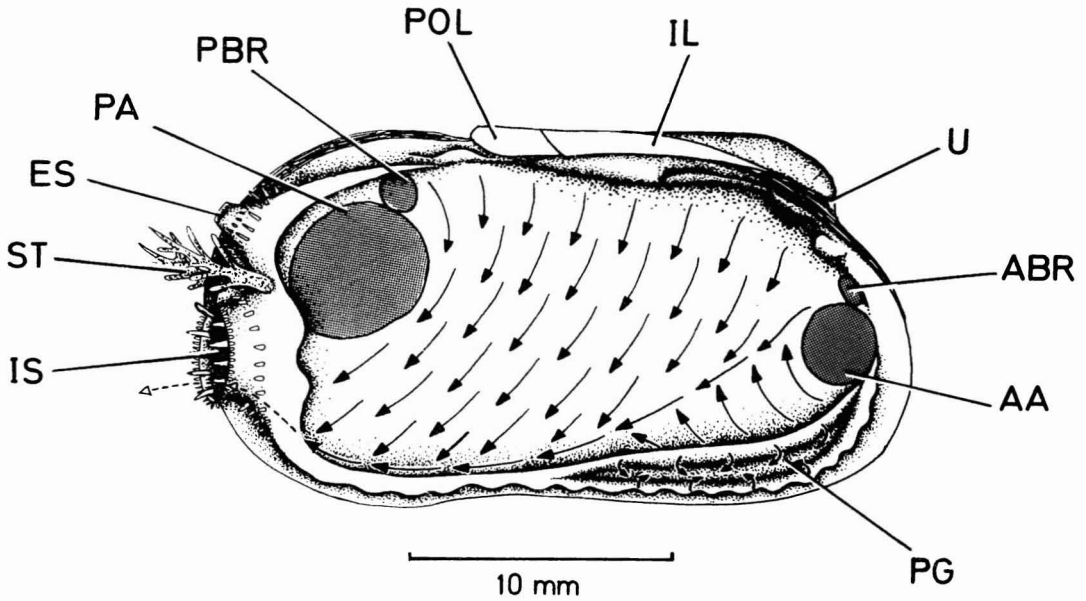


FIGURE 10. *Trapezium sublaevigatum*. The ciliary currents of the left mantle lobe.

AA, anterior adductor muscle; ABR, anterior byssal retractor muscle; ES, exhalant siphon; IL, inner ligament layer; IS, inhalant siphon; PA, posterior adductor muscle; PBR, posterior byssal retractor muscle; PG, pedal gape; POL, posterior outer ligament layer; ST, sensory tentacle; U, umbo.

