

CLEANSING MECHANISMS AND THE FUNCTION  
OF THE FOURTH PALLIAL APERTURE IN  
*SPISULA SUBTRUNCATA* (DA COSTA)  
AND *LUTRARIA LUTRARIA* (L.)

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(Text-figs. 1-8)

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INTRODUCTION

The investigations here recorded were the outcome of a preliminary study of *Lutraria lutraria* (L.) in connexion with a wider study on adaptation for deep burrowing in Lamellibranchiata. Examination of the ciliary currents concerned with the removal of waste material from the mantle cavity, which involved inquiry into the function of the fourth pallial aperture, revealed a variety of unrecorded facts. This led to an examination of conditions in *Spisula subtruncata* (da Costa) with which, on the basis of hinge characters, *Lutraria* is grouped in the family Mactridae (Thiele, 1935). Additional evidence of the close relationship between these two genera has been found.

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*SPISULA SUBTRUNCATA**External Appearance and Habits*

*Spisula subtruncata* is a stoutly built bivalve which inhabits silty sand, into which it burrows quickly by means of a thick, somewhat pointed foot. The siphons (Figs. 1 and 2) are united and, in a specimen 3.4 cm. long by 2.6 cm. deep, extend to a length of not more than 8 mm., usually somewhat less. When buried only their tips project above the surface. The fused siphons are surrounded by a sheath of periostracum which arises in a groove immediately anterior to the outer ring of tentacles. The siphons thus represent the fusion of the inner and middle lobes, with the marginal (periostracal) groove of the outer lobe, of the mantle edge (Yonge, 1948). The middle (sensory) lobe is represented by a ring of tentacles which surrounds both siphons (Fig. 2). The inner (muscular) lobe is represented by a ring of large, with intermingled small, tentacles round the opening of the inhalant siphon, and by a membrane round that of the exhalant siphon. These tentacles are very mobile and act as strainers, preventing large particles from entering with the inhalant current, while the membrane constricts and directs the exhalant current.

When the adductors relax, the ventral margins of the shell valves separate for a distance of about 2 mm., but the mantle lobes remain closely applied as shown in Fig. 1. They are actually free from the region of the anterior adductor to the base of the siphons, so providing an exceptionally long pedal opening. But this only functions when the foot is protruded; at other times the ventral surface is closed, except for a small area immediately posterior to the fusion of the mantle edges at the base of the siphons. Here a spherical opening, about 1-2 mm. in diameter, can be seen when the animal is expanded (Figs. 1 and 2, MA). Similar local separation of the mantle edges in this region was originally noted by Kellogg (1915) in *Mactra solidissima* Dilwyn.

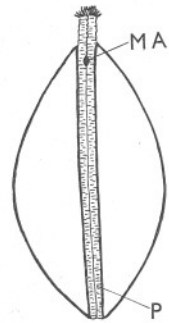


Fig. 1. *Spisula subtruncata*, animal fully expanded viewed from ventral surface.  $\times 1$ . MA, mantle aperture, margins fused on posterior side only; P, periostracum covering exposed mantle surfaces and siphons.

*The Mantle Cavity*

The appearance of the organs in the mantle cavity after removal of the right shell valve and mantle lobe is shown in Fig. 2. The flat and homorhabdic gills are large with the outer only about half the size of the inner demibranch. Their ciliation has been described by Atkins (1937 *a, b*). Small frontal cilia beat ventrally, carrying material into the marginal food grooves, except on the inner surface of the outer demibranch where they beat towards the gill axis.

But on this and on the adjacent surface of the inner demibranch there are additional long coarse frontal cilia which beat ventrally so that all large particles, such as sand grains, are carried into the food grooves, out of which they fall on to the surface of the mantle for extrusion with other waste material. Atkins associates the presence of these large cilia, which she notes are fully active only on mechanical stimulation, with life in silty sand. By their means many of the larger particles are removed from the gills, but mucus-laden strings of finer particles reach the long, strap-shaped palps by way of the food grooves and the gill axis. The palps function in the usual manner, further selection by them leading to the rejection of larger particles and masses from their tips.

