THE FUNCTIONAL MORPHOLOGY OF THE ANTARCTIC BIVALVE *THRACIA MERIDIONALIS* SMITH, 1885 (ANOMALODESMATA: THRACIIDAE)

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ABSTRACT

The functional morphology of the Thraciidae is poorly understood. Although some morphological aspects of several members have been described, only *Trigonothracia jinxingae* from Chinese waters is known in detail. *Thracia meridionalis* is the only representative of the family in Antarctic waters, and is common in Admiralty Bay, King George Island, where it inhabits muddy sediments. *Thracia meridionalis* shares many features with *Tr. jinxingae* that are typical of most Anomalodesmata, i.e. a secondary 'ligament' of thickened periostracum, extensively fused mantle margins, ctenidia of type E, a ctenidial-labial palp junction of category III, a stomach of type IV and simultaneous hermaphroditism. *Thracia meridionalis* is, however, strikingly different from *Tr. jinxingae* in a number of ways, such as the presence of a fourth pallial aperture, statocysts of type B_3, heterorhabdic ctenidia, direct communication between the mantle chambers, a deep-burrowing habit (individuals lying on the left shell valve), siphons that retract into mucus-lined burrows, a stomach with extensive sorting areas, a rectum which passes over the kidneys and separate male and female gonadial apertures. There is, therefore, a greater range of morphological diversity within the Thraciidae than previously suspected.

INTRODUCTION

The subclass Anomalodesmata Dall, 1889 comprises widely diverse extant families, exhibiting virtually all life habits found in the Bivalvia (Morton, 1981a). Nevertheless, knowledge of the morphology, habits and evolution of its species is still modest, since members of the Anomalodesmata are among the rarest bivalves, occupying extremely narrow niches (Morton, 1985a). The Thraciidae Stoliczka, 1870 is a good example of these statements. Although the family comprises about 30 species (Boss, 1982) distributed within nine genera, there is either little or no anatomical information available for most of them, and this is scattered in a vast malacological literature (for a review see Coan, 1990). Only the functional morphology of *Trigonothracia jinxingae* (Xu, 1980) has been described in detail. The author of that study (Morton, 1995) commented on the impossibility of reviewing the taxonomic status of the genera in the absence of detailed information on the morphology of any other thraciid. *Trigonothracia jinxingae* was, in fact, the only thraciid scored for the morphological characters selected in a cladistic analysis of the Anomalodesmata (Harper, Hide & Morton, 2000).

Thracia meridionalis Smith, 1885, the only representative of the Thraciidae reported in Antarctic waters, is a notable exception among the Anomalodesmata, along with *Tr. jinxingae* (Morton, 1995), for being rather common and widespread. It probably has a circum-Antarctic distribution, being found around the continent proper, extending through the Antarctic Peninsula, South Shetlands, South Orkneys, South Sandwich Islands and South Georgia to the Magellanic Region and the Falkland Islands, Kerguelen, Marion and Prince Edward Islands (Dell, 1990). The highest recorded density for the species is 13 individuals/m^2 off the west coast of the Antarctic Peninsula (Mühlenhardt-Siegel, 1989).

Throughout its geographic range, *T. meridionalis* has been recorded from depths of 5–752 m (Dell, 1990; Hain, 1990) in a wide variety of soft bottoms such as mud, muddy sand, sand and gravel (Nicol, 1966; Mühlenhardt-Siegel, 1989). Bottom temperatures from where individuals have been collected range from −1.5 to −5.34°C (Nicol, 1966; Dell, 1972).

Information on the morphology of *T. meridionalis* is restricted to prodissoconch length (Hain & Arnaud, 1992), detailed descriptions of the shell valves (Nicol, 1966; Narchi, Domaneschi & Passos, 2002) and reports of intraspecific variations in shell outline (Soot-Ryen, 1951; Dell, 1964). *Thracia meridionalis* has been included recently in a molecular phylogeny of the Anomalodesmata (Dreyer, Steiner & Harper, 2003).

Here we provide a detailed study of the functional morphology of *T. meridionalis* with the aim of providing biological information on one of the commonest Antarctic bivalves, as well as contributing to a better knowledge of the barely studied Thraciidae.

MATERIALS AND METHODS

During the austral summers of 1996/97, 1997/98 and 2000/01, living specimens of *T. meridionalis* were collected from muddy sediments at depths of between 40 and 60 m in Admiralty Bay, King George Island, Antarctica (62°05′ S – 58°23.5′ W), and kept in aquaria with natural sediment and circulating seawater (35‰) at the Brazilian Antarctic Station 'Comandante Ferraz'. Aquaria were housed in a room at $0 \pm 1°C$ where the animals' burial activities and the behaviour and functional morphology of the siphons were studied. Sorting mechanisms in the mantle cavity and stomach were elucidated using colloidal graphite, a suspension of carmine powder and fine, natural organic and mineral particles deposited on the sediment surface of the aquaria. For histological sections, specimens relaxed in a 4% magnesium chloride solution were fixed in Bouin's fluid, dehydrated in a graded ethanol series and embedded in resin according to instructions in the '7022 18500 Leica Historesin

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Embedding Kit'. Sections (1–6 μm thick) were stained with either Delafield's haematoxylin and eosin, or toluidine blue counterstained with basic fuchsin. For scanning electron microscopy (SEM), small pieces of organs and tissues were prefixed in a solution of 2.5% gluteraldehyde, 2% paraformaldehyde and 2.5 mM calcium chloride in 0.1 M cacodylate buffer at pH 7.4, the osmolarity being adjusted to 1000 mOsm by adding sucrose. Following primary fixation, samples were washed in three changes of cacodylate buffer solution and post-fixed in 1% osmium tetroxide in cacodylate buffer for 45 min. After secondary fixation, specimens were washed in three changes of buffer, immersed in 1% tannic acid in cacodylate buffer for 15 minutes, washed in distilled water, dehydrated in an acetone series and critical point dried. Finally, the biological material was mounted with silver paint on aluminium stubs, gold coated and viewed with a Zeiss DSM 940 scanning electron microscope. Shells were ultrasonically cleaned in distilled water for 10 min, dried overnight in a 60°C oven, mounted with silver paint on stubs and gold coated prior to examination on the SEM.

Voucher specimens of *T. meridionalis* are lodged in the collections of the Museu de Zoologia da Universidade de São Paulo, Brazil, and assigned the registration numbers MZSP 40934 (three whole specimens), MZSP 40935 (four whole specimens), MZSP 40936 (four complete shells; three isolated valves) and MZSP 40937 (six isolated valves).

RESULTS

Shell

Nicol (1966) and Narchi *et al.* (2002) give detailed descriptions of the shell valves of *T. meridionalis*, here complemented by details obtained mainly from SEM images. The external surface of the shell bears microscopic pustules (up to 30 μm in diameter) that show a tendency to align themselves commarginally, and numerous, fine commarginal growth lines. The pustules are made of calcified periostracum secreted by the internal surface of the outer mantle fold in advance of formation of the outer shell layer. Both outer and inner calcareous shell layers in *T. meridionalis* have a homogeneous, granular microstructure.

The hinge is edentulous, with a robust external, parivincular, opisthodetic ligament connected to a chondrophore in each valve (Fig. 1). The ligament comprises a thick, yellowish fibrous layer, covered by a thin, dark-brown lamellar layer that extends to just beyond the anterior and posterior limits of the fibrous layer. A secondary 'ligament' of periostracum (Yonge, 1982) assists in the alignment of the edentulous shell valves. A fragile, arch-shaped lithodesma is present at the anterior end of the ligament of juvenile specimens only.

The largest individual of *T. meridionalis* obtained for the present study measured 33 mm in length, 25 mm in height and 13.5 mm in width. The ratio of shell width:height:length ($n = 40$ specimens) has been calculated as 1:1.93 (± 0.13 SD): 2.46 (± 0.16 SD). The ratios of shell width:length, height:length, width:height and pre-umbonal length:post-umbonal length have also been calculated as 0.41 ± 0.02 SD, 0.78 ± 0.02 SD, 0.52 ± 0.03 SD and 1.02 ± 0.17 SD, respectively.

The larval shell was eroded in most individuals ($n = 40$). The smooth prodissoconch I measured 168.96 μm $\pm$ 1.99 SD in length ($n = 5$), and prodissoconch II, ornamented with faint commarginal growth lines, measured 222.78 μm $\pm$ 4.45 SD in length ($n = 5$).
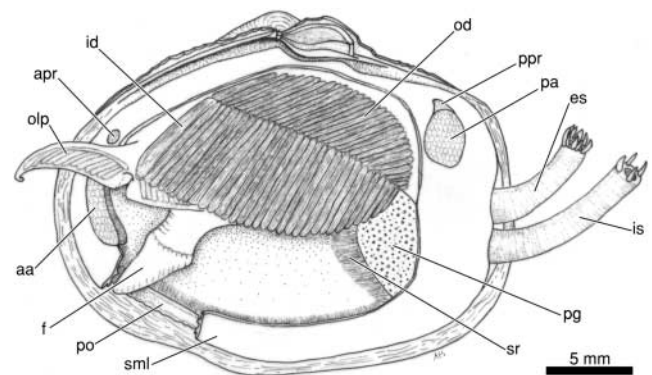
Mantle

The extensively fused mantle edges have four apertures: a small, anterior pedal gape, inhalant and exhalant openings and a tiny
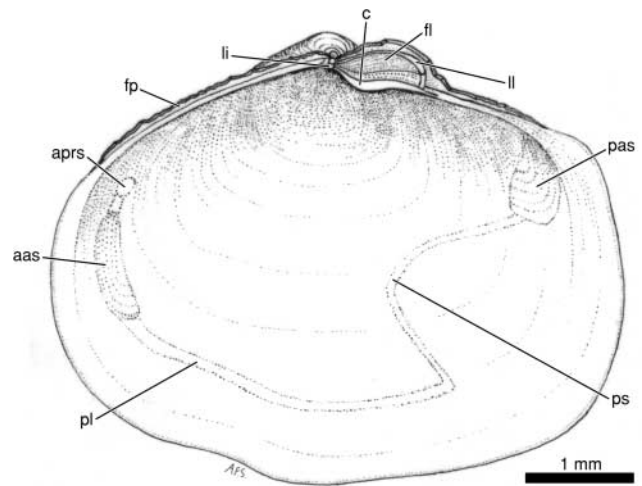

Figure 1. *Thracia meridionalis.* Internal view of the right shell valve. Abbreviations: aas, anterior adductor muscle scar; aprs, anterior pedal retractor muscle scar; c, chondrophore; fl, fibrous layer of ligament; fp, secondary ligament of fused periostracum; li, lithodesma; ll, lamellar layer of ligament; pas, posterior adductor muscle scar; pl, pallial line; ps, pallial sinus.

fourth pallial aperture, which opens into the siphonal embayment, close to the base of the inhalant siphon. Dorsally, between the adductor muscles, mantle fusion involves both the inner and middle folds (type C of Yonge, 1957), leading to the formation of a thick, extensive 'secondary ligament' of periostracum. Ventrally, posterior to the pedal gape, fusion involves the inner folds and the inner surfaces of the middle folds (type B of Yonge, 1957). Elsewhere, mantle fusions are of the inner folds only (type A of Yonge, 1957). At the pedal gape all folds hang free.

