The Biology of *Aporrhais pes-pelecani* (L.) and *A. serresiana* (Mich.).

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With 6 Figures in the Text.

CONTENTS.

INTRODUCTION.

THE genus Aporrhais comprises a small number of species which are easily recognizable owing to the greatly expanded outer lip of the shell, and which occur in the North Atlantic from West Africa to the Arctic. The animals are of especial interest on account of their habits and also of their close relationship to the tropical family Strombidae, the two most important genera of which, Strombus and Pterocera, are characteristic members of coral reef faunas, the latter in the Indo-Pacific, the former in both this region and the Atlantic.

Two species of Aporrhais occur in the Norwegian fjords, *A. pes-pelecani*, which is also a member of the Plymouth fauna, and *A. serresiana* (=*A. macandreae*) which is an inhabitant of deeper water and is found only off the northern shores of Great Britain. This paper is the result of observations carried out on these two species at the Bergens Museum Biological Station at Herdla during the month of August, 1936. The author wishes to express his sincere thanks to the Director of the Station, Professor A. Brinkmann, for his great kindness and help and also to Amanuensis D. Rustad for much assistance. Acknowledgements are also

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APORRHAIS PES-PELECANI.

This species (Fig. 1) is characterized by a solid shell, the spire of which is longer than the expanded lip or " body." The latter is prolonged into four conspicuous digitations and a fifth which is only very slightly
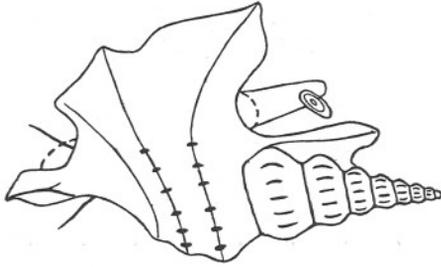

FIG. 1.—*Aporrhais pes-pelecani*, seen from above when moving over a hard surface. The head, except for the tentacles, is obscured by the blade-like terminal digitation. The operculum is attached to the upper side of the posterior end of the foot. The broken lines mark the positions, when the animal is buried, of the inhalent and exhalent apertures. $\times 1\frac{1}{2}$.

developed. The terminal or " caudal " digitation is notably stout and, owing to lateral dilation, blade-like (see Fig. 1). The point is directed downwards as shown in Fig. 2. This downward curve increases with age because, after the attainment of full size with the complete formation of the
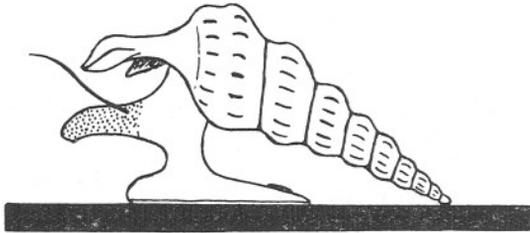

FIG. 2.—*A. pes-pelecani*, lateral view from left side showing the mode of progression over a hard surface.* The animal is raising the shell off the ground by extending the "neck," the body and shell will then be moved forward. $\times 1\frac{1}{2}$.

expanded lip, further shell formation is confined to an increase in thickness (very well-marked in the most worn shells), while, for reasons which will be made clear later, the frontal upper surface of the tip of the terminal digitation is worn away.

The exposed regions of the animal are yellowish-white with red

* Weber (Z. vergl. Physiol., II, 109 ; 1924) has described and figured this arhythmical movement in Chenopus (= Aporrhais) and also in Conus and Strombus.

speckling which often extends over the foot, including the sole. The snout and head are thickly speckled with scarlet, while the tentacles are mingled yellow and scarlet. The foot (Figs. 1 and 2) is narrow and very extensile and carries the small, elongated operculum (Fig. 1) on the upper surface near the posterior end. It is united to the body by a thick "neck" or stalk (Fig. 2). The head is prolonged into the characteristic proboscis, the mouth opening at the end of this and consisting of a perpendicular slit. The tentacles (Figs. 1, 2 and 4) are long and slender when fully expanded and at the base of these, situated on prominent bulbs, are the eyes (Fig. 4).

(a) Habitat and Habits.

