On the Structure and Adaptations of *Pandora inaequivalvis* and *P. pinna*

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SUMMARY

The two British species of *Pandora* are adapted for life on muddy-sand. *P. inaequivalvis* is taken from very sheltered shores at low-water mark and down to 10 fathoms. *P. pinna* is taken from depths of over 40 fathoms.

Both species are markedly inequivalve. This is probably connected with the habit of lying horizontally.

The mantle muscles and the ciliary mechanisms of the mantle and gills are described.

An account of the morphology and the functioning of the stomach is given and various modifications, due to the reduced typhlosole, are described.

PANDORA is the sole genus of the family Pandoridae (Eulamellibranchia) of the sub-order Anomalodesmata (Theile, 1935). There are two British species, *P. inaequivalvis* (Linné) and *P. pinna* (Montagu), but neither is common in British waters. Deshayes (1848) and Pelseneer (1911) have described the anatomy of *P. elongata* but, apart from observations by Ridewood (1903) and Atkins (1937a) on gill structure, there has been no study of living specimens. Observations have been made, therefore, on the structure and ciliary mechanisms of *Pandora* and comparisons have been made with species of related families, particularly the Lyonsiidae (Yonge, 1952) and Thraciidae (personal observations). Unless otherwise stated these observations apply to both the species *P. inaequivalvis* and *P. pinna*.

HABITAT

P. inaequivalvis is occasionally taken off Plymouth and Port Erin from muddy-sand in shallow water. The latter locality is apparently the northernmost record for this species. It is abundant at low water on sheltered sandy beaches in the Channel Isles and extends to the Mediterranean. Living specimens were obtained from Penpoull, a very sheltered muddy-sand beach near Roscoff on the Brittany coast. This beach shelved very slightly and much of it is used for oyster beds. The specimens of *Pandora* from this locality were not buried but lay at the surface on their sides. Although the animals were never seen to burrow, many had tufts of *Enteromorpha* and other algae attached to the siphonal end of the shell indicating possibly that they were often buried with only this part of the shell above the substratum.

P. pinna has a greater geographical range than *P. inaequivalvis* and extends from Scandinavian waters to the Mediterranean. It is found in deeper water than *P. inaequivalvis* and, whereas the latter is taken rarely from depths greater than 10 fathoms, *P. pinna* is always taken from 40 fathoms and below. Specimens of this species were obtained from the Sound of Jura from muddy-sand at a depth of 60 fathoms.

MANTLE/SHELL

Both species of *Pandora* are inequivalve with the right valve flat or even slightly concave (fig. 1). Yonge (1946) pointed out that, apart from *Aloidis*, *Pandora* appears to be the only lamellibranch in which an inequivalve shell is not associated with horizontal disposition. However, the observations at Penpoull suggest that at times *P. inaequivalvis* does lie horizontally. Usually,
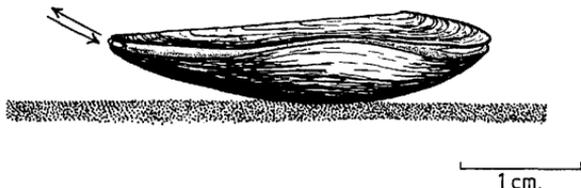

1 cm.

FIG. 1. *P. inaequivalvis* viewed from the free-margin and lying in its normal position on the left valve. The direction of the inhalent and exhalent currents are shown.

but not always, it was the right side that was found to be uppermost. The illustrations and description given by Forbes and Hanley (1853) show clearly the differences in shell shape between the two species. The maximum recorded measurements were: *P. inaequivalvis*, length 3·5 cm., height 1·9 cm., width 0·6 cm.; *P. pinna*, length 1·7 cm., height 0·8 cm., width 0·2 cm. The free margin of the right valve is poorly calcified and is similar to that of the smaller valve in *Aloidis* (Yonge, 1946). This margin of periostracum fits tightly against the marginal region of the left valve when the valves are closed. In addition, the margin of both valves is poorly calcified in the siphonal region.