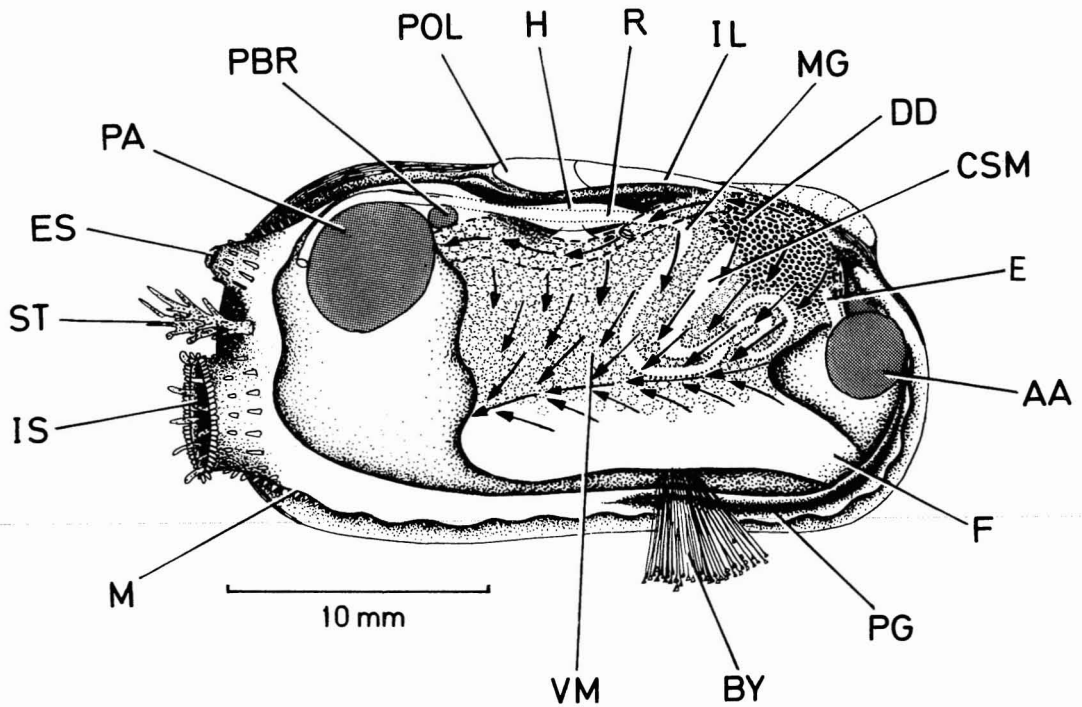


FIGURE 11. *Trapezium sublaevigatum*. The ciliary currents and structure of the visceral mass, viewed from the right side after removal of the right ctenidium, mantle lobe, and shell valve.

AA, anterior adductor muscle; BY, byssus; CSM, conjoined style sac and midgut; DD, digestive diverticula; E, esophagus; ES, exhalant siphon; F, foot; H, heart; IL, inner ligament layer; IS, inhalant siphon; M, mantle; MG, midgut; PA, posterior adductor muscle; PBR, posterior byssal retractor muscle; PG, pedal gape; POL, posterior outer ligament layer; R, rectum; ST, sensory tentacle; VM, visceral mass.

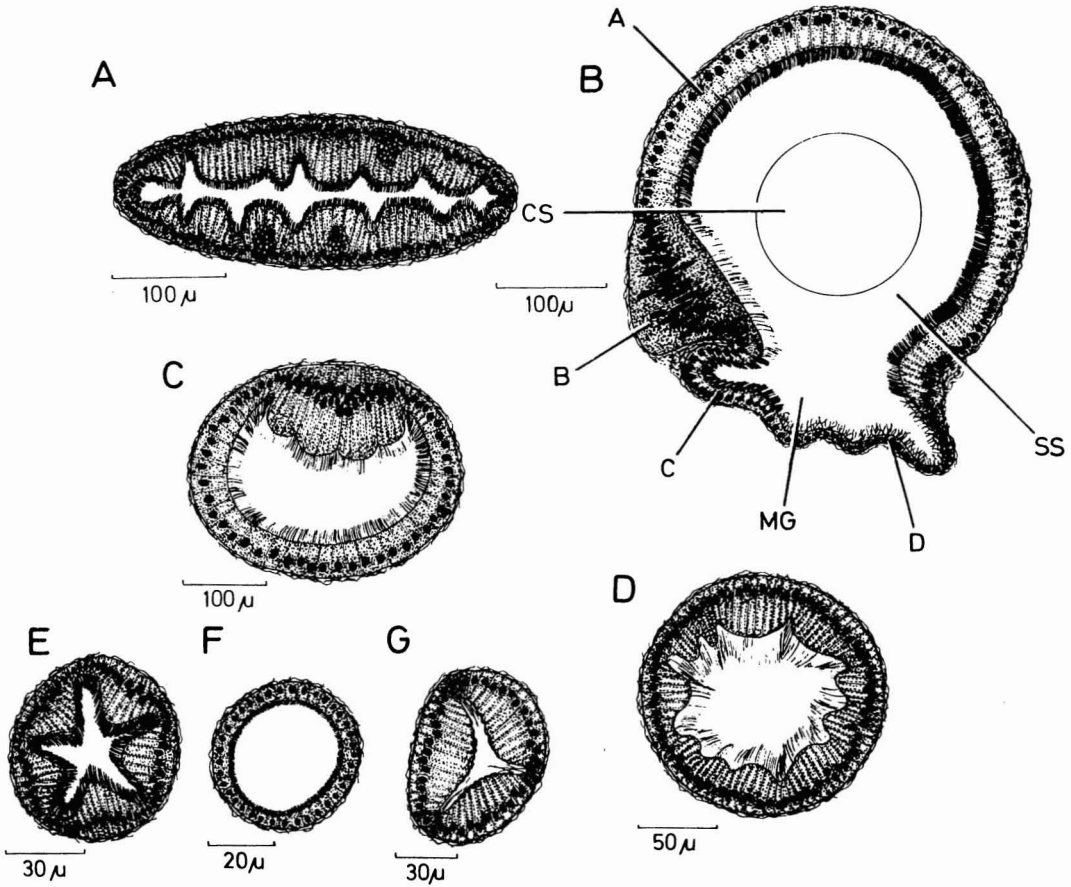


FIGURE 12. *Trapezium sublaevigatum*. Transverse sections through A, the esophagus; B, the conjoined style sac and midgut; C, the separated midgut; D, the rectum; E, the primary duct; F, the secondary duct; and G, a digestive tubule of the digestive diverticula.