The inner mantle epithelium within the limits of each siphonal retractor muscle is richly provided with gland cells with basal nuclei and a number of secretory globules, interspersed with supporting cells provided with apical nuclei and 10 μm-long cilia (Figs 2, 3). These glandular areas show a striking asymmetry, those on the right mantle lobe being wider and thicker (130 μm) than on the left (15 μm-thick). Both adults

Figure 2. *Thracia meridionalis.* The organs of the pallial cavity viewed from the left side after removal of left valve and partial section of the left mantle lobe. Abbreviations: aa, anterior adductor muscle; apr, anterior pedal retractor muscle; es, exhalant siphon; f, foot; id, inner demibranch; is, inhalant siphon; od, outer demibranch; olp, outer labial palp; pa, posterior adductor muscle; pg, pallial gland; po, pedal opening; ppr, posterior pedal retractor muscle; sml, sectioned mantle lobe; sr, siphonal retractor muscles.
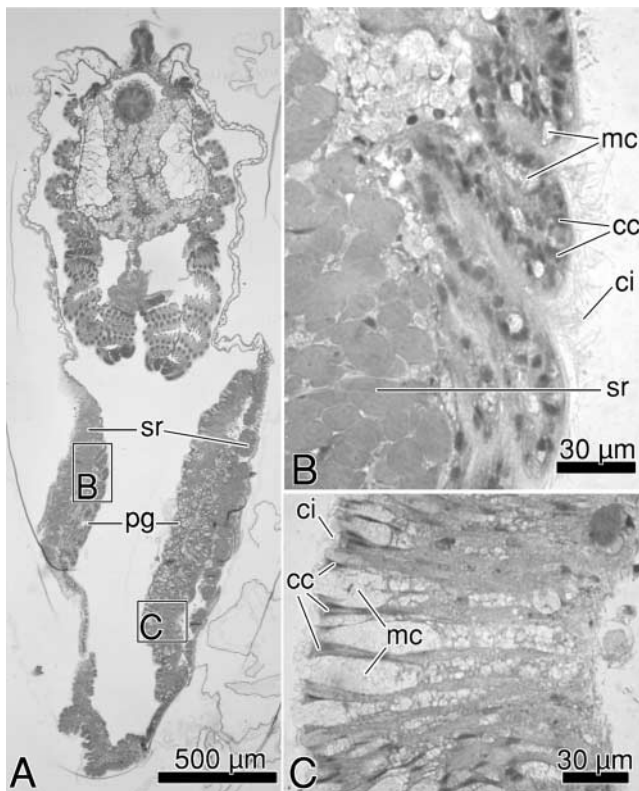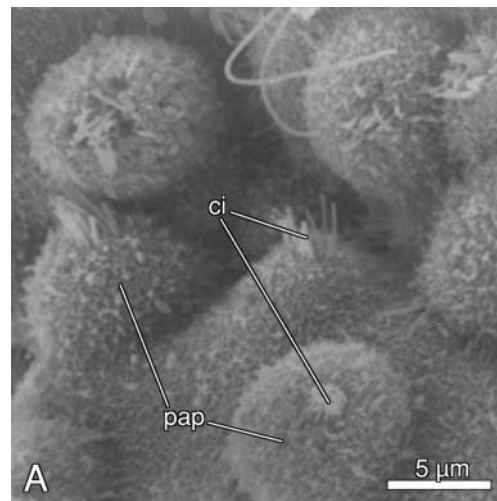
Figure 3. *Thracia meridionalis*. **A.** Light micrograph of a transverse section through the mantle in the region of the siphonal retractor muscles showing the asymmetry between the right and left pallial glands. Abbreviations: pg, pallial glands; sr, siphonal retractor muscles. **B** and **C.** Details of the corresponding framed areas in '**A**' showing the left and right pallial glands, respectively. Abbreviations: cc, ciliated cells; ci, cilia; mc, mucus cells; sr, siphonal retractor muscles.

and immature individuals have asymmetrical pallial glands with identical morphologies and restricted to the infrabranchial chamber.

Siphons

The siphons of *Thracia meridionalis* are separate and formed of the inner mantle folds only (type A of Yonge, 1948a, 1957, 1982). The longer inhalant siphon can extend to twice the shell length. The siphonal tips are fringed with a single row of finger-like tentacles, seven to 12 on the shorter exhalant siphon and four to eight on the inhalant. Not unusually, tentacles are unevenly spaced and some are bifid. SEM images revealed the presence of scattered tufts of >10 cilia which are 1.5−2.5 μm long, protruding from volcano-like papillae on the internal and external epithelium of both siphons; such ciliated papillae are especially abundant on the tentacles (Fig. 4).

In transverse section both siphons have a similar structure (Fig. 5). Beneath the outer epithelium lie a narrow band of circular muscles (c1) and a layer of scattered longitudinal muscle fibres (L1). Internal to the latter is a thick, loose band of circular muscles (c2), the inner portion of which overlaps with a zone of longitudinal muscles (L2) arranged in distinct blocks separated by radial muscle strands. Inside the longitudinal muscle layer (L2) is a wide haemocoel, partitioned by the radial fibres, and evenly spaced siphonal nerves (some 100 μm in maximum width). These nerves, four in the inhalant and six in the exhalant, are partially embedded in another zone of longitudinal bundles of muscle fibres (L3), which underlies the haemocoel. Further internally there is a band of circular muscles (c3)

Figure 4. *Thracia meridionalis*. Scanning electron micrograph of the ciliated sensory receptors on a tentacle of the exhalant siphon. Abbreviations: ci, cilia; pap, papillae.

followed by scattered individual longitudinal muscles (L4). The innermost layer comprises a narrow band of circular muscles (c4) juxtaposed to the inner epithelium.

Both siphons undertake peristaltic globular inflations as they open and line the sediment through which they pass with thick mucus. Once the mucus lining is completed, the siphonal tips are kept retracted from the sediment surface, enabling the animal to burrow deeper, using the mucus-lined tubes as siphonal extensions. Thus, in an undisturbed aquarium a 10 mm-long individual was found 80 mm below the sediment surface. The position adopted in the sediment is illustrated in Figure 6, the animal lying on the less convex, left valve with the sagittal plane almost parallel to the surface. The siphons rarely extend above the sediment surface and, when they do, the inhalant is held passively in a slightly curved position with the aperture some 10 mm above the sediment surface. The siphons of *T. meridionalis* are almost insensitive both to mechanical and photic stimulation, remaining indifferent to rough manipulation with forceps and high and low luminosities originating from an electronic flash or a microscope illuminator, respectively.

The siphonal burrows emerge at the sediment surface as round openings about 2.5–3.0 mm in diameter and about 15 mm apart, each bordered by a collar-like extension of the mucous lining (Fig. 6). Within the substratum, the mucous tubes converge and fuse near the bivalve, forming a common, short chamber at the posterior shell margin.

Fifteen individuals of *T. meridionalis* were observed for 32 days in aquaria. During that period all retained their siphonal tubes unaltered, even when clogged with sediment. Blocking the openings of the siphonal ends of the burrows with mud evoked the animal to expel a strong jet of water, unclogging them. Unclogging was also achieved by a sudden withdrawal of the siphons, which in turn pull the obstructive mud down the burrows. On the other hand, the addition of a 1−2 cm-thick layer of sediment over the siphonal burrow caused the animal to extend its siphons to the sediment surface, pushing aside such a barrier. Vertical migration occurred when the siphonal tips were unable to reach the sediment surface.
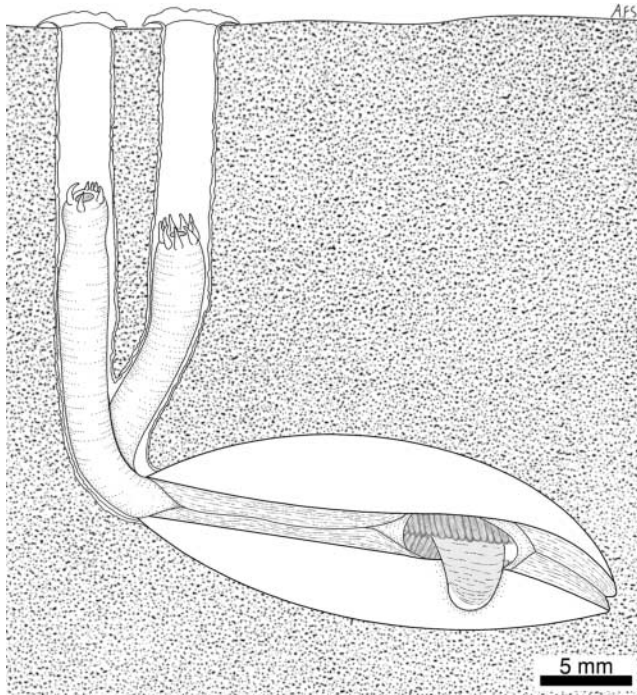
Ctenidia