The hinge teeth are simple and consist of a single cardinal tooth in each valve. The tooth on the right valve is the more prominent and lies at right angles to the hinge margin. This fits into a well-defined socket on the opposite valve. The internal ligament lies posterior to the tooth and usually has a posterior extension. Unlike the Lyonsiidae, there is no lithodesma, but like the latter group the valves of *Pandora* are united dorsally by periostracum. This is probably a primitive feature (see Yonge, 1952; Owen, Trueman, and Yonge, 1953). The periostracum extends posteriorly almost to the siphons and anteriorly to the anterior adductor muscle.

There is extensive fusion of the mantle edges, the pedal gape occupying less than one-third of the ventral margin (fig. 2 A). Unlike the Lyonsiidae and the
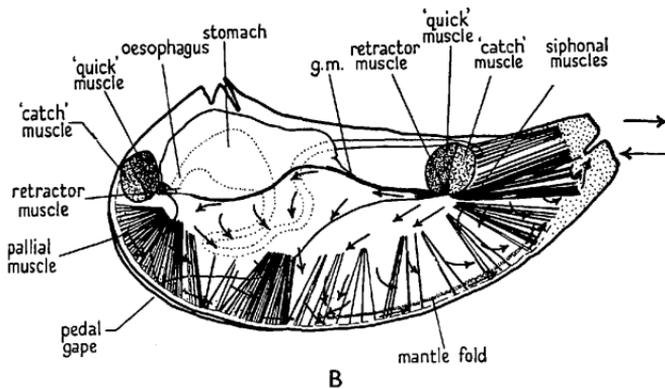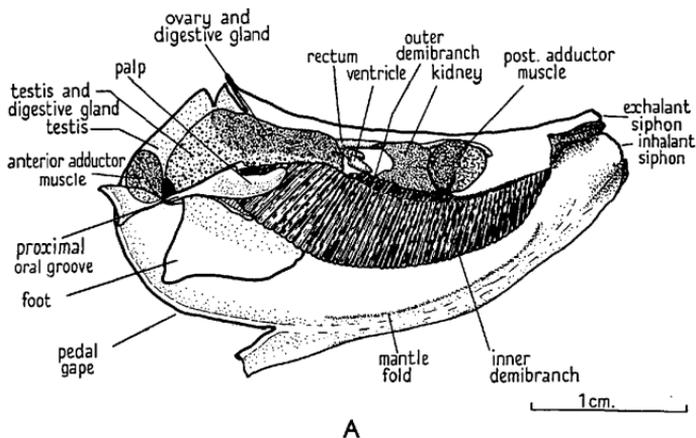
FIG. 2. A, lateral view of *Pandora* with the left valve removed and mantle cut away. B, lateral view of *Pandora* with the left valve removed to show the ciliary currents of the mantle and the mantle musculature. *g.m.*, line of attachment of the gill lamella.

Thraciidae there is no fourth pallial aperture. There is complete fusion of the tissues and not merely a cuticular junction (Atkins, 1937*b*). Both inner and middle lobes of the mantle edge are involved in tissue fusion.

The siphons of *Pandora* are short and are not capable of extending more than a few millimetres. There is no siphonal embayment such as is found in *Thracia*. The apertures are slightly lobed and are fringed with a number of short papillae. There is no well-defined periostracal groove and the periostracum is secreted here, as it is ventrally, by the epidermal cells in the region *P* shown in fig. 3. The periostracum is apparently secreted in a semi-fluid state.
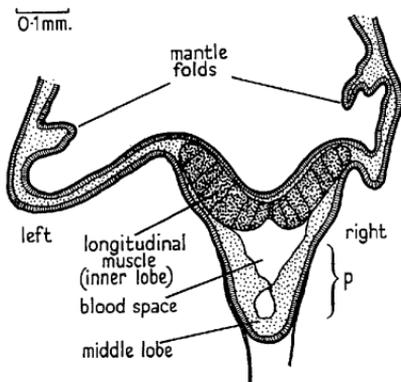

FIG. 3. Transverse section of the fused ventral mantle edge showing the position of the mantle folds. *P*, region of the secretion of the periostracum.

This is particularly the case at the base of the siphons where sand grains become incorporated in it. Yonge (1952) describes a similar condition in the Lyonsiidae where in the case of *Enteodsma* and *Lyonsia* the shell may be covered by sand grains attached to the periostracum. In *Pandora* the sand is restricted to the base of the siphons and is never found attached to the surface of the shell.