A, A cell layer of style sac; B, B cell layer of style sac; C, C cell layer of style sac; CS, crystalline style; D, D cell layer of style sac; MG, midgut; SS, style sac.

of veneroids. The stomach has a relatively large gastric shield and extensive sorting areas, notably SA₃ and SA₅. The minor typhlosole is small and the major typhlosole penetrates first the right and then the left caeca. The conjoined style sac and midgut leaves the stomach posteroventrally and in transverse section (Figure 12B) is seen to comprise a number of epithelial types earlier recognized in a number of other bivalves (Kato and Kubomura 1954, Morton 1969, 1976, 1978). The style sac (SS) is bounded by the A cell layer (Figure 12B) which comprises a columnar epithelium of cells 48 μ m tall, each with a basal nucleus 7 μ m

in diameter and fringed distally by cilia 12 μ m long. The B cell layer (Figure 12B) is the major typhlosole which comprises more densely staining cells 55 μ m long, each with a centrally located, elongate nucleus (10 μ m) and cilia 10 μ m long. The minor typhlosole, located opposite the major typhlosole, quickly disappears when it passes from the stomach into the conjoined style sac and midgut (MG). Internal to the B cell layer and forming one region of the midgut is the C cell layer (Figure 12B) which comprises cells 24 μ m tall (on average), each with a basal nucleus 5–6 μ m in diameter and short (6 μ m), stiff cilia. Within the cell the rootlets

of these cilia are clearly seen as in *Dreissena polymorpha*, *Geloina erosa*, and *Claudiconcha japonica* (Morton 1969, 1976, 1978). The remainder of the midgut epithelium, connecting A and C epithelial types, is the D cell layer (Figure 12B) which comprises cuboidal cells 12–14 μm tall with a central nucleus 7 μm in diameter and long (10 μm), sparse cilia. The style sac of *T. sublaevigatum* thus closely resembles those of *Geloina erosa* and *Claudiconcha japonica* (Morton 1976, 1978).

The separated midgut (Figure 12C) comprises a round tube 260 μm in diameter. The major typhlosole penetrates the midgut and is seen as a high ridge in transverse section. The cells of the midgut are 100 μm tall (on average) with a small (5–6 μm) nucleus and long (14–15 μm) cilia. After separation from the style sac, the midgut undertakes a number of convolutions in the visceral mass before turning dorsally and then posteriorly to penetrate the ventricle of the heart as the rectum (Figure 11, R). The rectum, as seen in transverse section (Figure 12D), is 150–160 μm in diameter and comprises a convoluted epithelium with cells that are 55 μm tall (on average). Each has a basal nucleus 5 μm in diameter and is fringed by long (20 μm) cilia.

The digestive diverticula open into the stomach from the right and left caeca, from the left pouch, and from three ducts opening independently on the right wall of the stomach, dorsal to the orifice of the right caecum (Purchon 1960). In transverse section ciliated primary ducts (Figure 12E) 60 μm in diameter divide, forming secondary ducts (Figure 12F) 48 μm in diameter. The latter have a brush border of microvilli which are only 2.5 μm long. The secondary ducts divide to form digestive tubules (Figure 12G) approximately 60–70 μm in diameter and from the crypts of which arise long (26 μm) cilia. The digestive tubules are typical of those seen in a wide range of bivalves (Owen 1955, Yonge 1926).

The Pericardium

The heart (Figure 13, H) lies posterior to the umbones under the long ligament. It

comprises a single ventricle (V) and a pair of lateral auricles (AU). From the antero-ventral floor of the pericardium (P) arise a pair of renopericardial apertures (RPA) which open into the very extensive saclike distal limb of the kidney (DK). The kidney is located largely under the posterior region of the pericardium and extends up to the posterior byssal retractor muscles (PBR). The distal limb of the kidney encloses and opens into a pair of ciliated proximal limbs (PK). These in turn open into the supra-branchial chamber via an excretory aperture (EA). Located close and anterior to the excretory aperture is the gonadial aperture (GA) which has a pair of fleshy lips. The pericardial gland (PE) is largely associated with the auricles and not with the pericardium as in *Dreissena* and *Geloina* (Morton 1969, 1976).