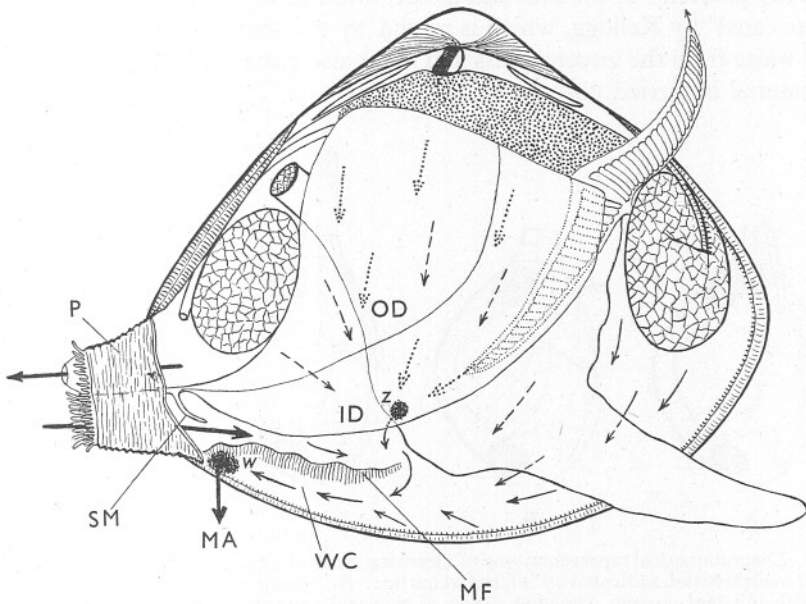


Fig. 2. *Spisula subtruncata*, animal viewed from right side after removal of right shell valve and mantle lobe, siphons intact.  $\times 2\frac{1}{2}$ . ID, inner demibranch; MA, mantle aperture with arrow showing direction in which waste (*w*) ejected; MF, mantle fold (left); OD, outer demibranch; P, periostracum surrounding siphons; SM, siphonal membrane; WC, waste canal; *z*, temporary accumulation of waste on visceral mass at base of the foot. Solid and broken arrows indicate course of ciliary currents on mantle (exposed or beneath other organs), dotted arrows currents on visceral mass. Currents on gills and palps (apart from rejection from tips of latter) not shown.

On the posterior third of the mantle surface a pair of horizontally extending mantle folds (Fig. 2, MF) form, by apposition, a roof over the applied mantle edges. Similar folds have been described by Kellogg (1915) in three other species of Mactridae, *Schizothaerus nuttalli* (Conrad), *Mactra solidissima* Dilwyn and *Spisula polynyma* Stimpson, although not in *S. planulata* (Conrad). Somewhat similar folds occur in various deposit-feeding Lamellibranchiata, species of *Scrobicularia*, *Abra* and *Macoma*, but they have a somewhat different

function. From the roof of the inner opening of the inhalant siphon a flap or siphonal membrane (Kellogg) hangs down (Fig. 2, SM). This, as shown below, is probably associated functionally with the mantle folds.

#### Removal of Waste Material

All currents on the mantle surface and visceral mass, but *not* on the gills, are shown in Fig. 2. The foot, as usual, is not ciliated. On the visceral mass the cilia (dotted arrows) carry material to an area ( $z$ ) behind the posterior margin of the foot, which also receives matter rejected from the inner palps. On the mantle surface ciliary currents (broken and solid arrows) converge mid-ventrally posterior to the foot and at the entrance to the ventral tract, termed 'waste canal' by Kellogg, which is roofed by the mantle folds. The accumulated waste from the visceral mass and palps also passes into this canal in which all material is carried posteriorly.