A. pes-pelecani is found on comparatively firm muddy gravel bottoms. In the neighbourhood of Herdla it was most abundant near Rossland on a bottom of this type at a depth of some 20 metres. It is characteristic of the shallower depths in which such bottoms occur; both Forbes and Hanley (1853) and Sars (1878) give the vertical distribution as from about 5 to 100 fathoms.

The animal is, in the words of Jeffreys (1867), "shy, slow and backward in its movements." When placed in a dish of sea-water the animals soon expand, locomotion taking place by a series of somewhat ungainly movements. The body is first raised by extending the "neck" (as shown in Fig. 2) which may stretch to a length of 1 cm., especially when faced with obstacles. Then, the foot remaining motionless, the body and the shell are carried forward in one convulsive movement for a distance up to about 8 mm. The shell and body then fall and the foot glides forward for the same distance, after which the "neck" is again raised and the process repeated. When placed upside down the animals can right themselves. This they do by extending the foot and head to the maximum extent around the base of the terminal digitation on the side away from the expanded lip. Extension proceeds until the foot is placed firmly on the substratum and, with the aid of the purchase so obtained, the shell is righted by a convulsive contraction of the body musculature.

It is interesting to compare these movements with those of the related "spider-shell" of the tropical Indo-Pacific, *Pterocera crocata*, which, although very much larger, has a shell of somewhat similar type. This animal lives on sandy areas on coral reefs. As previously observed (Yonge, 1932), it progresses by a series of sudden movements not unlike those of Aporrhais, but in this case not with the aid of a creeping sole, which has been lost, but by means of the stout operculum, long and very sharp, which is dug into the sand before each movement, after which it is dragged forward and pushed into the sand again.* In this case the animal

* Parker (J. Exp. Zool., XXXVI, 205; 1922) records similar progression in *Strombus gigas.*

can right itself by extending the foot around the same side of the shell as in Aporrhais until the operculum is hooked under the shell where this rests on the ground. Then, by a convulsive movement, the animal turns over.

When *A. pes-pelecani* was placed in a vessel containing a thick layer of gravelly mud it soon became apparent that the animal is actually specialized for burrowing and that progression on the surface must normally be of rare occurrence. After moving about for a short time on the surface the animals invariably began to burrow. The process is interesting. The terminal digitation, in shape admirably fitted for this, is first pushed beneath the substratum. Then, as a result of a succession of movements, the animal gradually progresses at first obliquely downward and then horizontally beneath the surface. The movements, which at first occur at intervals of between 40 seconds and one minute, become less frequent as the obstacles to progression increase. At each
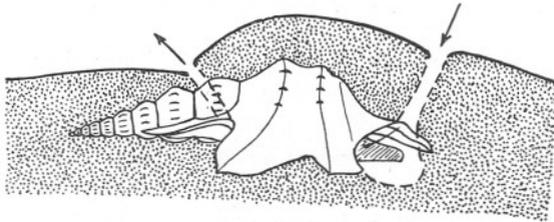
FIG. 3.—*A. pes-pelecani*, semi-diagrammatic representation of the position of the animal when buried, from the right side. The inhalent and exhalent apertures are indicated by arrows showing the direction of the currents. × 1½.

movement the animal turns over a little to the right side (that with the expanded lip) and the shell, as indicated by the movement of the mud above it, is raised. The action is clearly the same as when the animal is moving on the surface. As the animal sinks below the surface a small mound is raised in front of it and it is when this is some 5 mm. above the highest point on the terminal whorl of the shell that the direction of movement becomes horizontal. The upper surface of the apical whorls of the shell are still uncovered but lie in an elongated depression into which material falls from the sides and particularly from the mound raised in front. Finally, by a combination of the effect of continued forward movement and the falling in of material from all sides the shell is completely covered, as indicated in Fig. 3.

At this stage further movements can still be detected though with little or no progression. Each movement, by causing a raising and lowering of the expanded lip, results in the ejection of water from under the hinder margin of the expanded lip. In this way a temporary opening is

formed in the gravel. There is no other opening at this stage. These movements probably serve to clear away the softer mud before the animal finally settles down ; they may also clear a space below the expanded, horizontally disposed lip.