DISCUSSION

Trapezium sublaevigatum is a member of the Arcticeae, a superfamily of the huge and successful order Veneroida. Within this order representatives have colonized a wide range of habitats so that there are shallow and deep burrowers of soft deposits, both intertidal and sublittoral; nestlers on rocky shores; and borers of soft rocks and shales. Though most families are marine or estuarine, there are freshwater veneroids, e.g., the Corbiculacea and Dreissenacea. In four extant superfamilies there is a trend toward a heteromyarian form, i.e., the Gaimardiacea, Carditacea, Dreissenacea, and Arcticeae, the latter represented by *Trapezium*. It is thus pertinent to identify and comment upon the characters that link *Trapezium* to other veneroids and then to compare body form and function in this species with other heteromyarian veneroids, notably *Cardita* and *Dreissena*.

Within the Veneroida the structure and mineralogy of the shell is particularly uniform, comprising (except in some members of the Veneracea where the shell is three-layered) an outer crossed lamellar layer and an inner, complex crossed lamellar layer. The

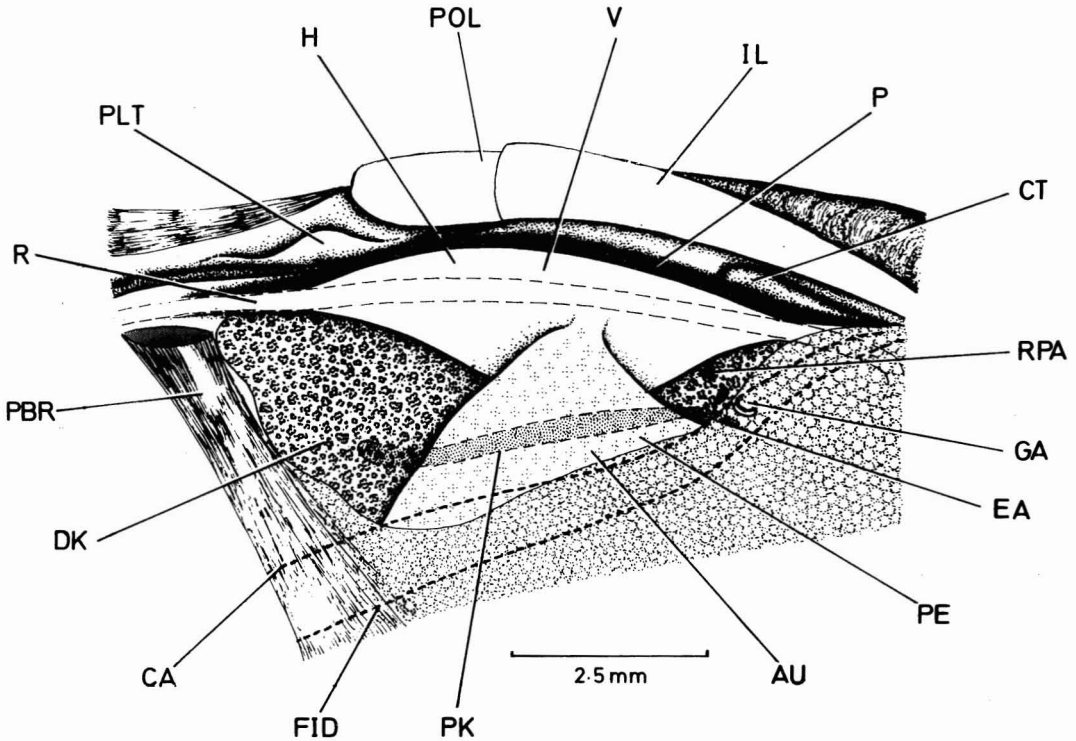


FIGURE 13. *Trapezium sublaevigatum*. The pericardium and associated organs viewed from the right side. AU, auricle; CA, ctenidial axis; CT, cardinal tooth; DK, distal limb of kidney; EA, excretory aperture; FID, point of fusion of inner demibranch with visceral mass; GA, gonadial aperture; H, heart; IL, inner ligament layer; P, pericardium; PBR, posterior byssal retractor muscle; PE, pericardial gland; PK, proximal limb of kidney; PLT, posterior lateral tooth; POL, posterior outer ligament layer; R, rectum; RPA, renopericardial aperture; V, ventricle.

shell of *Arctica*, though comprising two shell layers, has a homogeneous structure (as in *Gaimardia trapezina*) which is different from *Trapezium*; the latter shell conforms to the basic veneroid plan (Taylor, Kennedy, and Hall 1973).