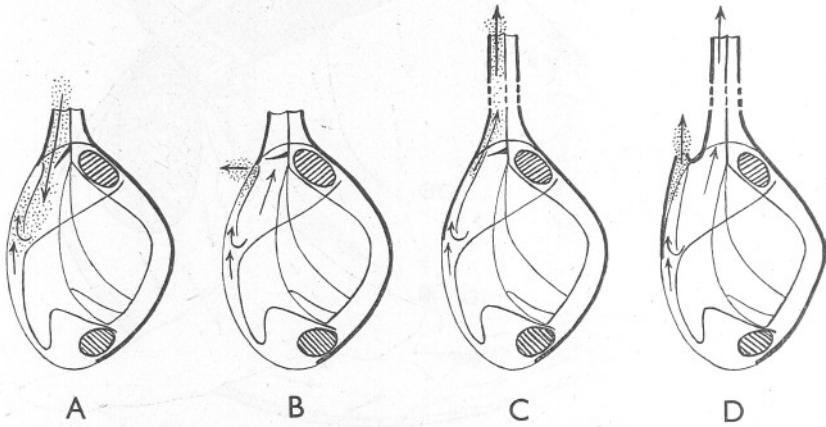


Fig. 3. Diagrammatical representations of cleansing mechanisms in various Mactridae. Extent of mantle fusion indicated by thickened outline. A, *Spisula subtruncata*, intake of sediment with inhalant current, showing action of siphonal membrane and passage of waste into canal guarded by mantle folds; B, *S. subtruncata*, ejection of waste ventrally through mantle aperture; C, *Schizothaerus nuttalli*, ejection of waste posteriorly through inhalant siphon owing to backward extension of waste canal behind siphonal membrane (based on Kellogg); D, *Lutraria lutraria*, ejection of waste posteriorly through fourth pallial aperture, mantle folds but *not* siphonal membrane being retained.

The siphonal membrane opens inward and so offers no resistance to the inflowing current. Kellogg suggests that 'its function is to throw the current downward on to the mantle edges, and away from the gills, when much sediment is present'. This view, implying that the membrane is an adaptation for life in silty water, appears correct. This deflexion of the water current necessitates some means of preventing the accumulation of waste at the base of the siphon from being swept forward. This, as Kellogg points out, explains the presence of the mantle folds which over-arch the waste canal. The action of both the membrane and the folds is shown diagrammatically in Fig. 3 A, B.

In *Schizothaerus nuttalli* the mantle edges, as Kellogg has shown, are fused as far forward as the anterior end of the mantle folds (see Fig. 3 C). But here the mantle folds and the waste canal terminate *behind* the siphonal membrane so that when the adductors contract for cleansing, the accumulated waste is ejected through the long inhalant siphon in the usual manner (Fig. 3 C). This animal, the Pacific horse-clam or gaper, is one of the largest of lamellibranchs, with a shell attaining a length of 8 and a breadth of 5 in. The fused siphons, encased in periostracum as in all Mactridae, are very long so that the animal often occurs at depths of up to 2 ft. or over (Quayle, 1941). But in the shallow burrowers, such as *S. subtruncata* and, judging from Kellogg's figure, in *S. polynyma*, these folds terminate, and the waste accumulates, *in front of* the membrane as shown in Fig. 2. This would appear to explain the local separation of the mantle edges in this region in *S. subtruncata*. Kellogg makes no mention of a similar opening in *S. polynyma*, but his account of this species is brief. In the former species a slow current of water is drawn in through this opening when the adductors are relaxed, but when they contract the waste is ejected through it. Back pressure of water will drive the siphonal membrane back and largely, if not completely, block the lumen of the siphon. The differences between this condition and that described by Kellogg in *Schizothaerus* are indicated in Fig. 3 B and C.

Conditions are somewhat different in *Mactra solidissima*, where Kellogg found that cilia and muscle combine to remove the waste ventrally. In the unrelated *Cardium corbis* Martyn all waste matter is so removed by ciliary action alone. In neither of these species is the posterior end of the animal buried, and this method of cleansing represents, Kellogg states, 'the usual procedure in forms with free mantle margins, and which are not completely buried in a burrow'. Waste could certainly not be removed ventrally by ciliary action in *Spisula subtruncata* which is completely covered with sand when it burrows.

The expulsion of waste ventrally following contraction of the adductors in *S. subtruncata* thus involves the presence of what is in effect, if not structurally, a fourth pallial aperture. This gives the key to the explanation of conditions here for the first time fully described in *Lutraria lutraria*.

#### LUTRARIA LUTRARIA

##### *External Appearance and Habits*

*Lutraria lutraria* (Fig. 4) is adapted for deep burrowing usually in rather shifting sands, although it also lives in mud where this is overlaid with sand. It occurs on the shore near low water of spring tides and in the sublittoral zone. The large oval shell with a wide posterior gape closely resembles that of the other genera of deep-burrowing lamellibranchs, *Mya* and *Panope*. This resemblance is the result of convergence due to similarity of habits. Attention



is here confined to the less obvious but fundamental relationship between *Lutraria lutraria* and the shallow burrowing species of the Mactridae, in particular *Spisula subtruncata*.