The pallial muscles are well marked. Anteriorly there are two well-developed groups in association with the pedal gape while posteriorly a similar group of muscles form the siphonal retractors. Between the pedal and siphonal groups there are scattered muscles controlling the fused mantle margins (fig. 2 B). The anterior and posterior adductor muscles are well developed and approximately equal in size. The 'quick' muscles are very well developed and, as in *Aloidis*, are probably associated with very large amounts of bottom material entering with the inhalent current (Yonge, 1946). The anterior and posterior pedal retractor muscles are unusual in that they are inserted by the *ventral* side of the adductor. The posterior retractor may be wedged between the 'quick' and 'catch' muscles.

A pair of mantle folds, dorsal to the fusion of the inner mantle lobes, extend from a few millimetres behind the pedal gape to a position anterior to the inhalent aperture (figs. 2 and 3). The folds are not wide enough to form a roof as in *Spisula* (Yonge, 1948). The mantle currents are as shown in fig. 2, B. A main ciliary tract for the rejected particles extends from a position opposite the tip of the palps posteriorly to the mantle fold. Particles are carried along the groove formed by the mantle fold and the fused inner lobes of the mantle. The cilia in the groove are longer (70μ) than those of the general mantle surface ($<40\mu$). The rejected particles do not collect at the ventral side of the inhalent aperture but are carried on to the lateral and dorsal walls. Particles falling on to the mantle from the heel of the foot and from the anterior portion of the gill lamella are carried to the anterior end of the mantle fold. Those from the posterior end of the gill lamella are deflected ventrally and posteriorly and are not carried along the ventral groove. Dorsally, where the mantle and gill margins meet, the cilia beat anteriorly so that particles are carried anteriorly on to the gill lamella.

ORGANS IN THE MANTLE CAVITY

There is a moderately developed foot with a byssus groove and gland. The latter is not functional in the adult. The labial palps are of medium size and function in the usual manner. The dorsal edge of the palp is unusual in that it has numerous fine ridges running in the same direction as the normal palp ridges. The proximal oral grooves are long and deep. They run forward on either side of the foot and, anteriorly, the outer sides of each groove unite to form a hood over the mouth.

The ctenidia are plicate and heterorhabdic; *P. pinna* has nine filaments to each plica and *P. inaequivalvis* seven, confirming the observations of Ridewood (1903). The outer demibranch is very much reduced. It is reflected dorsally and only the direct lamella remains. Atkins (1937a) has suggested that as there is a relatively small number of filaments to each plica it might be expected that the sorting mechanism will be different from that of the *Pinna* type which she describes and figures (pp. 347 et seq.). But examination shows that the sorting mechanism is the same as in the deeply plicate species.

All frontal cilia beat towards the free margins of the inner demibranch, those on the outer demibranchs beating towards the axis and so to the outer surface of the inner demibranch. The marginal groove is scalloped and fine particles moving down the principal filaments are carried into the depth of the marginal groove. Larger particles, that cannot reach the principal filaments because of the narrowness of the interplical space, arrive at the gill margin and are carried anteriorly outside the groove along the tips of the filaments (Atkins 1937a, p. 347). Many of these will then fall on to the foot and mantle. The gills are sufficiently muscular for the opposing tips of the apical filaments to close over the marginal groove. Examination under high power of the edges of the apical and adjacent ordinary filaments shows that sorting of the particles also occurs

here. The long terminal cilia which move the larger particles anteriorly extend only over two-thirds of the tip of the filament while the remainder are unmodified frontal cilia. The latter allow any fine particles to pass into the marginal groove (fig. 4.). A similar sorting mechanism has been described by Yonge (1946) in the case of *Aloidis*.
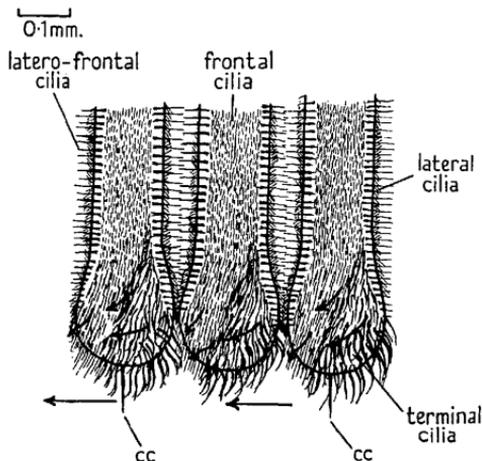

Fɪɢ. 4. Sorting mechanisms at the edge of the apical and ordinary filaments of the inner gill lamella. *CC*, coarse cirrus-like cilia.