Finally all movements cease. An inhalent opening is then made by the highly extensile proboscis which extends around the right-hand side of the terminal digitation, in front of the expanded lip, and upward until it breaks the surface. It then moves round actively in all directions curling back over the opening, so that the inhalent opening, at first irregular in outline, becomes finally rounded and some 2 mm. in diameter. Mucus is secreted by numerous unicellular glands in the wall of the proboscis (demonstrated in sections) and this consolidates the wall of the inhalent opening. The proboscis is then withdrawn, turned backward under the expanded lip and protruded upwards around the edge of the bay at the hinder end of the lip. An exhalent opening is formed in exactly the same manner as the inhalent one, the positions of both being shown in Fig. 3. The function of these becomes at once apparent when carmine is added to the water around them, a steady flow of water passing into the anterior one and out by way of the posterior one. The formation of two siphonal openings by the same agency, and at such considerable distance from one another—an animal of shell length 3·8 cm. had siphonal openings 2·3 cm. apart—has not, as far as can be ascertained, been observed in any other animal. It provides a most interesting example of adaptation in a burrowing Gastropod. The formation of siphonal tubes consolidated with mucus is also unusual in Mollusca although, during the same period at Herdla, it was found that the lamellibranch, *Thracia pubescens*, forms siphonal tubes in somewhat the same manner (Yonge, 1937).

After the inhalent and exhalent apertures have been made and consolidated the proboscis is withdrawn and only very occasionally protruded through them again, apparently to strengthen the lining of the tubes. It can always be induced to protrude by obliterating either of the openings which it promptly proceeds to reconstruct. The animals remain motionless beneath the surface, the only indication of their presence the two small openings, for long periods. One animal remained so for three days before uncovering itself, when it moved about for a short distance and then burrowed again. The proboscis can presumably range about at will under the surface of the expanded wing and both in front of and behind this, and it is to be assumed that the animal remains in one position so long as sufficient food can be obtained within this area.

(b) Currents in the Mantle Cavity.

The powerful inhalent and exhalent currents which enter and leave the apertures constructed by the proboscis reveal the presence of strong

ciliary currents within the mantle cavity. It is also clear that, living buried beneath mud, the animals must be exposed to great danger from silt blocking the mantle cavity and must possess adequate mechanisms for dealing with this. The nature of the various ciliary mechanisms was
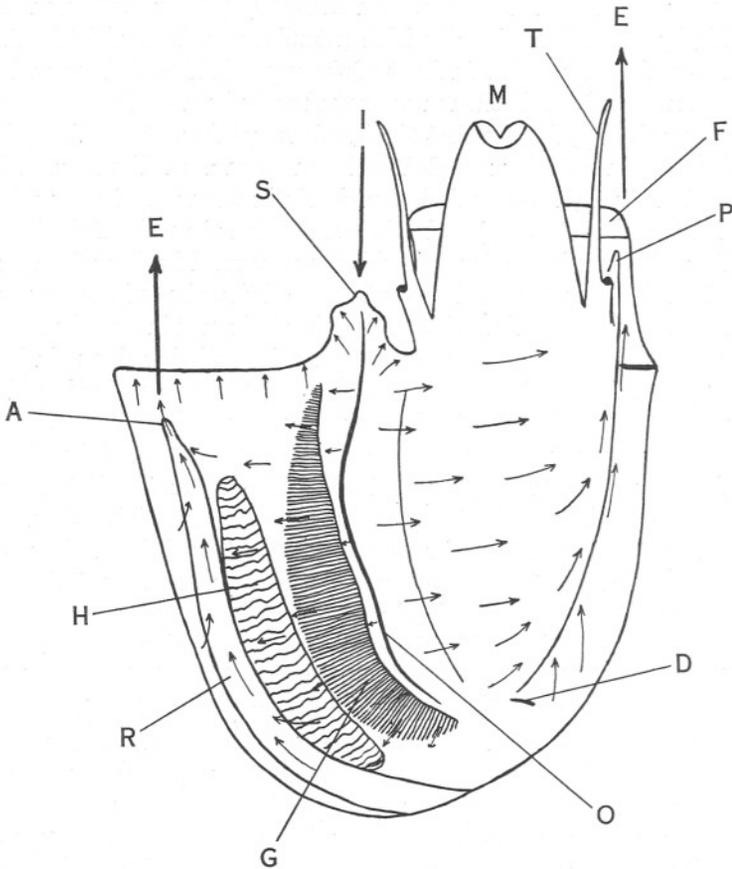

FIG. 4.—*A. pes-pelecani*, mantle cavity opened along the right side, seen from above. ×5. A, anus; D, opening of the male reproductive duct; E, exhalent current; F, anterior margin of foot; G, gill; H, hypobranchial gland; I, inhalent current; M, mouth; O, osphradium; P, penis; R, rectum; S, siphonal extension; T, tentacle with eye on bulb at base. Arrows indicate direction of ciliary currents.

revealed when the mantle cavity was opened, by cutting along the right side, as shown in Fig. 4.