The shell attains a size of some 13 cm. long by 7 cm. broad. The massive, fused siphons extend for up to three times the length of the shell and, apart from their size, resemble in all respects those of *S. subtruncata*, being similarly covered with periostracum and fringed with tentacles and with a membrane round the exhalant siphon. There is also a true fourth pallial aperture. As shown in Fig. 4, the distended mantle edges extend for some distance beyond the margin of the shell and, at the base of the inhalant siphon, form a posteriorly directed papilla which marks the site of this aperture (FA).

#### The Mantle Cavity

The disposition of the organs when exposed by the removal of the right shell valve and mantle lobe is shown in Fig. 5. Compared with *S. subtruncata*, they are extended longitudinally, especially in the posterior half of the body. The visceral mass is large, but the foot, though big for a deep burrower, is relatively smaller than in that species. The pedal gape is confined to the antero-ventral surface. The gills are large and the outer demibranch only a little smaller than the inner one. Atkins (1937 *b*) describes them as plicate and homorhabdic, and has shown that currents run oralward along the marginal food grooves and along the gill axis, as in *S. subtruncata*. The long frontal cilia found in that species are absent. The palps are large but broad at the base which approaches in length the two free margins.

Between the wide pedal gape and the small fourth aperture, the mantle edges are fused for rather more than half the length of the ventral surface (between FA and PG). Atkins (1937 *c*) has shown that it is the cuticular linings of the applied epithelia that fuse, as shown in Fig. 8 (CF). She notes that, unlike *Ensis siliqua* (L.), *E. arcuatus* Jeffreys, and *Cultellus pellucidus* (Penn.), where cuticular fusion of the mantle edges also occurs, there is no rupture along the line of fusion when the animal dies and gapes widely. She thinks, therefore, that there may be fine cross-connecting strands of muscle in *Lutraria lutraria*. Owing to the folds into which the epithelia are thrown in fixation, she found it impossible to

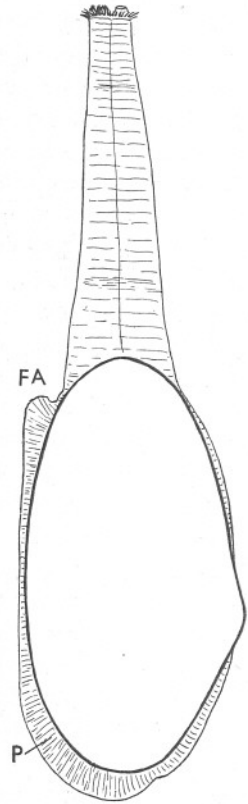


Fig. 4. *Lutraria lutraria*, fully expanded animal viewed from right side.  $\times \frac{1}{2}$ . FA, fourth pallial aperture; P, periostracum covering exposed mantle surfaces and siphons.

determine this matter in sections. However, when examining stocks of specimens that had been preserved for several years in formalin it was found that the fused surfaces had either come apart or could be separated with the greatest ease. The exposed surfaces were perfectly smooth with no trace of any ruptured tissues. Apparently long exposure to formalin softens the cuticle along the line of fusion and this represents the only means whereby the two lobes are united. But they are certainly fused much more firmly than in *Ensis* or *Cultellus*.

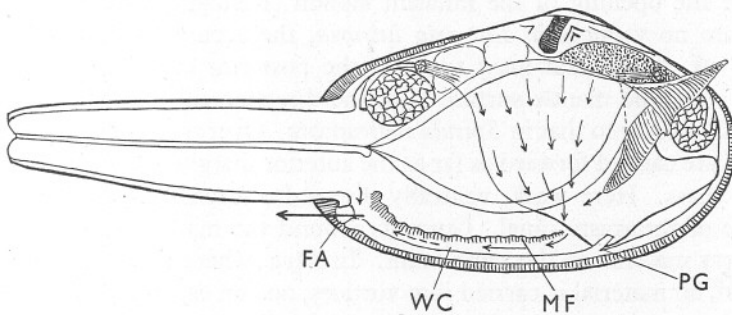


Fig. 5. *Lutraria lutraria*, animal viewed from right side after removal of right shell valve and mantle lobe, siphon cut longitudinally.  $\times \frac{1}{2}$ . PG, posterior end of pedal gape. Other lettering as before. Arrows indicate course of ciliary currents on the visceral mass and within the waste canal.