The veneroid hinge plate typically has either two or three cardinal teeth and both anterior and posterior laterals. However, some diversity of structure is encountered within the order, so that in the (British) Veneracea (Ansell 1961), for example, there are typically three cardinals and a single anterior lateral, whereas in the Petricolidae there are no laterals and either two or three cardinals, e.g., *Petricola pholadiformis* (Purchon 1955a) and *Claudiconcha japonica* (Morton 1978). In the Corbiculacea the (posterior and anterior) lateral teeth are serrated, e.g., *Corbicula fluminea*. In *Glossus humanus*

(Owen 1953), however, the anterior laterals are reduced, and the cardinals and posterior laterals are elongate and extend almost parallel to the sides of the hinge plate. In members of the Carditacea, a distinct anterior lateral tooth is often present, e.g., *C. carpenteri* (Yonge 1969), but cardinals and posterior teeth are similarly elongate. In the distinctively heteromyarian *Dreissena* and *Mytilopsis* (Morton 1969, in preparation) there are no true hinge teeth, but the latter genus often develops secondary hinge teeth on the anterior shell margin. In *Arctica islandica* there are three cardinals and, as in *Trapezium*, a single posterior lateral tooth located behind the ligament. However, *Arctica* also has an assortment of anterior lateral teeth (Tebble 1966).

In these few examples of veneroid hinge configuration there would seem to be some

degree of consistency, with a basic structure of three cardinals and both anterior and posterior laterals. In some members of the order there seems to be a trend toward a reduction in the anterior slope of the shell and an enhancement of posterior growth. Many thus have an (either external or internal) opisthodontic ligament and there is an associated trend toward the loss of the anterior laterals and the elongation of the cardinals and posterior laterals posteriorly.

The veneroid ligament has been described on a number of occasions and is either amphidetic, e.g., *Crassinella* (Allen 1968), or opisthodontic, as in *Glossus* (Owen 1953), *Venus* (and other venerids) (Ansell 1961), *Glauconome* (Owen 1959), *Petricola* (Purchon 1955a), *Dreissena* (Yonge and Campbell 1968), and *Cardita* (Yonge 1969). In *Trapezium*, a ligament of the same structure is found and its elongation in this bivalve can be correlated with the assumption of partial heteromyarianism as in *Cardita* and *Beguinia* (Yonge 1969).

Mantle fusion in *Trapezium* is simple and of the inner folds only (type A). Within the Veneroida this situation is probably primitive, and the inner surfaces of the middle folds fuse (type B) in many of the Cardiacea, Veneracea, and Solenacea (Yonge 1957). Only in a few veneroids such as *Zirphaea* and in members of the myoid superfamily *Saxicavacea*, e.g., *Hiatella* (Hunter 1949), do the outer surfaces of the middle folds become fused. The Lucinacea (Allen 1958) and Leptonacea possess an anterior inhalant stream, though in the former superfamily a posterior inhalant siphon is exclusively associated with the expulsion of pseudofeces. The remaining veneroids are more typical in possessing posterior inhalant and exhalant siphons and this situation can be correlated with a deeper burrowing mode of life and simplification of the life-style. In the Cardiacea, only fusion of the inner mantle folds occurs and no true siphons are formed; the exhalant aperture results only from the apposition of the inner folds (Yonge 1969). This is probably a primitive feature, since these bivalves have close affinities with the infaunal Crassatellacea, a group with many

primitive and lucinoid adaptations (Allen 1968).

In the infaunal Veneroida and Myoida, a deeper burrowing mode of life can often be correlated with the fusion of more of the mantle folds in forming the siphons. In the shallow burrowing Cardiacea, Veneracea, and Isocardiacea (Ansell 1961, Yonge 1957), the siphons are formed by fusion of the inner and middle mantle folds (type B, Yonge 1957). In the deep-burrowing members of the Mactracea (*Lutraria*), Saxicavacea (*Panope*), and Myacea (*Mya*), mantle fusion encompasses the inner surface of the outer folds also (type C, Yonge 1957). In the epifaunal heteromyarian *Dreissena*, the siphons are formed by fusion of the inner folds only (type A, Yonge 1957), as they are in *Trapezium*. This feature is associated with the general absence of long, protected siphons in bivalves assuming this life-style. The siphons of *Trapezium* and *Petricola* (Purchon 1955a) are complex, with an elaborate arrangement of papillae and two unusually long tentacles that are almost certainly sensory.