The ctenidia of *T. meridionalis* are eulamellibranch, deeply plicate and heterorhabdic. The inner demibranch comprises both lamellae with a ventral marginal food groove, while the
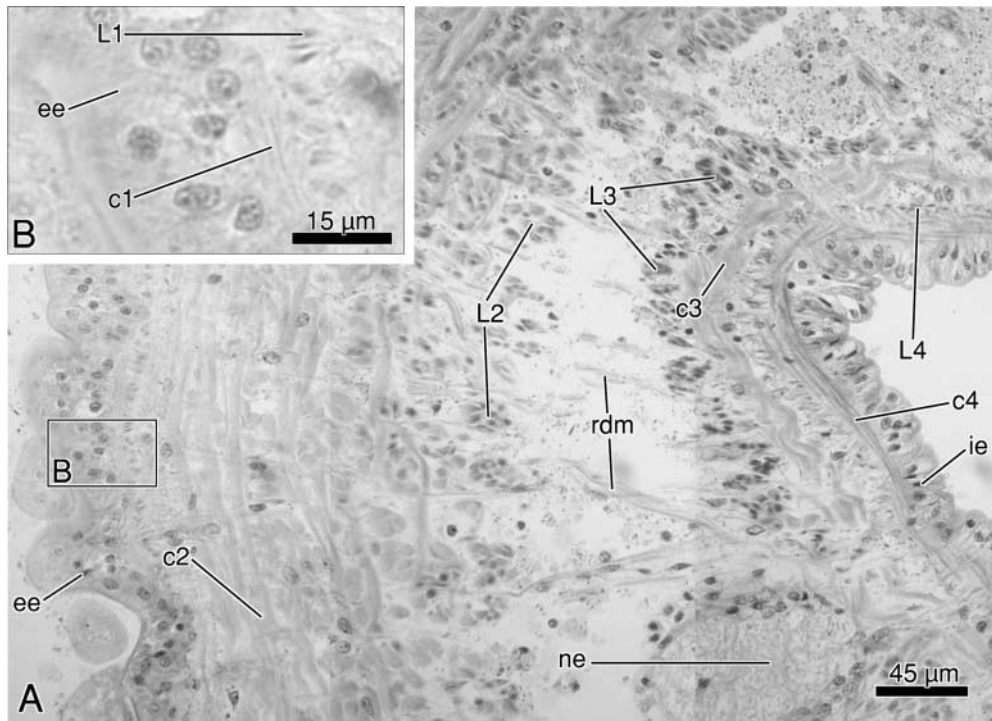
Figure 5. *Thracia meridionalis*. **A.** Light micrograph of a transverse section through the inhalant siphon showing the musculature. Abbreviations: c2 to c4, circular muscle layers; ee, external epithelium; ie, internal epithelium; L2 to L4, longitudinal muscle layers; ne, nerve; rdm, radial muscle strands. **B.** A detail of the corresponding framed area in '**A**' showing the outermost layers of longitudinal and circular muscles. Abbreviations: c1, circular muscle layer; ee, external epithelium; L1, longitudinal muscle layer.

outer comprises the upturned descending lamella only (Fig. 7A). The ventral tips of the anterior filaments of the inner demibranch are not inserted into the distal oral groove and the ctenidial–labial palp junction is thus of category III (Stasek, 1963).

Figure 6. *Thracia meridionalis*. A ventral view of the animal in its natural position lying on the left valve.
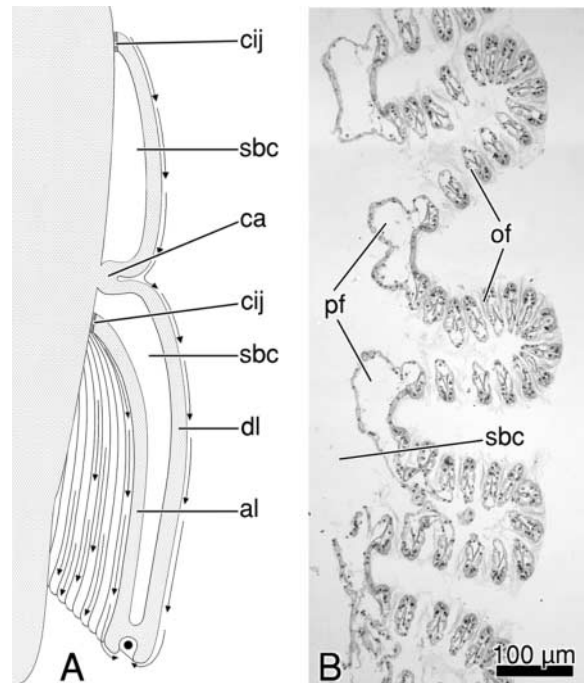
Figure 7. *Thracia meridionalis*. **A.** Diagrammatic vertical section through the right ctenidium to show the ventralward (arrows) and oralward (•) ciliary currents. Abbreviations: al, ascending lamella; ca, ctenidial axis; cij, ciliary junction; dl, descending lamella; sbc, suprabranchial chamber. **B.** Light micrograph of a cross-section through the outer demibranch, showing ordinary and principal filaments. Abbreviations: of, ordinary filaments; pf, principal filaments; sbc, suprabranchial chamber.

The frontal, latero-frontal and lateral cilia are about 15, 25 and 20 μm long, respectively; abfrontal ciliary tufts are numerous and widespread on principal filaments but scattered and rare on the ordinary ones. Frontal cilia do not differentiate into terminal cilia on the free end of the inner demibranch filaments. The frontal ciliary currents on both demibranchs beat toward the ventral marginal food groove and the ctenidia can thus be ascribed to type E (Atkins, 1937a).
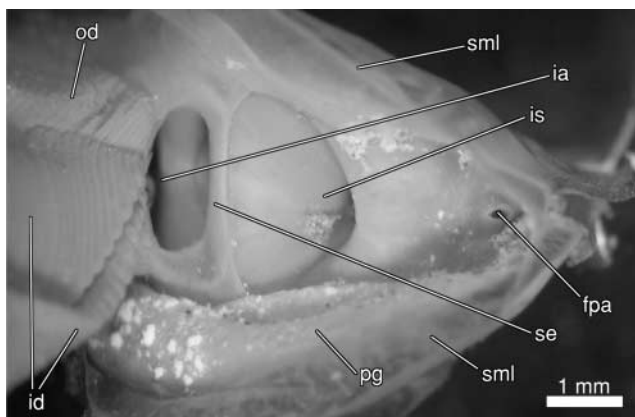
The principal filaments have an expanded 'U'-shaped frontal surface, their sides frequently sloping away (Fig. 7B). High and low alternate interlamellar septa unite the abfrontal surfaces of the descending and ascending portions of each principal filament. High septa almost reach the ctenidial axis while low ones extend but a short distance up from the ventral margin. Numerous and regularly spaced interfilamentar junctions compartmentalize the full extent of the intraplical spaces.

The ascending lamella of the inner and the upturned descending lamella of the outer demibranchs attach to the visceral mass by ciliary junctions. Posterior to the visceral mass, the ctenidial axes hang free from the body and the ascending lamellae of left and right demibranchs unite with each other by ciliary junctions, forming a capacious suprabranchial chamber. The posterior end of the ctenidial axes and inner demibranchs do not fuse with the inter-siphonal septum, as one would expect in a typical siphonate bivalve (Fig. 8). Supra- and infrabranchial chambers are thus in direct communication, the functional separation of the mantle cavity being accomplished by the juxtaposition of the aperture borders.

Sorting mechanisms on the ctenidia are of the '*Pinna* type' (Atkins, 1937b), i.e. fine particles travelling along the troughs between adjacent plicae are passed to an active oralward current within the ventral marginal food groove, while coarse particles travelling on the plical surfaces are transferred to the rejectory tracts on the mantle and visceral mass. By adjusting the distance among plicae and between the lateral edges of the marginal food groove, the animal can further regulate the oralward uptake of particles. Apposition of the plicae and lateral walls of the food groove hide the acceptance tracts exposing oncoming particles to an entirely rejectory surface; divergence leads to acceptance of a greater proportion of particles.

Foot

The small, thin, wedge-shaped foot has a poorly developed postero-ventral byssal groove, but no byssal gland. The epithelium on the distal portion of the foot is densely ciliated and comprises numerous mucus-secreting cells whilst on the basal portion of the organ, the epithelium bears a few scattered tufts of 2–3 μm-long cilia similar to those on the siphons. Ciliary currents were not detected on the surface of the foot.
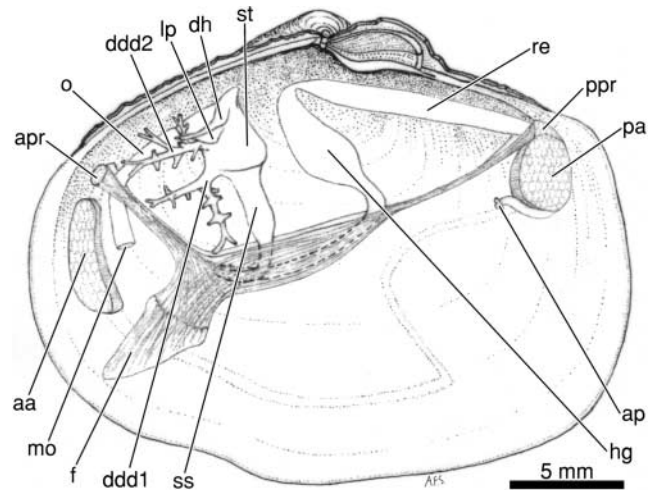
Within the basal portion of the foot lie the pedal ganglia and two statocysts. The latter conform to type B_3 of Morton (1985b) in that they are separate from the pedal ganglia and each possesses numerous irregular, inorganic statoconia. The statocyst capsule is some 60 μm in diameter and formed by a cuboidal, ciliated epithelium, the cilia being some 5 μm long.

The extrinsic pedal musculature consists of bilateral pairs of thin anterior and posterior pedal retractor muscles, the latter thinner (Fig. 9). Each anterior retractor attaches to the shell valves by a round insertion, dorsally placed and slightly separated from the anterior adductor muscle scar. Both anterior muscles converge on the sagittal plane of the animal where most of their fibres pass separately into the foot. Only the innermost bundles of each muscle criss-cross the ones arising from the opposite side, the left ones penetrating deeply into the right side of the foot and vice versa.