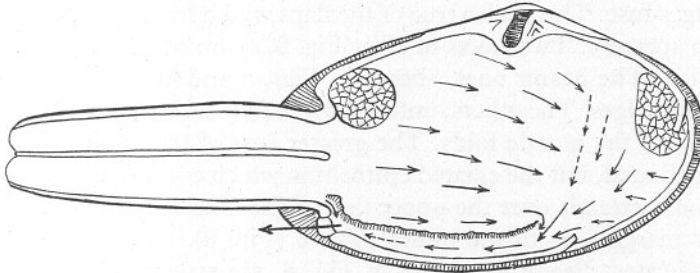


Fig. 6. *Lutraria lutraria*, as in Fig. 5, but with organs removed to expose the mantle surface and with arrows indicating the direction of the ciliary currents on this, weaker ones shown by broken arrows.

The fourth aperture is short, not more than 5 mm. long in an animal of shell length 11.5 cm. The mantle margins are here somewhat thicker, owing to a greater development of the pallial muscles. Well-developed mantle folds, shown in section in Fig. 8, extend from the base of the inhalant siphon, i.e. just posterior to the fourth aperture, to near the posterior margin of the foot and visceral mass, exactly as in *Spisula subtruncata* only for a relatively longer distance owing to the posterior extension of the body in *Lutraria lutraria*. There is no trace of a siphonal membrane.

### *Removal of Waste Material*

The course of the ciliary currents on the visceral mass and of those on the surface of the mantle is shown in Figs. 5 and 6. On the former, material is carried ventrally to the posterior margin adjacent to the hinder surface of the foot. Conditions therefore resemble those in *Spisula subtruncata* and not in *Mya arenaria* L., where all currents beat towards vortices on either side of the posterior end of the more longitudinally extended visceral mass and nearly opposite the opening of the inhalant siphon (Kellogg, 1915; Yonge, 1923). There are no vortices in *Lutraria lutraria*, the accumulated waste material passing off the visceral mass to enter the posterior end of the waste canal (Fig. 5). On the mantle surface also, the direction of the ciliary currents is essentially similar to that in *Spisula subtruncata*. Over the posterior two-thirds, particles are carried forward as far as the anterior margin of the currents on the visceral mass. Here weak, ventrally directed, currents convey them to the entrance of the waste canal. Currents around the margin of the wide pedal gape carry material to the same point. In *Mya*, where the currents are more powerful, all material is carried into vortices, one on each side of the posterior end of the pedal gape.

The currents in the waste canal, when viewed from above with the mantle folds drawn apart, are shown in Fig. 7. All waste, as shown above, enters this canal. There are no cilia along the mid-line, where the cuticular surfaces of the mantle edges fuse. This is also true of the flaps which fringe the pedal gape and the fourth aperture. Two tracts of cilia (Fig. 8, c) are present on either side of the mid-line. The nearer ones, shown in Figs. 7 and 8, lie on the surface of a pair of low ridges. The others, only shown in the section (Fig. 8), are situated at the bases of the mantle folds. The greater part of the under surface of the folds is unciliated, but the ciliated epithelium which covers the general surface of the mantle extends over the upper face of the folds and for a short distance over their margins on to the under surface (Fig. 8). Subepithelial mucous glands, indicated diagrammatically in Fig. 8, are associated with all ciliated areas. The unciliated epithelium is much lower and almost devoid of glands.

Within the anterior half of the canal particles travel back with some speed, but behind this, in the region indicated by the broken arrows, the currents are very weak. More powerful currents exist between the base of the inhalant siphon and the fourth aperture towards which they carry particles. Conditions are thus very different from those in *Mya*. There an exceptionally powerful posteriorly beating tract of cilia occupies a broad mid-ventral area formed by the complete fusion of the mantle edges. Elongated areas of mucous cells on either side of the pedal opening (originally described by Vlès, 1909) supply mucus in which the waste particles are consolidated in masses at the base of the inhalant siphon through which they are periodically ejected. No such glandular areas are present in *Lutraria lutraria*.