ALIMENTARY CANAL

The course of the alimentary canal is indicated in figure 2, ʙ. A short oesophagus leads into a relatively large stomach. The mid-gut and style sac are in communication, the intestine curves anteriorly, ventral to the stomach and then loops posteriorly and dorsally to terminate posterior to the posterior adductor. The ventricle lies ventral to the hind gut. The stomach was dissected from various aspects and with the aid of carmine and fine carborundum particles the ciliary currents investigated. The nomenclature proposed by Graham (1949) and Owen (1953) has been followed.

The morphology of the stomach and the ciliary currents can be followed with reference to fig. 5. Particles accepted by the palps are carried through the oesophagus within a string of mucus which is wrapped around the tip of the crystalline style. The style is relatively large in *Pandora*—0·5 cm. in a specimen 3·2 cm. in length—and it rotates in a clockwise direction when viewed from the oesophageal end of the stomach. It is prevented from entering the dorsal hood by means of the tooth that is present on the recurved portion of the gastric shield. The gastric shield is held in place by flanges extending into the dorsal hood and left pouch.

dorsal dorsal
hood groove   left pouch

rejection
tract

posterior
sorting area

oesophagus

acceptance
tract

left
caecum

tooth

right
duct

groove

area 'a'

gastric
shield

lateral
rejection grooves

right
caecum

extension of
post. sorting area

major
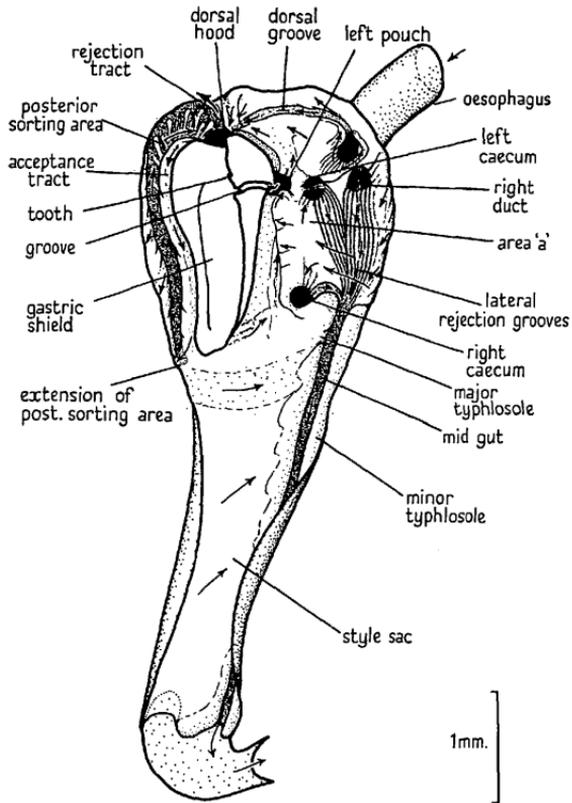typhlosole

mid gut

minor
typhlosole

style sac

1mm.

FIG. 5. The stomach opened from the right side to show the direction of the ciliary currents.

The ciliary mechanisms of the dorsal hood and the posterior sorting area are similar to those described by Owen (1953) for *Glossus*. Released particles from the tip of the crystalline style are carried, probably by the revolving style, on to the posterior sorting area which is moderately well developed with a small backward extension ventral to the posterior end of the acceptance tract. The cilia of the grooves and ridges of this area exercise a quantitative selection; lighter particles are carried into the dorsal hood while heavier particles are conveyed to the rejection tract. The rejected particles are conveyed to the mid-gut by way of the lateral rejection grooves (fig. 5).