The respiratory current is created by lateral cilia on the gill filaments, each of which consists of an elongate triangle, broadest at the base but slightly flattened at the tip. The large size of the gill (G) explains the powerful nature of this current. The inhalent current (I) enters on the

left side of the head, where the mantle is extended to form a short siphonal process (S). The exhalent current (E) leaves the mantle cavity on the right side (topographically behind the other).

In the intact animal the siphonal process when distended is considerably larger than it appears in Fig. 4. It then extends for some distance forward under the terminal digitation and around the adjacent edge of the bay on the front edge of the expanded lip of the shell. The largest particles which are carried in with the inhalent current come in contact with the surface of the mantle in this region and are caught in powerful outwardly directed ciliary currents which also extend all around the edge of the mantle, as indicated by the arrows in Fig. 4.

The osphradium (O) is unusually elongated. It arises a short distance anterior to the extreme posterior end of the gill (G), running parallel to the base of this for some two-thirds of its course then diverging somewhat to the right and extending for some distance anterior to the gill along the middle line of the siphonal extension. The line of the osphradium marks the extreme left-hand side of the mantle cavity and therefore the middle line of this when it is cut open and extended as in Fig. 4. Under these conditions the ciliary currents on the mantle carry particles in opposite directions on either side of the osphradium. On the right-hand (ventral) side particles are carried over the floor of the mantle cavity to the exhalent region where they pass forward alongside the genital groove. On the dorsal side (left side in the figure) particles are carried to the gills, in between the filaments of which the water passes, where they are carried to the tip by the frontal cilia and thence, over the surface of the large hypo-branchial gland (H) which secretes large quantities of mucus, to the region of the rectum (R) where they pass forward. The two mucus-laden streams of particles from the ventral and dorsal surfaces of the mantle cavity thus combine on the right or exhalent side of the mantle cavity and pass out, together with faeces discharged by the anus (A) at the side of the head. They are then carried downwards over the " neck " region into a groove running around the base of the foot in which all this waste material is conveyed backwards. All material which drops on to the foot is also carried into this tract.

The powerful respiratory currents, necessary possibly in view of the probably lowered oxygen tension in the water immediately in contact with mud containing much organic matter, are thus provided by the lateral ciliation on the filaments of the very well-developed gill. Disposal of material in suspension is brought about by three agencies. (1) Largest particles are immediately carried to the edge of the inhalent region, in essentially the same manner as similar material is ejected from the inhalent cavity of Lamellibranchia (see Kellogg, 1915 ; Yonge, 1923, 1926). (2) Somewhat lighter particles, which settle to the surface farther

within the mantle cavity, are carried across the floor of the mantle cavity to the exhalent region. (3) The lightest particles of all, which are retained in suspension, are carried to the tip of the gills when the water passes through this and are then entangled in mucus secreted by the hypo-branchial gland before passing out with the medium particles and the faeces by way of the exhalent opening.