Each posterior retractor muscle attaches to the shell by a triangular insertion joined to the dorsal margin of the posterior adductor muscle scar. The right and left posterior retractors converge on the sagittal plane as they proceed anteriorly and fuse into a single bundle beneath the kidneys. This bundle extends further anteriorly into the proximal portion of the foot, where its fibres spread fanwise enveloping the visceral mass ventrally before entering the distal portion.

Apart from the extrinsic muscles, the foot contains a large number of isolated bundles of transverse muscle fibres whose extremities intermingle with and attach to those that form the lateral muscular walls of the organ.

Once removed from the substratum, adult specimens of *T. meridionalis* were able to re-burrow, though slowly. The largest collected individual (about 38 mm in shell length) remained unburied in aquaria for 23 days before starting its burrowing activities. Eight of 13 other individuals (10–28 mm in shell length) lying on either the left or right shell valve re-burrowed within 16 h of being placed on muddy sediment.

Figure 8. *Thracia meridionalis*. Ventral view of the posterior portion of the infrabranchial chamber showing the well-dilated direct communication (ia) with the suprabranchial chamber. Abbreviations: fpa, fourth pallial aperture; ia, inter-chamber aperture; id, inner demibranchs; is, proximal aperture of the inhalant siphon; od, outer demibranch; pg, pallial gland; se, inter-siphonal septum; sml, sectioned mantle lobe.

Figure 9. *Thracia meridionalis*. Left view of the musculature and alimentary canal. Abbreviations: aa, anterior adductor muscle; ap, anal papilla; apr, anterior pedal retractor muscle; ddd1 and ddd2, ducts from the digestive diverticula; dh, dorsal hood; f, foot; hg, hind gut; lp, left pouch; mo, mouth; o, oesophagus; pa, posterior adductor muscle; ppr, posterior pedal retractor muscle; re, rectum; ss, conjoined mid gut and style sac; st, stomach.
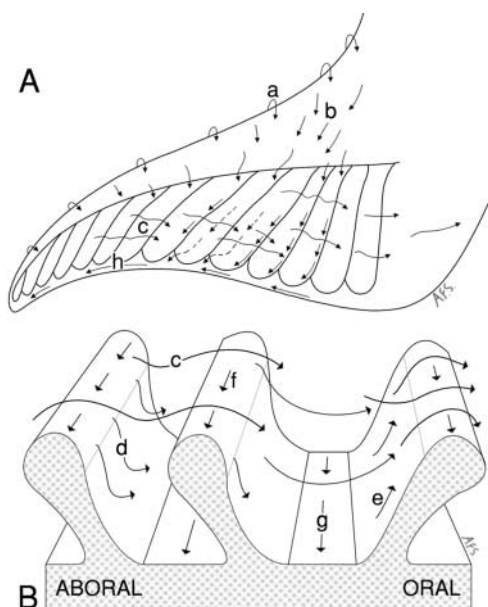
Figure 10. *Thracia meridionalis*. Diagram of the folded surface of (**A**) the left, outer labial palp with (**B**) a detail of three folds and respective ciliary currents. The arrows show the path taken by particles. Lettering: a to h, ciliary currents (see text for details).

Figure 11. *Thracia meridionalis*. Ciliary currents on the surface of the visceral mass (broken arrows) and right mantle lobe (solid arrows). Abbreviations: idil, line of insertion of the ascending lamella of the inner demibranch with the visceral mass; pf, pseudofaeces; pg, pallial gland.

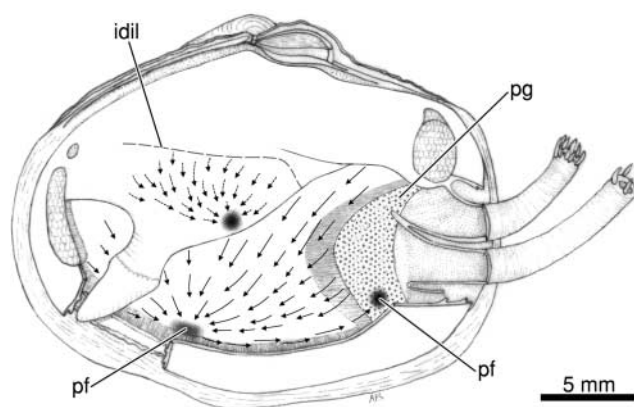Having burrowed, the animals remained relatively immobile, exhibiting no horizontal or vertical migration.

Labial palps

The labial palps are long and triangular. Their structure and ciliary sorting mechanisms are shown in Figure 10. The following ciliary currents were observed:

(1) dorsalward currents (Fig. 10A: a) on the smooth outer surface, conveying particles onto the folded inner surface;
(2) ventralward currents (Fig. 10A: b) on the smooth dorsal margin of the inner surface pass particles onto the folds;
(3) transversely directed currents (Fig. 10: c), operating oralward across the folds act as either acceptance or rejection currents, depending on either the size and/or total volume of particles;
(4) downward currents (Fig. 10B: d) on the oral fold surface pass excess material, or dense particles onto the floor between adjacent folds;
(5) upward currents (Fig. 10B: e) on the aboral fold surface recover light and small particles from currents 'd' and deliver them to currents 'c';
(6) rejection currents on, respectively, the crests (Fig. 10B: f) and grooves (Fig. 10B: g) of the folds, driving particles to the rejection current 'h';
(7) rejection current (Fig. 10A: h) on the smooth ventral margin of the inner surface, carrying particles to the tip of the palp, thence throwing them off to the mantle and visceral mass.

Ciliary currents of the visceral mass and mantle

The ciliary currents on the visceral mass are shown in Figure 11. Cilia on the anterior end of the visceral mass beat postero-ventrally, whereas those on the posterior end beat antero-ventrally. Waste material thus accumulates at a point on the postero-ventral edge of the visceral mass whence it eventually falls on to the mantle.

The ciliary currents of the mantle (Fig. 11) take material to the posterior end of the pedal gape where it accumulates in large masses. Thence, particles are either pushed by the foot and/or water jets through the pedal gape, or carried posteriorly by a powerful ventral rejectory tract to be expelled from the inhalant siphon as pseudofaeces after being bound in sticky mucus secreted from the pallial glands.

Alimentary canal

The mouth opens into a long, flattened oesophagus that enters antero-dorsally the globular, capacious stomach (Fig. 9). A long, conical-shaped, almost straight dorsal hood extends anteriorly from the left dorsal side of the stomach. Slightly anterior and ventral to the dorsal hood, arises a shallow, blind, well-defined left pouch. Two ducts from the digestive diverticula (Fig. 9: ddd1 and ddd2) enter the left wall of the stomach; two other closely disposed ducts (Fig. 12: ddd3 and ddd4) enter the right wall.

The conjoined style sac and mid gut leaves the floor of the globular region of the stomach and extends postero-ventrally into the visceral mass. Thence, the isolated mid gut turns abruptly anteriorward, makes a simple loop to the right side, and extends posteriorly as the hind gut. The hind gut greatly increases in diameter and accumulates faeces as it ascends to the umbonal region. Here it returns to a narrow diameter as it goes through the anterior wall of the pericardial cavity, penetrates the ventricle, passes over the kidneys and terminates in the anal papilla. This last portion of the gut varies in diameter depending on the amount of retained faeces.

Internally, the oesophageal epithelium is thrown into a dorsal and a ventral series of longitudinal ciliated folds, separated from each other by lateral ciliated grooves (Fig. 12). Cilia on the crests of the folds propel the mucus-bound food strand towards the crystalline style in the stomach where isolated particles fall on the sorting area surrounding the entrance of the oesophagus into the stomach (Fig. 12: sa8). Ciliary currents along the folds of this area beat anteriorward, conveying particles to the rim (Fig. 12: rm) of the oesophageal orifice. Here, transverse ciliary currents drive particles towards a longitudinal ridge (Fig. 12: r) on the roof of the stomach, then deep into the dorsal hood.

On the roof of the dorsal hood, another ridge (Fig. 12: r2) conveys material outward, into a blind depression on the rear
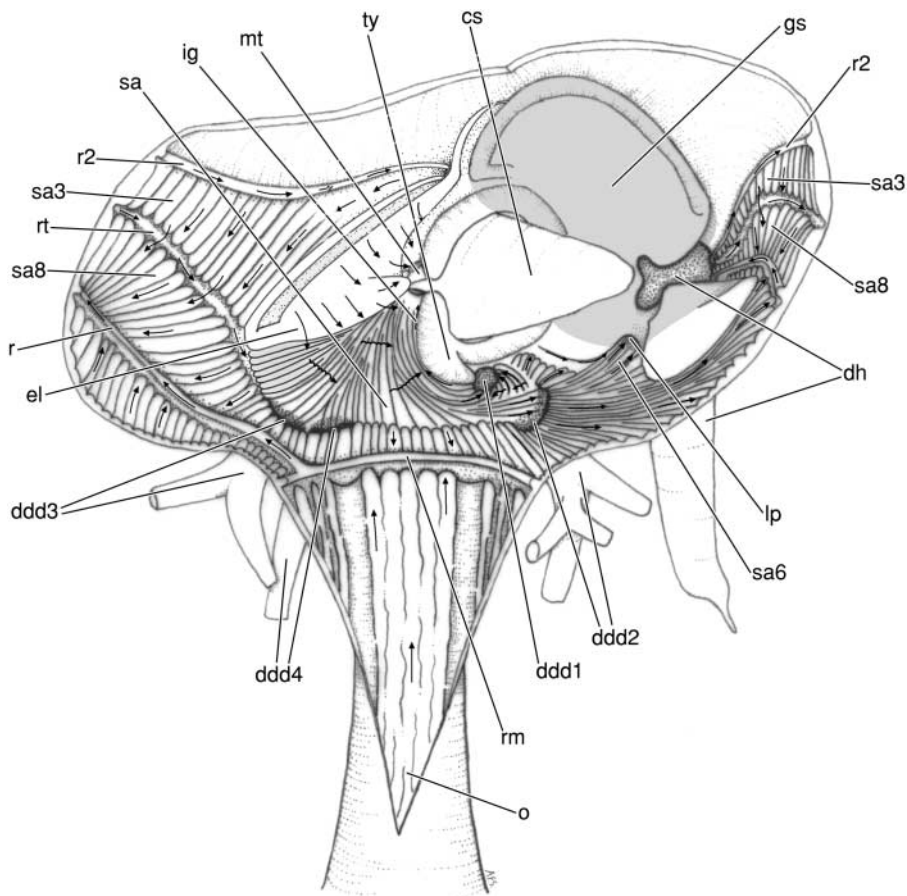
Figure 12. *Thracia meridionalis*. Diagram of an internal view of the oesophagus and stomach after being opened by an incision along the dorsal wall. Abbreviations: cs, crystalline style; ddd1 to ddd4, orifices of ducts from the digestive diverticula; dh, dorsal hood; el, forwardly projecting elevation; gs, gastric shield; ig, intestinal groove; lp, left pouch; mt, minor typhlosole; o, oesophagus; r, ridge passing from the oesophageal orifice over the roof of the stomach to the interior of the dorsal hood; r2, ridge on the posterior wall of the dorsal hood; rm, rim around the opening of the oesophagus into the stomach; rt, rejection tract; sa, sorting area on the anterior floor of stomach; sa3, sorting area of the dorsal hood and right side of the stomach; sa6, sorting area in the left pouch; sa8; sorting area on the anterior roof of the stomach; ty, major typhlosole.