The necessity for removing waste must be no less in *Lutraria* than in *Mya*, but the mechanism is certainly different. When fully expanded, as shown in Fig. 4, the fourth aperture is normally closed. But the immediate effect of contraction by the locally enlarged pallial muscles, which accompanies that of the adductors, is to pull the lips apart so that a longitudinal slit is converted

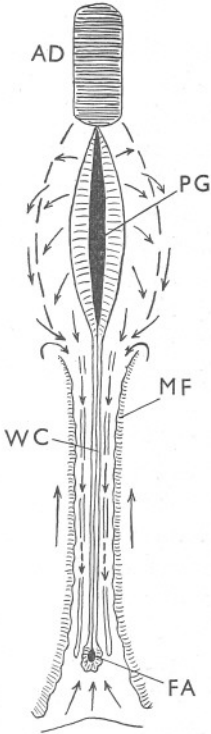


Fig. 7.

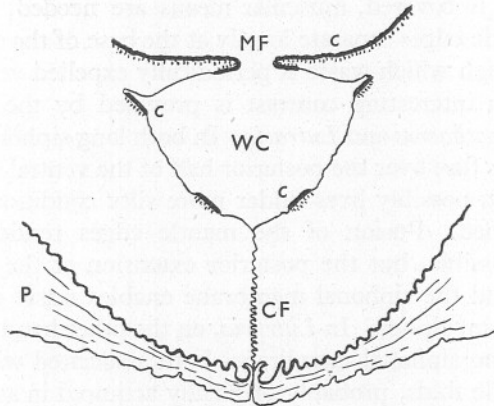


Fig. 8.

Fig. 7. *Lutraria lutraria*, mid-ventral region of the mantle viewed from above.  $\times \frac{3}{4}$ . AD, anterior adductor; PG, pedal gape. Other lettering as before. Arrows indicate direction of ciliary currents carrying material to fourth aperture.

Fig. 8. *Lutraria lutraria*, semi-diagrammatic drawing of section through the fused mantle edges and waste canal.  $\times 2$ . c, areas of ciliated epithelium with underlying mucous glands; cf, cuticular fusion of mantle edges. Other lettering as before.

into a circular opening. As already noted, this points posteriorly and is in line with the waste canal. Hence all material within this will be ejected through the fourth aperture. Bloomer (1903) noted that *Lutraria* uses this 'aperture frequently in suddenly ejecting water or any objectionable matter from the pedal cavity'. Atkins (1937 c) agrees with him. Neither, however, notes the presence of the pallial folds. The absence of a siphonal membrane in *Lutraria*, possibly correlated with the less silty environment, enables the greater part of

the water in the large inhalant chamber to be expelled at the same time through the inhalant siphon, as in the even larger *Schizothaerus* where the waste is carried out by this route. In Fig. 3 D conditions in *Lutraria* are shown diagrammatically in comparison with those in *Spisula subtruncata* and in *Schizothaerus*.

#### DISCUSSION

It would appear from the foregoing account that a siphonal membrane has evolved in shallow-burrowing Mactridae, such as *Spisula subtruncata* and *S. polynyma*, as an adaptation to life in silty water. The long frontal cilia on the gills of the former, described by Atkins (1937 *a, b*), represent a further adaptation to these conditions. The protection of the waste canal by mantle folds is correlated initially with the presence of the siphonal membrane, as postulated by Kellogg. Where the hind end of the shell is not covered when the animal burrows, as in *Mactra solidissima*, ciliary currents may be adequate to remove the waste ventrally from the canal. But in *S. subtruncata*, where the entire shell is covered, muscular means are needed, and correlated with this the mantle edges separate locally at the base of the siphons, providing an aperture through which waste is periodically expelled ventrally.

An interesting contrast is provided by the two deep-burrowing genera, *Schizothaerus* and *Lutraria*. In both long siphons are formed while the mantle edges fuse over the posterior half of the ventral surface. But in *Schizothaerus*, which possibly lives under more silty conditions, the siphonal membrane is retained. Fusion of the mantle edges renders ventral ejection of waste impossible, but the posterior extension of the mantle folds and waste canal behind the siphonal membrane enables waste to be carried out through the inhalant siphon. In *Lutraria*, on the other hand, there are no long frontal cilia and no siphonal membrane, both associated with life in silty water, but the mantle folds, probably originally acquired in association with the membrane, remain. They retain their function because a true fourth aperture is present which, owing to the protrusion of the mantle edges, is directed posteriorly. The waste is thus expelled along a passage parallel to, but owing to the intervention of the mantle folds distinct from, the inhalant siphon. Owing to its descent from some form not unlike *Spisula subtruncata*, the cleansing mechanisms of *Lutraria* are very unlike those of *Mya*, despite the similarity of external form and of habit in the two genera.