(c) *Feeding.*

The animals will feed on the surface as readily as when buried and so the process can be observed. The proboscis continually moves about, being capable of extension from base of tentacles to tip up to a length of 1 cm., while the mouth continually searches the ground for food. The lateral lips are very sensitive and repeatedly open, exposing the small, but powerful, radula and the jaws (capable of firmly seizing a needle inserted into the mouth) which are protruded between them. Aporrhais has been described as a carnivore (Woodward, 1875), but is actually, as will be shown, a specialized herbivore. The presence of animal matter (shredded out tissues of bivalves) may even cause the animals to move away, sometimes backwards, or this may first be tasted and the proboscis then withdrawn sharply, the animal passing elsewhere. Finely cut up pieces of Fucus were not accepted, but fine green algae, such as shredded strips of Enteromorpha, were taken readily. This was seized by the jaws and radula and swallowed whole. The radula consists of a single hooked and denticulate tooth with three laterals, the first two transverse and the third claw-shaped (see Woodward, 1875, Fig. 100). A radula of this type has usually been considered characteristic of carnivorous Gastropoda (e.g. by Digby (1902) in Chytra and Limnotrochus), but is actually adapted for seizing, as opposed to scraping, which is the more usual method of feeding in herbivorous Gastropoda. The radula of Aporrhais, as Woodward has pointed out, most closely resembles those of Strombus and Pterocera (both herbivorous, Yonge, 1932) and of the Heteropod Carinaria, a carnivore which is specialized for seizing larger members of the zooplankton. This misapprehension as to the true significance of this type of radula is probably responsible for the statements that Aporrhais is a carnivore.

The animal presumably feeds normally by collecting, by means of the extensile proboscis, all particles of plant matter which occur in the mud in the region below and around the expanded lip. This material will consist largely of detritus of vegetable origin, the remains of algae or of diatoms which have dropped from the surface, together with bottom-living diatoms. Hunt (1925) in his work on the food of the bottom fauna around Plymouth classified *Aporrhais pes-pelecani*, together with one other Gastropod, *Turritella communis*, as a selective deposit-feeder. He

did so as a result of examination of the stomach contents which he found always consisted of " roughly sorted bottom material."

(d) The Alimentary Canal.

Further evidence as to the nature of the food is provided by a study of the gut. A straight and comparatively wide oesophagus carries material into the large and complex stomach (Fig. 5). Into the lumen of this projects a stout crystalline style, 8 mm. long and 1 mm. wide in an adult animal. This structure, the presence of which was noted by Digby (1902), is secreted within a wide style-sac (S) in restricted communication
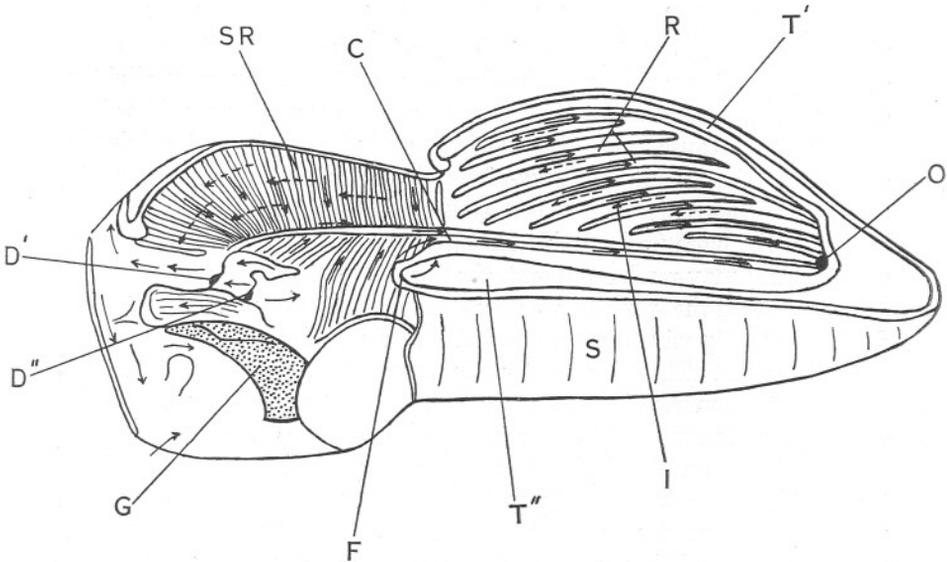

Fig. 5.—*A. pes-pelecani*, stomach with initial region of intestine and style-sac opened along mid-dorsal side. ×9. C, channel leading into initial region of intestine from sorting region in stomach; D′, D″, ducts into digestive diverticula; F, flap guarding entrance from oesophagus; G, gastric shield; I, initial region of intestine; O, opening into second region of intestine; R, ridges in initial region of intestine; S, style-sac; SR, sorting region; T′, T″, typhlosoles which separate style-sac from intestine. Arrows indicate direction of ciliary currents.