stomach floor. This ridge limits posteriorly a sorting area (Fig. 12: sa3) on which particles are passed to sorting area 'sa8' and so returned to the dorsal hood. Some particles travelling on 'sa3' may be captured by cilia on a rejection tract (Fig. 12: rt) between 'sa3' and 'sa8'. From here, particles are carried to the anterior sorting area (Fig. 12: sa), which extends among and enters the ducts from the digestive diverticula. Transversely directed ciliary currents on the folds of this area carry material into the intestinal groove, while cilia in the troughs pass particles towards the digestive diverticula.

Interposed between 'sa3' and 'sa' lies a long forward-projecting elevation of the right wall of the stomach (Fig. 12: el) by which particles are either discharged into the mid gut or passed to 'sa'.

The minor typhlosole terminates at the aperture of the conjoined style sac and mid gut into the stomach. Immediately after entering the stomach, the major typhlosole and accompanying intestinal groove extend a short distance to the left, to penetrate and finish at the aperture of the duct from the digestive diverticula, which enters the left, anterior floor of the stomach (ddd1).

The posterior part of the left wall of the stomach is covered by an extensive gastric shield that sends lobes into the style sac, dorsal hood and left pouch. Sorting area 'sa6' carries and concentrates particles into the shallow, blind left pouch.
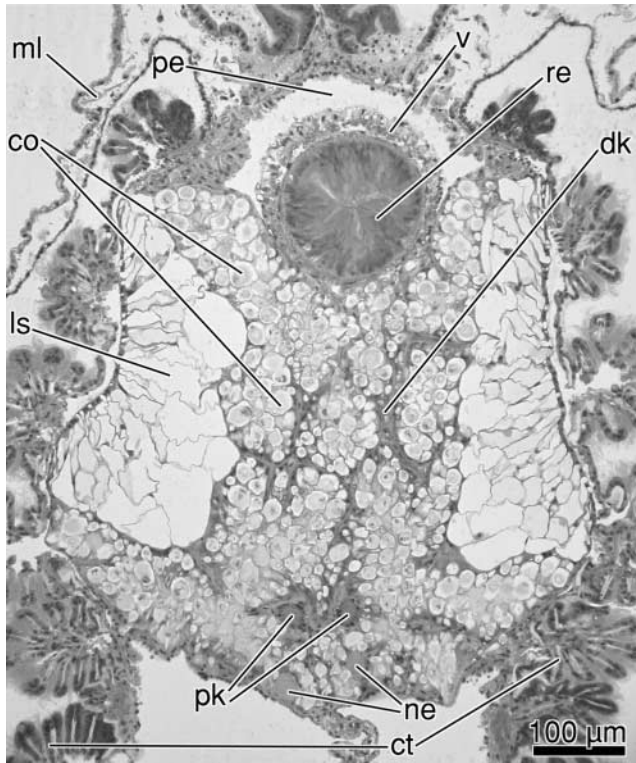
Pericardium and kidney

The pericardial cavity is located just below the umbones. The heart comprises a ventricle, penetrated by the rectum, and lateral auricles that broaden as they leave the ventricle and approach the ctenidial axes.

On the postero-ventral floor of the pericardium lies a pair of renopericardial apertures that lead into the narrow proximal ducts of the kidneys. These ducts are ciliated, nearly straight and long, extending to the posterior end of the organ, where they continue as the distal limbs. The latter portion comprises a system of broad meandering tubules whose cells are filled with spherical excretory concretions up to 30 μm in diameter (Fig. 13). Each kidney discharges into the suprabranchial chamber via a ciliated renal aperture located close to the female aperture on each side of the body.

A lacunal system flanks the kidneys, occupying the space between the distal limbs and outer epithelium of the visceral mass. Such lacunae are delimited by a thin, squamous epithelium.

Reproductive system

Thracia meridionalis is a simultaneous hermaphrodite, with a complete separation of the paired male and female gonads (Fig. 14).

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Figure 13. *Thracia meridionalis.* Light micrograph of a transverse section through the pericardial cavity and kidneys. Abbreviations: co, excretory concretions within the distal lobes of the kidneys; ct, ctenidia; dk, distal lobes of the kidneys; ls, lacunal system; ml, mantle lobe; ne, nerves; pe, pericardial cavity; pk, proximal lobes of the kidneys; re, rectum; v, ventricle in systole.

The large, bag-like ovaries occupy a dorsal position in the visceral mass, enclosing the stomach and part of the digestive diverticula. Numerous large ovocytes, each encased in a thick gelatinous capsule, can be seen through the translucent walls of the follicles. The mean ($\pm$SD) diameter of the mature ovocytes, free in the lumen of the follicles, is 200 ± 24 μm ($n = 60$), while the largest ovocyte found measured 247 μm in diameter. The thick capsule (about 10% of cell diameter) is considered to be a vitelline membrane, secreted by the ovocyte itself while it is still attached to the ovarian wall. The point of attachment to the follicle is easily identified as a micropyle even in spawned ovocytes (Fig. 15A).

The testes form the ventral portion of the visceral mass, partially encompassing the style sac, ovaries and digestive diverticula. The spermatozoa possess a conical, 3 μm-long head with no obvious acrosome, a middle piece which comprises four to five mitochondrial spheres and a long flagellum (about 70 μm) (Fig. 15B).

DISCUSSION

This study of the functional morphology of *T. meridionalis* broadens our current understanding of the mode of life of the Thraciidae, which hitherto was largely based on a single species, *Trigonothracia jinxingae* (Morton, 1995), and provides new anatomical features that may be useful for any discussion of the puzzling relationships within the subclass Anomalodesmata (compare Harper *et al.*, 2000 with Dreyer *et al.*, 2003).

Taylor, Kennedy & Hall (1973) have shown that outer and inner layers of the shells of *Thracia* (*Homeodesma*) *convexa* Wood, 1815, *T.* (*Odoncineta*) *phaseolina* (Lamarck, 1818) and *T.* (*O.*) *villosiuscula* (Macgillivray, 1827) have a homogeneous microstructure. The shells of *Trigonothracia jinxingae* (Morton, 1995) and *Thracia meridionalis* (this study) similarly possess two homogeneous layers, a condition that has evolved in the Thraciidae
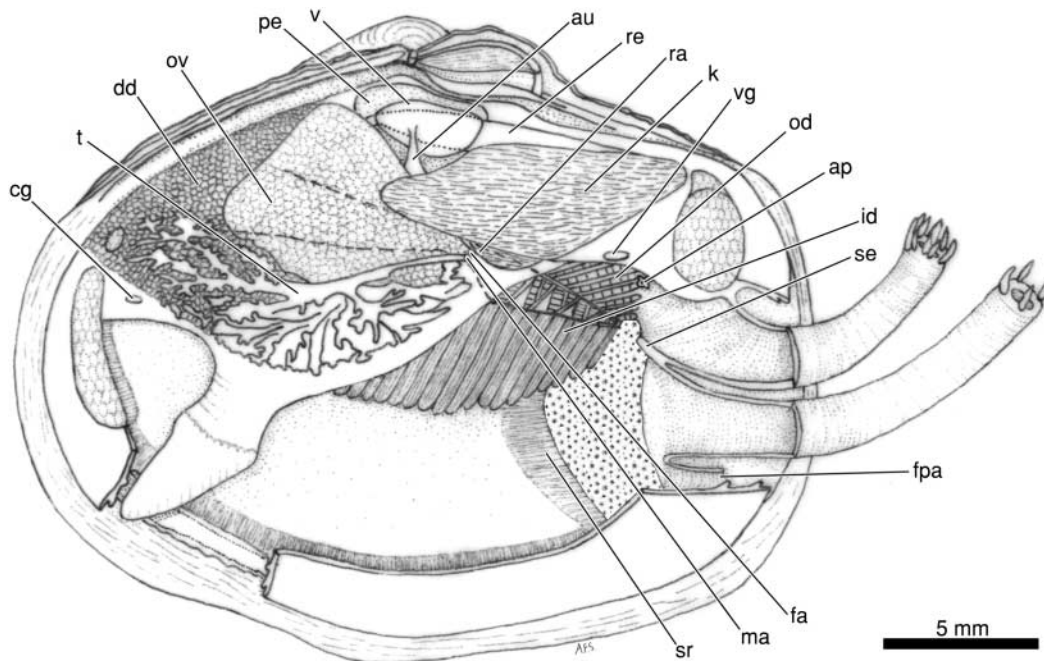
Figure 14. *Thracia meridionalis.* The organs of the visceral mass viewed from the left side after removal of the left valve, mantle lobe and ctenidium. Abbreviations: ap, anal papilla; au, auricle; cg, cerebral ganglion; dd, digestive diverticula; fa, female aperture; fpa, fourth pallial aperture; id, inner demibranch of right ctenidium; k, kidney; ma, male aperture; od, outer demibranch of right ctenidium; ov, ovary; pe, pericardial cavity; ra, renal aperture; re, rectum; se, inter-siphonal septum; sr, siphonal retractor muscle; t, testis; v, ventricle; vg, visceral ganglion.
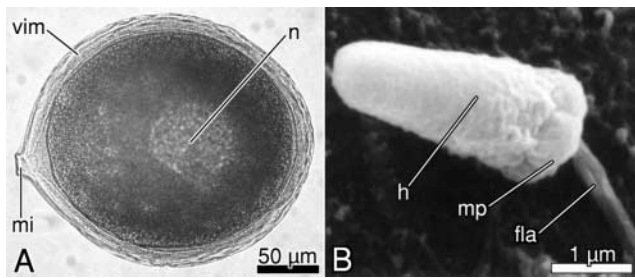
Figure 15. *Thracia meridionalis*. **A.** Light micrograph of an ovocyte. Abbreviations: mi, micropyle; n, nucleus; vim, vitelline membrane (capsule). **B.** Scanning electron micrograph of a spermatozoon. Abbreviations: fla, flagellum; h, head; mp, middle piece.

from prismato-nacreous shells typical of most anomalodesmatans (Boss, 1978).