A fourth aperture is present in a number of other Lamellibranchiata, in species of *Ensis* and *Cultellus pellucidus* and in many of the Anatinacea (Pelseneer, 1890, 1911). The nature of the opening in the former has been discussed by Bloomer (1903), Graham (1931) and Atkins (1937 *c*). In *Ensis* it lies in about the middle of the ventral surface, in *Cultellus* it is more anterior. The mantle edges between the fourth and pedal apertures are united only by cuticular fusion (Atkins, 1937 *c*), and very readily separate when the animals

are removed from the sand or mud which normally presses against the shell valves. Atkins considers that the function of the fourth aperture in these animals is to act 'normally as an additional inhalant aperture, and, on sudden closure of the valves, for ejection of unwanted particles'. The former function can be at best merely incidental; any opening into the inhalant cavity will admit water when the lateral cilia on the gills are beating. The same criticism can be made of the second function ascribed to it. Graham (1931) has shown that waste material is conveyed, in the usual manner, to the base of the inhalant siphon in *Ensis siliqua*. It appears more probable that the fourth aperture in these animals is essentially a safety valve which permits the ventral extrusion of some of the water in the mantle cavity when these rapidly burrowing animals make the sudden muscular contractions involved in downward movement. It is certainly not associated with special mechanisms concerned with collection of waste as it is in *Lutraria*.

In the Anatinacea the aperture lies, as in *Lutraria*, at or near the base of the inhalant siphon. The mantle edges are extensively fused along the ventral surface. Atkins (1937c) has shown that there is complete tissue fusion in *Thracia villosiuscula* F. & H., and this is probably true of all Anatinacea. Kellogg is the only worker to examine the mantle cavity in life, and he has shown that waste collects in the vicinity of the fourth aperture in *Mytilimeria nuttalli* (Conrad) and *Lyonsia saxicola* Baird. But there are no associated mantle folds, and he was unable to determine with certainty the significance of the opening. In the abyssal genera, *Asthenothaerus* and *Periploma*, Pelseener (1911) describes a third ventral adductor immediately posterior to the fourth aperture. Such evidence as there is would therefore seem to indicate that the function of the fourth aperture in the Anatinacea is similar to that in *Lutraria*. But further study in life of species of this little-known group is needed.

#### SUMMARY

*Spisula subtruncata* is a shallow-burrowing member of the Mactridae which inhabits silty sand. Adaptations to such conditions include long frontal cilia on the gills (Atkins), and the presence of a siphonal membrane with associated mantle folds over-arching a waste canal, as postulated by Kellogg for allied species.

The mantle edges are free ventrally, but are normally closely applied except for a short distance at the base of the inhalant siphon, an effective fourth pallial aperture being so formed. Through this opening material from the waste canal is ejected.

*Lutraria lutraria* is a deep-burrowing species belonging to the same family. The general resemblance to *Mya arenaria* is due to convergence. Cleansing currents resemble those of *Spisula subtruncata* and there is a similar waste canal, but the siphonal membrane and the long frontal cilia associated with a silty environment are absent.

The mantle edges are firmly united along the posterior half of the ventral surface by fusion of the bounding cuticle (Atkins), but there is a true morphological fourth aperture at the base of the inhalant siphon. This is directed posteriorly and all waste is probably ejected through it.

*Schizothaerus nuttalli*, described by Kellogg, is another deep-burrowing member of the Mactridae, but here the mantle edges are fused without leaving a fourth aperture. Waste is ejected through the inhalant siphon owing to the extension behind the siphonal membrane of the waste canal and mantle folds.

It is suggested that the fourth aperture in species of *Ensis* and *Cultellus* acts as a safety valve through which some of the water leaves the mantle cavity following the sudden contractions which occur in these rapidly burrowing species.

The fourth aperture in many Anatinacea has never been adequately studied. Existing data indicate that it may be concerned with the ejection of waste, but there is no associated waste canal with mantle folds.

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