The ciliary currents of the organs of the mantle cavity of *Trapezium sublaevigatum* are similar to those possessed by a wide range of veneroids. The ctenidia are plicate as in *Glossus* (Owen 1953) and *Claudiconcha* (Morton 1978), and the ctenidial ciliation is of type C(Ib) as in *Venus* (Ansell 1961). Within the Veneroida a very wide range of ctenidial ciliation is seen and there is often an overall reduction in the height of the outer demibranch in relation to the inner. Similarly, the category 3 ctenidial/labial palp junction (Stasek 1964) is seen in a very wide range of veneroids, and the size and ciliation of the ctenidia and labial palps is related to the mode of life of the individual concerned. In the case of *T. sublaevigatum* the plication increases the surface area of the ctenidia, despite a reduction in the dorsoventral height of the outer demibranch. The labial palps are relatively large and cope with the large amounts of material the ctenidia have the potential to collect. The stomach of *T. sublaevigatum* is similar to that of a wide range of eulamellibranchs and is of type V (the

internal morphology is only discretely modified in different species, which adapts them to a particular mode of life). Thus, the relatively large gastric shield and the large sorting areas indicate that liberal amounts of material may enter the stomach for processing. Similarly, the conjoined style sac and midgut of *T. sublaevigatum* has a structure typical of a wide range of eulamellibranchs but most notably *Geloina erosa* and *Claudiconcha japonica* (Morton 1976, 1978).

In *Dreissena polymorpha*, *Geloina erosa* (Morton 1969, 1976), and *Barnea candida* (Purchon 1955b), the renopericardial apertures are located on the floor of the pericardium behind the heart; the kidney extends under the posterior byssal retractor in *Dreissena* and up to the posterior pedal retractor in *Geloina*. In *Trapezium sublaevigatum*, the renopericardial apertures open into the pericardium in front of the heart and the kidney extends under the heart to the posterior byssal retractor muscle as in *Laevicardium crassum* (White 1942). In *Dreissena*, *Geloina*, and *Barnea*, the pericardial gland is associated with the pericardium and not with the auricles, whereas in *T. sublaevigatum* (as in *Pholas dactylus* and *Pholadidea loscombiana*, Purchon 1955b) the opposite is true. White (1942) has reviewed the location of this gland in many bivalves.

In general, the Veneroidea are infaunal bivalves with the byssus retained late into life in representatives of only a few superfamilies, e.g., the Carditacea, Gaimardiacea, Dreissenacea, and Arcticacea. In all these bivalves there is a trend toward the heteromyarian form, especially in the Dreissenacea. *Trapezium sublaevigatum* shows some heteromyarian features in that the anterior adductor and byssal retractors are reduced relative to the posterior. The modifications to the hinge plate have already been alluded to. *Trapezium* is not so modified as the rocky shore mytilids or freshwater dreissenids, however, and the lateral slimness of the ventral region of the shell enables it to nestle deep into crevices. In *Dreissena* and *Septifer* (Yonge and Campbell 1968) the shell is widest ventrally; this adaptation enables them to withstand rapid water movement.

Yonge (1969) considers that the hetero-

myarian Carditacea have affinities with the isomyarian Crassatellacea; Morton (1970) considers that the Dreissenacea have affinities with the Corbiculacea (the freshwater epifaunal niche is just as available as the rocky intertidal). However, it is difficult to arrive at similar conclusions with regard to *Trapezium* because the bivalves it is supposed to be closely related to (*Arctica* and *Cyprina*) have yet to be adequately studied.

Assuming that the interpretation of the superfamily Arcticacea is correct, however, it would seem likely that the ancestors of *Trapezium*, as with the other heteromyarian bivalves mentioned above, must be sought among a wide range of isomyarian forms. Thus, a study of *Arctica* in particular would be extremely valuable in helping to determine how the heteromyarian form in *Trapezium* could have evolved. When more studies of this kind have been undertaken we will be better able to determine common criteria and evaluate the heteromyarian condition in the Bivalvia as a whole.

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