Ornamentation of the shell surface by calcified periostracal structures, a primitive feature according to Carter & Aller (1975), has been identified in many species of Thraciidae, Laternulidae, Lyonsiidae and Pholadomyidae (Allen, 1961a; Aller, 1974; Carter & Aller, 1975; this study). In the Thraciidae, these structures occur in all genera, except *Lampeia* MacGinitie, 1959 and *Thraciopsis* Tate & May, 1900 (for a review see Kamenev, 2002). The formation of such ornamentation in *T. meridionalis* follows essentially the same mechanism proposed for *Laternula* by Aller (1974), i.e. the pustules are formed by the mantle in advance of the growing shell margin and subsequently incorporated into the outer shell layer.

Yonge & Morton (1980) considered that the function of the lithodesma was to assist in the alignment of the valves of the Thracioidea. This is certainly not the case in adult specimens of *T. meridionalis*, which lack a lithodesma. Valve alignment is achieved by the robust primary ligament assisted by a secondary 'ligament' of periostracum that extends well beyond the primary ligament. The lithodesma is only present in juvenile specimens, a condition that also occurs in many *Thracia* subgenera, e.g. *Thracia s.l.*, *Homeodesma*, *Cetothrax*, *Crassithracia*, and *Ixartia* (Coan, 1990).

As in most anomalodesmatans, *T. meridionalis* possesses extensively fused mantle margins. At the pedal gape, however, the outer, middle and inner mantle folds can be identified, hanging free on each mantle margin as in a typical bivalve. Such a condition differs from that described for the pedal gape of *Trigonothracia jinxingae* where each mantle margin comprises the free outer mantle fold and unified middle and inner mantle folds (Morton, 1995). Posterior to the pedal gape, *T. meridionalis* shares with *T. (O.) villosiuscula* (Atkins, 1937c) and *Tr. jinxingae* (Morton, 1995) a ventral mantle fusion of type B (Yonge, 1957).

In addition to *T. meridionalis*, a fourth pallial aperture is also present in other thraciids, e.g. *Thracia (H.) convexa* (Pelseneer, 1890), *Asthenothaerus* sp. (Pelseneer, 1911), *Parvithracia (Pseudoasthenothaerus) lukini* Kamenev, 2002 and *P. (P.) sirenkoi* Kamenev, 2002 (Kamenev, 2002), but not *Bushia elegans* Dall, 1886 (Dall, 1886) and *Trigonothracia jinxingae* (Morton, 1995). Atkins (1937c) and Yonge (1948b) have shown that pseudofaeces are expelled through this aperture in the Mactridae. In the Anomalodesmata, however, examination of living specimens (Yonge, 1952; Narchi, 1968; Morgan & Allen, 1976; Morton, 1974, 1977a, 1981b, 2002a; this study) has not demonstrated any function, pseudofaeces being expelled via the inhalant siphon. In *T. meridionalis*, pseudofaeces are also expelled through the pedal opening, where cleansing ciliary currents on the mantle surface predominantly concentrate material; thence water jets and/or pushing caused by the foot sweep pseudofaeces out of the animal.

Although the first description of a pallial gland in the Thraciidae is probably that of Pelseneer (1911), who noticed a thick glandular covering over the right siphonal retractor muscle of an unidentified species of *Thracia*, such a gland was clearly illustrated by Kiener (1834, pl. I, fig. b), bordering the anterior end of the siphonal retractor muscle on the right mantle lobe of *Thracia (Homeodesma) corbuloidea* Blainville, 1827. Nevertheless, Kiener (1834) neither described nor identified the gland in his figure.

The pallial glands of *T. meridionalis* correspond in structure to the so-called 'hypobranchial glands' (reviewed by Morton, 1977b) present in the supra- and infrabranchial chambers of the thracioideans *Periploma (Offadesma) angasai* Crosse & Fischer, 1864 and *Trigonothracia jinxingae* (Morton, 1981b, 1995). Morton (1977b) suggested reproductive functions for the glands of the heterodonts *Corbicula fluminea* (Müller, 1774) and *Fimbria fimbriata* (Linnaeus, 1758), the former species presenting larger and more active glands during the periods in which it incubates its larvae. Large pallial glands with a different function were described by Morton & Harper (2001) in the infrabranchial portion of the right mantle lobe of small individuals of *Cleidothaerus albidus* (Lamarck, 1819), a species that is closely related to *T. meridionalis* according to the molecular phylogenetic studies of Dreyer *et al.* (2003). In *C. albidus*, the glands are presumably the source of the cement by which juvenile specimens attach to the substratum (Morton & Harper, 2001). In *T. meridionalis*, the glands are equally developed in both adults and immature individuals, and restricted to the infrabranchial chamber where their mucus secretion entraps unwanted particles. The glands thus retain their ancient cleansing function in *T. meridionalis*.

Globular inflations of the siphons and mucus lining of their passage through the sediment, as here described for *T. meridionalis*, have been recorded for a number of anomalodesmatans, i.e. *T. (Ixartia) distorta* (Montagu, 1803) by Forbes & Hanley (1853), *T. (H.) conradi* Couthouy, 1839 by Morse (1919), *T. pubescens* (Pulteney, 1799) by Yonge (1937) [Coan (1990) noted that Yonge (1937) was actually studying *T. (O.) phaseolina*] and *Periploma (O.) angasai* by Morton (1981b). The mechanism of tube formation was first elucidated by Yonge (1937) and conforms to the process herein described for *T. meridionalis*. Once the mucous lining is completed, *T. meridionalis* retains the siphonal tubes unaltered, unlike *T. (H.) conradi* which frequently changes the position of its siphons in the sediment (Thomas, 1967).

On both siphons of *T. meridionalis*, the length and number of cilia protruding from each volcano-like papillae are similar to the type I sensory receptors of Hodgson & Fielden (1984), who linked them to chemoreception in *Donax serra* Röding, 1798 and *D. sordidus* Hanley, 1845. That is probably also the case in *T. meridionalis* although no test was performed with chemicals. Significantly, however, the siphons do not react to mechanical or light stimulation.

The removal or translocation of macrobenthos by iceberg impacts into the seabed is common in Antarctic shallow-water sites (Peck *et al.*, 1999). The retention of an ability to burrow by *T. meridionalis* throughout its life increases the probability of survival for specimens dislodged by such events. Among the Thraciidae, this capability is also retained by *T. pubescens* (Yonge, 1937) and *Trigonothracia jinxingae* (Morton, 1995), but not *Thracia (H.) conradi* (Thomas, 1967).

Statocysts of type B_3 (Morton, 1985b), common in the Myochamidae (Harper & Morton, 2000) and Clavagellidae (Morton, 1984a, b, 2002b) are herein recorded for the first time in a thracioidean, other members of the superfamily possessing either types B_1 or B_2 (Morton, 1985b).

Type E ctenidia (Atkins, 1937a) are typical of the Anomalodesmata (Morton, 1985a), except for the septibranch

Poromyidae and Cuspidariidae (Yonge, 1928; Morton, 1987). Among the Thraciidae, the type E ctenidia are homorhabdic in *Trigonothracia jinxingae* (Morton, 1995) and heterorhabdic in *Thracia* (*H.*) *corbuloidea*, *T.* (*O.*) *papyracea* (Poli, 1791) [*T.* (*O.*) *phaseolina* according to Coan, 1990] (Ridewood, 1903), *T.* (*O.*) *villosiuscula*, *T.* (*I.*) *distorta* (Atkins, 1937a) and *T. meridionalis* (this study). Although the ctenidia of *Trigonothracia jinxingae* attach to the visceral mass by cuticular junctions (Morton, 1995), those of *Thracia meridionalis* do so by ciliary junctions.

Hancock (1853) refers to an inter-chamber aperture in the same position as that of *T. meridionalis* in a single specimen of *Myochama anomioides* Stutchbury, 1830, although he states (p. 290): 'It is quite possible that this aperture may be the result of injury, for these parts are so exceedingly delicate that the examination of more than one specimen is necessary to determine this point with certainty'. Harper & Morton (2000) do not mention such an aperture in their work on the functional morphology of *M. anomioides*, which reinforces the idea that it was an artefact in the specimen studied by Hancock (1853). Another presumably artefactual, differently-located aperture was described by Burne (1920) in a seriously damaged specimen of *Laternula elliptica* (King & Broderip, 1832) whose external demibranchs were free from the body wall for a short extent, allowing direct communication between the mantle chambers.