with the first portion of the intestine (I). The head of the style bears, in life, against a similarly well-developed gastric shield (G). The presence of these organs immediately indicates that the animal is herbivorous, because, for reasons given elsewhere (Yonge, 1930), the presence of a crystalline style is incompatible with that of an extracellular protease, and, as already noted, the only possible substitute for this mechanical trituration by the radula, is absent. A second structure of great significance in the stomach is the series of parallel ridges which constitute

a sorting region (SR). Fine particles are carried over these ridges from summit to summit (as indicated by the broken arrows in Fig. 5) and so passed to the vicinity of the openings of the two ducts into the digestive diverticula (D', D''), while larger particles pass into the grooves between the ridges and are conveyed by different ciliary tracts into a channel (C) which carries them rapidly into the first portion of the intestine.

The stomach of Aporrhais thus bears a remarkably close resemblance to that of a typical Lamellibranch in the presence of a style with an associated gastric shield and of a complicated sorting region (identical in function with those of Modiolus (Nelson, 1918), Mya (Yonge, 1923), Ostrea (Yonge, 1926) and Ensis (Graham, 1931)). It resembles the stomach of Pterocera and *Vermetus novae-hollandiae* (Yonge, 1932) in the presence of a style, but a sorting mechanism is absent or only very slightly developed in these animals. In Pterocera such an organ is probably of no importance, because the food, which is exclusively of plant origin, is exposed to the action of a powerful cellulase—absent (as experiments proved) in Aporrhais—which breaks down the larger food masses. In Vermetus the more finely divided nature of the food (collected by ciliary mechanisms) may render elaborate further sorting unnecessary.

The action of the stomach, therefore, is to convey fine particles into the ducts of the digestive diverticula and larger ones into the first portion of the intestine. There is an outward passage of particles along the floor of the ducts from the digestive diverticula (indicated by arrows in Fig. 5) and an inward movement above this. It is therefore possible for material to be carried in, and for the indigestible remnants of intracellular digestion to be later expelled. Muscular movements may also assist in this ; the walls of the stomach were observed to make frequent contractile movements even after being opened out, and this applied particularly to the flap which separates the two ducts and that which guards the entrance from the oesophagus (F). Within the stomach circulation of particles will be assisted by the rotation of the style, the dissolution of which will bring about extracellular digestion of starch. Sections of the digestive diverticula revealed the absence of secreting cells. The cells are presumably concerned exclusively with intracellular digestion as in other herbivorous Prosobranchia, such as Patella (Graham, 1932), and in all Lamellibranchia.

The intestinal regions of the gut are three in number and are concerned exclusively with consolidating the particles passed on from the stomach into firm faecal pellets. The regions consist of a wide initial region (I, Fig. 5) which is largely separated from the adjacent style-sac (S) by two typhlosoles (T', T''), a narrow " small " intestine which ramifies for some distance through the viscera, and a terminal, much wider

"rectum" (R, Fig. 4), which runs along the right side of the mantle cavity to open at the anus (A) in the exhalent region.

The channel (C) into which material is passed from the sorting region of the stomach is continued throughout the wide initial region of the intestine, which also possesses an interesting series of ridges (R) which run obliquely around it as shown in Fig. 5. On the summits of these powerful ciliary currents carry material into the opening into the "small" intestine (O) towards which the ridges converge. In the grooves between the ridges less powerful currents beat in the opposite direction. There is a great production of mucus in this region of the intestine and the purpose of the ridges and grooves with their different tracts of cilia is apparently that of thoroughly mixing the particles with mucus. Muscular movements play an important part in this process, continual contractions, causing the temporary obliteration of the grooves, being frequently observed even after this region had been opened out. The material passed into the opening of the "small" intestine is thoroughly mixed into a homogeneous mass with large quantities of mucus.