The dorsal hood, which is of moderate size, is directed anteriorly and to the left. Accepted particles are carried to the tip of the hood, those on the dorsal side being passed on to the acceptance tract while those on the ventral side are carried on to the flange of the gastric shield and the head of the style (see Owen, 1953, fig. 8.). Fine particles are conveyed posteriorly by the acceptance tract which lies along the dorsal side of the gastric shield. These particles are then carried ventrally over the posterior wall of the stomach to the right and left caeca and to the left pouch. This movement across the posterior wall is in an opposite direction to that of the style, i.e. in an anticlockwise direction when viewed from the anterior end of the stomach. Particles are carried either directly to the openings of the digestive ducts or fall on to the area *A* next to the ventral and lateral side of the gastric shield. In the latter case, those particles near the right caecum are carried towards its aperture, while the remainder are directed towards the gastric shield to a poorly defined groove and then anteriorly to the left pouch.

The stomach of *Pandora* is unusual in that the major typhlosole is very poorly developed. In many of the specimens examined it terminated just within the entrance to the right caecum and in the remainder, just before the entrance. It does not continue towards the left caecum and form a flap-like cover to an intestinal groove as it does in *Glossus* (Owen, 1953) and other Eulamellibranchia (Graham, 1949). In place of an intestinal groove there is a series of ten to fifteen grooves (lateral rejection grooves) which extend from the openings of the right duct and the right and left caeca to the mid-gut. Rejected particles from these ducts are carried along the grooves. In addition, cilia on the crests of the ridges between these grooves beat ventrally, conveying accepted particles towards the area *A*.

The path of rejected particles from the left pouch is not clear. Careful examination shows no rejection path joining those from other ducts. The only material observed leaving the pouch was carried on to the flange of the gastric shield. Apparently rejected material returns to the general circulation of the stomach and is probably pulled over the groove lying below the tooth of the gastric shield and so on to the style.

Particles failing to enter the digestive ducts are carried towards the oesophageal region of the stomach. These particles, together with any stray particles entering by the oesophagus, are carried dorsally on either side of the oesophageal opening to the dorsal groove. From here they are carried to the

base of the dorsal hood. Some of these particles are carried directly to the right duct.

The differences between the stomach of *Pandora* and those of other Eulamellibranchia are a possible consequence of elongation. The right and left caeca of *Pandora* are widely separated and, as the poorly developed major typhlosole extends no further than the right caecum, there is no flap covering an intestinal groove. Instead a series of lateral rejection grooves are present which function in a similar way to the ridges and grooves of the posterior sorting area. Thus, while rejected material is carried in the grooves, accepted particles are passed across this region by the cilia on the crest of the ridge between each adjacent groove.

It seems probable that the area *A* is homologous to that portion of the stomach in other Eulamellibranchia, e.g. *G. humanus* (see Owen, 1953, p. 98), that lies between the gastric shield and the flap of the major typhlosole.

DISCUSSION

Pandora is apparently adapted for life on the surface of the substratum. *P. inaequivalvis* was found to be abundant on *very* sheltered and slightly shelving beaches around L.W.S.T. level. No buried specimens were found, but algal growth confined to the siphonal region suggests that *Pandora* is sometimes buried with only the siphons showing. The animals were not observed to burrow either in the field or in the laboratory, although there is a moderately developed foot and the pedal gape is sufficiently wide for this foot to be extended. Although no observations have been recorded, it is possible that the foot is used to uncover and orientate the animal if it becomes silted over.

The shell is markedly inequivalve and the animals lie on the surface on the left, convex side. The siphons are very short and never extend more than a few millimetres. They are directed upwards at an angle to the substratum and not horizontally along the surface (fig. 1). Even so, large quantities of sediment will almost certainly be taken into the mantle cavity. This is removed by the sudden contractions of the well developed 'quick' portion of the adductor muscles.

In addition lateral compression in *Pandora* is very great. This may be why the retractor muscles lie in the unusual position ventral to the adductor muscles.

This, also, may be why the ctenidia only extend over the posterior portion of the visceral mass, and thus there are necessarily long proximal oral grooves present.

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