Thracia meridionalis, like the cemented *Cleidothaerus maorianus* Finlay, 1827, possesses a true aperture between the infra- and suprabranchial chambers but with a distinct morphological origin. Whereas in the latter species the aperture arises from the loss of contact between the asymmetrical posterior portion of the right and left ctenidia (Morton, 1974), in the former the symmetrical ctenidia remain united with each other for their whole extent but do not fuse with the intersiphonal septum, thus leaving an aperture in the posterior portion of the mantle chamber. The functional significance of this interchamber aperture in *T. meridionalis* is presumably to allow water previously retained within the suprabranchial chamber and exhalant siphon to be transferred into the infrabranchial chamber during the burrowing process, thereby enhancing the jet of water expelled through the small pedal opening so as to facilitate penetration into the substratum. A similar mechanism of water retention and corresponding use in the burrowing process was described by Bromley & Asgaard (1990) for *Solecurtus strigilatus* (Linnaeus, 1758). Unlike *T. meridionalis*, however, *S. strigilatus* expels the jet through a small orifice just posterior to the pedal opening.

Morton (1995) regards the Thraciidae as deposit-feeding ancestors of the suspension-feeding Laternulidae and Periplomatidae, largely based on the mode of life and exceedingly simple stomach morphology of *Trigonothracia jinxingae*. While that species is a shallow-burrower that lies just below the sediment surface with the inhalant siphon parallel and closely applied to the surface taking in deposited material (Morton, 1995), *T. meridionalis* burrows to a depth of at least twice its shell length, keeping the siphons perpendicular to and more often retracted away from the sediment surface. Nearby deposited material is prevented from falling into the siphonal apertures by the mucus lining the passage of the siphons through the sediment and which extends beyond the surface. *Thracia meridionalis* is thus a suspension-feeder, like members of the related thracioidean families Laternulidae and Periplomatidae.

Thracia meridionalis possesses a stomach of type IV (Purchon, 1958) with extensive sorting areas, as opposed to the exceedingly simple one of *Trigonothracia jinxingae* that practically lacks sorting areas. The complexity of the stomach allied with the large amount of pseudofaeces and faeces within the mantle cavity and hind gut, respectively, shows that in spite of its suspension feeding habit, *T. meridionalis* deals with and ingests large amounts of material.

Thracia meridionalis is similar to *Parvithracia* (*A.*) *lukini* and *P.* (*A.*) *sirenkoi* (Kamenev, 2002) in that its rectum penetrates the ventricle and passes dorsal to the kidneys, but differs from the thracioideans *Laternula truncata* (Lamarck, 1818), *Periploma* (*O.*) *angasai* and *Trigonothracia jinxingae* in which the rectum penetrates both the ventricle and the kidneys (Morton, 1973, 1981b, 1995; Harper *et al.*, 2000).

The lacunal system that flanks the kidneys of *T. meridionalis* closely resembles that of *Lyonsiella formosa* (Jeffreys, 1881). Morton (1984c) inferred that in the latter species the lacunal system is an important blood reservoir for the functioning of the raptorial inhalant siphon, providing the necessary volume of fluid for its complete eversion. The lacunal system of *T. meridionalis* presumably works in a similar fashion, allowing both siphons to perform great extensions, both in length and width. Nevertheless, Morton (1981b) described similar siphonal behaviour in *Periploma* (*O.*) *angasai*, with no lacunal blood system, so that more studies are required before the function of the system is fully elucidated.

Thracia meridionalis is a simultaneous hermaphrodite as are all other Anomalodesmata, except *Clavagella australis* Sowerby, 1830 (Morton, 1984a) and Cuspidariidae (Morton, 1985a), and the first studied member of the Thracioidea to have a complete separation of the male and female gonads and their respective apertures. Pelseneer (1891) described distinct testes and ovaries, opening side by side on a common prominence of an individual attributed to *Thracia*. Nevertheless, since neither the species name is given nor the shell figured, its identity is uncertain. Thorson (1936) described *Thracia truncata* Brown (which is *T. devexa* Sars, 1878 according to Ockelmann, 1958) as hermaphroditic, with distinct male and female gonads but no information on the gonopores was provided. The other members of the superfamily in which this aspect was studied, i.e. *Laternula elliptica*, *L. truncata*, *Periploma* (*O.*) *angasai* and *Trigonothracia jinxingae* (Burne, 1920; Morton, 1973, 1981b; Harper *et al.*, 2000, respectively), all possess a common male and female aperture, which is either separate from the nephridiopore (*Periploma* and *Trigonothracia*) or united with it (*Laternula*).

The spermatozoa of *T. meridionalis* are similar to those described by Franzén (1955) for *T.* (*O.*) *papyracea* (= *T.* (*O.*) *phaseolina*), in that both species possess spermatozoa with a conical, about 3 μm-long head with no obvious acrosome, a middle piece with four to five mitochondrial spheres and a long flagellum. The large encapsulated ovocytes are similar to those already described for several anomalodesmatans (Burne, 1920; Ockelmann, 1958, 1965; Allen, 1961b; Morgan & Allen, 1976; Morton, 1980, 1981b, 1982; Ansell & Harvey, 1997; Harper & Morton, 2000). Nevertheless the mechanism of formation of the capsules seems to differ among species, casting some doubts on whether or not they are homologous structures. In *T. meridionalis* (this study) and *Laternula elliptica* (Bigatti, Penchaszadeh & Mercuri, 2001) the capsule is a vitelline membrane while in *Pholadomya candida* Sowerby, 1823 and *Parilimya fragilis* (Grieg, 1920) the structure appears to be produced by amoebocytes rather than by the ovocyte itself (Morton, 1980, 1982).

ACKNOWLEDGEMENTS

REFERENCES

ALLEN, J.A. 1961a. The British species of *Thracia* (Eulamellibranchia). *Journal of the Marine Biological Association of the United Kingdom*, **41**: 723–735.

ALLEN, J.A. 1961b. The development of *Pandora inaequivalvia* (Linné). *Journal of Embryology and Experimental Morphology*, **9**: 252–268.

ALLER, R.C. 1974. Prefabrication of shell ornamentation in the bivalve *Laternula*. *Lethaia*, **7**: 43–56.

ANSELL, A.D. & HARVEY, R. 1997. Protected larval development in the Antarctic bivalve *Laternula elliptica* (King & Broderip) (Anomalodesmata: Laternulidae). *Journal of Molluscan Studies*, **63**: 285–286.

ATKINS, D. 1937a. On the ciliary mechanisms and interrelationships of Lamellibranchs. Part III: Types of lamellibranch gills and their food currents. *Quarterly Journal of Microscopical Science, New Series*, **79**: 375–421.

ATKINS, D. 1937b. On the ciliary mechanisms and interrelationships of Lamellibranchs. Part II: Sorting devices on the gills. *Quarterly Journal of Microscopical Science, New Series*, **79**: 339–373.

ATKINS, D. 1937c. On the ciliary mechanisms and interrelationships of Lamellibranchs. Part IV: Cuticular fusion, with special reference to the fourth aperture in certain Lamellibranchs. *Quarterly Journal of Microscopical Science, New Series*, **79**: 423–445.

BIGATTI, G., PENCHASZADEH, P.E. & MERCURI, G. 2001. Aspects of the gonadal cycle in the Antarctic bivalve *Laternula elliptica*. *Journal of Shellfish Research*, **20**: 283–287.

BOSS, K.J. 1978. Taxonomic concepts and superfluity in bivalve nomenclature. *Philosophical Transactions of the Royal Society of London, Series B*, **284**: 417–424.

BOSS, K.J. 1982. Mollusca. In: *Synopsis and classification of living organisms* (S.P. Parker, ed.), **1**: 945–1166. McGraw-Hill, New York.

BROMLEY, R.G. & ASGAARD, U. 1990. *Solecurtus strigilatus*: a jet-propelled burrowing bivalve. In: *The Bivalvia – Proceedings of a Memorial Symposium in Honour of Sir Charles Maurice Yonge, Edinburgh 1986* (B. Morton, ed.), 313–320. Hong Kong University Press, Hong Kong.

BURNE, R.H. 1920. Mollusca. Part IV: Anatomy of Pelecypoda. *British Antarctic ('Terra Nova') Expedition, 1910, Natural History Report. Zoology*, **2**: 233–256.

CARTER, J.G. & ALLER, R.C. 1975. Calcification in the bivalve periostracum. *Lethaia*, **8**: 315–320.

COAN, E.V. 1990. The recent Eastern Pacific species of the bivalve family Thraciidae. *Veliger*, **33**: 20–55.

DALL, W.H. 1886. Reports on the results of dredging, under the supervision of Alexander Agassi, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80), by the U.S. Coast Survey steamer 'Blake', Lieut.-Commander C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., commanding. XXIX. Report on Mollusca – Part 1. Brachiopoda and Pelecypoda. *Bulletin of the Museum of Comparative Zoölogy*, **12**: 171–318.

DELL, R.K. 1964. Antarctic and Subantarctic Mollusca: Amphineura, Scaphopoda and Bivalvia. *Discovery Reports*, **33**: 93–250.

DELL, R.K. 1972. Antarctic benthos. *Advances in Marine Biology*, **10**: 1–216.

DELL, R.K. 1990. Antarctic Mollusca with special reference to the fauna of the Ross Sea. *Bulletin of the Royal Society of New Zealand*, **27**: 1–311.

DREYER, H., STEINER, G. & HARPER, E.M. 2003. Molecular phylogeny of Anomalodesmata (Mollusca: Bivalvia) inferred from 18S rRNA sequences. *Zoological Journal of the Linnean Society*, **139**: 229–246.

FRANZÉN, A. 1955. Comparative morphological investigations into the spermiogenesis among Mollusca. *Zoologiska Bidrag Fran Uppsala*, **30**: 399–456.

FORBES, E. & HANLEY, S. 1853. *A history of British Mollusca, and their shells. Vol. I. Including the Tunicata, and the families of Lamellibranchiata as far as Cyprinidae*. John Van Voorst, London.

HAIN, S. 1990. Die beschalten benthischen Mollusken (Gastropoda und Bivalvia) des Weddellmeeres, Antarktis. *Berichte zur Polarforschung*, **70**: 1–184.

HAIN, S. & ARNAUD, P.M. 1992. Notes on the reproduction of high-Antarctic molluscs from the Weddell Sea. *Polar Biology*, **12**: 303–312.

HANCOCK, A. 1853. On the animal of *Myochama anomioides*. *Annals and Magazine of Natural History, Series. 2*, **11**: 287–291.

HARPER, E.M., HIDE, E.A. & MORTON, B. 2000. Relationships between the extant Anomalodesmata: a cladistic test. In: *The Evolutionary Biology of the Bivalvia* (E.M. Harper, J.D. Taylor & J.A. Crame, eds), 129–143. Geological Society of London, London.

HARPER, E.M. & MORTON, B. 2000. The biology and functional morphology of *Myochama anomioides* Stutchbury, 1830 (Bivalvia: Anomalodesmata: Pandoroidea) with reference to cementation. *Journal of Molluscan Studies*, **66**: 403–416.

HODGSON, A.N. & FIELDEN, L.J. 1984. The structure and distribution of peripheral ciliated receptors in the bivalve molluscs *Donax serra* and *D. sordidus*. *Journal of Molluscan Studies*, **50**: 104–112.

KAMENEV, G.M. 2002. Genus *Parvithracia* (Bivalvia: Thraciidae) with descriptions of a new subgenus and two new species from the Northwestern Pacific. *Malacologia*, **44**: 107–134.

KIENER, L.C. 1834. Genre *Thracia*. In: *Spécies général et iconographie des coquilles vivantes, comprenant le Musée Masséna, la Collection Lamarck, celle du Muséum d'Histoire Naturelle, et les découvertes récentes des voyageurs*, **5**: 1–7. Ballière, Paris. *BioSophia Archive 00000004*.

MORGAN, R.E. & ALLEN, J.A. 1976. On the functional morphology and adaptations of *Entodesma saxicola* (Bivalvia: Anomalodesmacea). *Malacologia*, **15**: 233–240.

MORSE, E.S. 1919. Observations on living lamellibranchs in New England. *Proceedings of the Boston Society of Natural History*, **35**: 139–196.

MORTON, B. 1973. The biology and functional morphology of *Laternula truncata* (Lamarck, 1818) (Bivalvia: Anomalodesmata: Pandoracea). *Biological Bulletin*, **145**: 509–531.

MORTON, B. 1974. Some aspects of the biology and functional morphology of *Cleidothaerus maorianus* Finlay (Bivalvia: Anomalodesmata: Pandoracea). *Proceedings of the Malacological Society of London*, **41**: 201–222.

MORTON, B. 1977a. Some aspects of the biology and functional morphology of *Myadora striata* (Quoy & Gaimard) (Bivalvia: Anomalodesmata: Pandoracea). *Journal of Molluscan Studies*, **43**: 141–154.

MORTON, B. 1977b. The hypobranchial gland in the Bivalvia. *Canadian Journal of Zoology*, **55**: 1225–1234.

MORTON, B. 1980. Anatomy of the 'living fossil' *Pholadomya candida* Sowerby 1823 (Bivalvia: Anomalodesmata: Pholodomyacea). *Vindenskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjobenhavn*, **142**: 7–101.

MORTON, B. 1981a. The Anomalodesmata. *Malacologia*, **21**: 35–60.

MORTON, B. 1981b. The biology and functional morphology of *Periploma (Offadesma) angasai* (Bivalvia: Anomalodesmata: Periplomatidae). *Journal of Zoology*, **193**: 39–70.

MORTON, B. 1982. The functional morphology of *Parilimya fragilis* (Bivalvia: Parilimyidae nov. fam.) with a discussion on the origin and evolution of the carnivorous septibranchs and a reclassification of the Anomalodesmata. *Transactions of the Zoological Society of London*, **36**: 153–216.

MORTON, B. 1984a. The biology and functional morphology of *Clavagella australis* (Bivalvia: Anomalodesmata). *Journal of Zoology*, **202**: 489–511.

MORTON, B. 1984b. Adventitious tube construction in *Brechites vaginiferus* (Bivalvia: Anomalodesmata: Clavagellacea) with an investigation of the juvenile of 'Humphreyia strangei'. *Journal of Zoology*, **204**: 461–484.

MORTON, B. 1984c. Prey capture in *Lyonsiella formosa* (Bivalvia: Anomalodesmata: Verticordiacea). *Pacific Science*, **38**: 283–297.

MORTON, B. 1985a. Adaptive radiation in the Anomalodesmata. In: *The Mollusca*. **10**: *Evolution* (E.R. Trueman & M.R. Clarke, eds), 405–459. Academic Press, London.

MORTON, B. 1985b. Statocyst structure in the Anomalodesmata (Bivalvia). *Journal of Zoology*, **206**: 23–34.

MORTON, B. 1987. Siphon structure and prey capture as a guide to affinities in the abyssal septibranch Anomalodesmata (Bivalvia). *Sarsia*, **72**: 49–69.

MORTON, B. 1995. The ecology and functional morphology of *Trigonothracia jinxingae* (Bivalvia: Anomalodesmata: Thracioidea) from Xiamen, China. *Journal of Zoology*, **237**: 445–468.

MORTON, B. 2002a. Biology and functional morphology of the watering pot shell *Brechites vaginiferus* (Bivalvia: Anomalodesmata: Clavagelloidea). *Journal of Zoology*, **257**: 545–562.

MORTON, B. 2002b. The biology and functional morphology of *Humphreyia strangei* (Bivalvia: Anomalodesmata: Clavagellidae): an Australian cemented 'watering pot' shell. *Journal of Zoology*, **258**: 11–25.

MORTON, B. & HARPER, E.M. 2001. Cementation in *Cleidothaerus albidus* (Lamarck, 1819) (Bivalvia: Anomalodesmata: Pandoroidea). *Molluscan Research*, **21**: 1–15.

MÜHLENHARDT-SIEGEL, U. 1989. Antarktische Bivalvia der Reisen des FS 'Polarstern' und des FFS 'Walther Herwig' aus den Jahren 1984 bis 1986. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, **86**: 153–178.

NARCHI, W. 1968. The functional morphology of *Lyonsia californica* Conrad, 1837 (Bivalvia). *Veliger*, **10**: 305–313.

NARCHI, W., DOMANESCHI, O. & PASSOS, F.D. 2002. Bivalves Antárticos e Subantárticos coletados durante as Expedições Científicas Brasileiras à Antártica I a IX (1982–1991). *Revista Brasileira de Zoologia*, **19**: 645–675.

NICOL, D. 1966. Descriptive ecology and geographic distribution of some antarctic pelecypods. *Bulletins of American Paleontology*, **51**: 1–102.

OCKELMANN, W.K. 1958. The zoology of East Greenland marine lamellibranchiata. *Meddelelser om Gronland*, **122**: 1–256.

OCKELMANN, K.W. 1965. Development types in marine bivalves and their distribution along the Atlantic coast of Europe. *Proceedings of the European Malacological Congress*, **1**: 25–35.

PECK, L.S., BROCKINGTON, S., VANHOVE, S. & BEGHYN, M. 1999. Community recovery following catastrophic iceberg impacts in a soft-sediment shallow-water site at Signy Island, Antarctica. *Marine Ecology Progress Series*, **186**: 1–8.

PELSENEER, M.P. 1890. Sur le quatrième orifice palléal des Pélécypodes. *Comptes Rendus Hebdomadaires des Séances de L'Académie des Sciences*, **110**: 154–156.

PELSENEER, P. 1891. Sur l'existence d'un groupe entier de Lamellibranches hermaphrodites. *Zoologischer Anzeiger*, **14**: 5–8.

PELSENEER, P. 1911. Les lamellibranches de L'Expédition du Siboga. Partie anatomique. In: *Siboga-Expeditie*. **34** (Monogr. 53a) (M. Weber, ed.), 1–125. Brill, Leiden.

PURCHON, R.D. 1958. The stomach in the Eulamellibranchia: Stomach type IV. *Proceedings of the Zoological Society of London*, **131**: 487–525.

RIDEWOOD, W.G. 1903. On the structure of the gills of the Lamellibranchia. *Philosophical Transactions of the Royal Society of London, Series B*, **195**: 147–284.

SOOT-RYEN, I. 1951. Antarctic pelecypodes. *Scientific Results of the Norwegian Antarctic Expeditions 1927–1928*, **32**: 1–46.

STASEK, C.R. 1963. Synopsis and discussion of the association of ctenidia and labial palps in the bivalved Mollusca. *Veliger*, **6**: 91–97.

TAYLOR, J.D., KENNEDY, W.J. & HALL, A. 1973. The shell structure and mineralogy of the Bivalvia. II. Lucinacea-Clavagellacea. Conclusions. *Bulletin of the British Museum (Natural History), Zoology*, **22**: 253–294.

THOMAS, M.L. 1967. *Thracia conradi* in Malpegue Bay, Prince Edward Island. *Nautilus*, **80**: 84–87.

THORSON, G. 1936. The larval development, growth, and metabolism of artic marine bottom invertebrates compared with those of other seas. *Meddelelser om Gronland*, **100**: 1–155.

YONGE, C.M. 1928. Structure and function of the organs of feeding and digestion in the septibranch, *Cuspidaria* and *Poromya*. *Philosophical Transactions of the Royal Society of London, Series B*, **216**: 221–263.

YONGE, C.M. 1937. The formation of siphonal openings by *Thracia pubescens*. *Proceedings of the Malacological Society of London*, **22**: 337–338.

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

YONGE, C.M. 1948b. Cleansing mechanisms and the function of the fourth pallial aperture in *Spisula subtruncata* (da Costa) and *Lutraria lutraria* (L.). *Journal of the Marine Biological Association of the United Kingdom*, **27**: 585–596.

YONGE, C.M. 1952. Structure and adaptation in *Entodesma saxicola* (Baird) and *Mytilimeria nuttalli* Conrad. *University of California Publications in Zoölogy*, **55**: 439–450.

YONGE, C.M. 1957. Mantle fusion in the Lamellibranchia. *Publicazione della Stazione Zoologica di Napoli*, **29**: 151–171.

YONGE, C.M. 1982. Mantle margins with a revision of siphonal types in the Bivalvia. *Journal of Molluscan Studies*, **48**: 102–103.

YONGE, C.M. & MORTON, B. 1980. Ligament and lithodesma in the Pandoracea and the Poromyacea with a discussion on the evolutionary history in the Anomalodesmata (Mollusca: Bivalvia). *Journal of Zoology*, **191**: 263–292.