The "small" intestine has a narrow lumen with no typhlosole, but with a fine groove on one side which probably represents the continuation of the channel in the stomach and initial region of the intestine. A powerful anally-directed ciliary current is present in this groove. The faeces are here consolidated into a firm, continuous thread with an outer envelope of mucus. In this form they enter the wide "rectum." The groove with its powerful ciliary current is continued and provides the propulsive force towards the anus. The remainder of the wall of the rectum is ciliated, but the direction of the currents could not be determined with accuracy. When carborundum was placed upon this surface it merely trembled to and fro. The same action is always observed when similar particles are placed on the surface of the style-sac epithelium of any Lamellibranch (or style-bearing Gastropod), indicating that in the rectum also the cilia may only act when material is pressed tightly against them (Yonge, 1926). Additional evidence is provided by a similar velvety appearance of the surface of the living epithelium in both rectum and style-sac and by a general resemblance of both epithelia in section. It is certainly true that both epithelia have the same function, that of moulding material into a rod-like form. In the rectum of Aporrhais the fine threads which enter from the "small" intestine are converted into elongated, thick pellets, each of which contains a twisted coiled mass of these finer threads enclosed in a second, thicker envelope secreted by the walls of the rectum. Thus it is in the form of large pellets, which cannot foul the water in the mantle cavity, that the faeces are expelled from the anus.

APORRHAIS SERRESIANA.

This species provides an interesting contrast in structure and habitat
to *A. pes-pelecani*. The shell, illustrated in Fig. 6, attains a slightly
greater size than that of *A. pes-pelecani*, but is somewhat more delicate,
notably in the expanded lip. Owing to the greater length of the terminal
digitation in this species (compare Figs. 1 and 6) the spire is shorter than
the " body " of the shell. The expanded lip is much larger than in the
other species and there are five, instead of four, prominent digitations,
which are prolonged into fine points instead of ending bluntly. The ter-
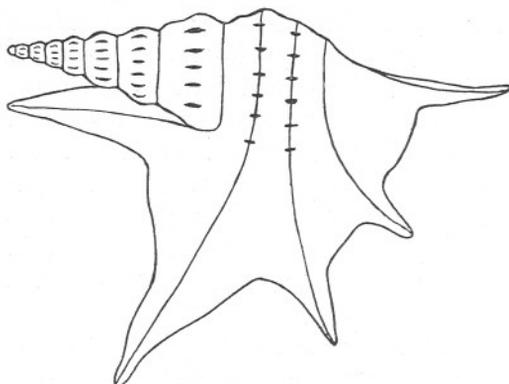minal digitation is notably long and narrow, being straight and pointed

FIG. 6.—*A. serresiana*, shell seen from above, the great
extent of the expanded lip is shown, also the five
sharply pointed digitations, the terminal one being
notably fine. ×1½.

instead of broad and blade-like as it is in *A. pes-pelecani*. The animal is
more delicate than that of the other species and the tissues are white and
translucent except for the head and proboscis. The former possesses a
triangular patch of red on the dorsal surface, while the latter is speckled
with scarlet along the dorsal surface, with a white line, widening near
the tip, running along the middle line. The tentacles are translucent
with an opaque white band running along the upper side. They are also
longer and more extensile than those of *A. pes-pelecani*, being capable,
in a fully grown animal, of extending to a length of 1·5 cm.

  A. serresiana is an inhabitant of deeper water than *A. pes-pelecani*.
Sars (1878) states that the vertical distribution is from 80–300 fathoms.
It was collected in greatest numbers, although it is never so abundant as
A. pes-pelecani, at depths of about 200 metres in the Herdla fjord, where
it was the only species of the genus taken. At intermediate depths,
notably about 60 metres at Ypsøsund, both species were taken in

proportions of roughly seven *A. pes-pelecani* to one *A. serresiana*. Neither species was as abundant as they are in shallower or greater depths respectively.

The distribution of the two species is clearly dependent on the nature of the bottom. *A. pes-pelecani*, as already stated, occurs on comparatively firm bottoms of muddy gravel, but *A. serresiana* is an inhabitant of softer bottoms of fine mud found in deeper water.

The habits of *A. serresiana* are the same as those of *A. pes-pelecani*. It moves in the same manner over the bottom of a glass dish and burrows into soft mud. When placed on muddy gravel taken from the normal habitat of *A. pes-pelecani*, one specimen burrowed into the side of a small mound and moved slowly horizontally under the surface. No attempt was made to push downwards nor was there the same "shouldering" action as in the other species. Only with much greater effort and over a much longer period did the animal finally bury itself. *A. serresiana* is definitely less powerful than *A. pes-pelecani* and possibly in its natural habitat tends to sink in the mud and then push forward rather than actively to burrow downwards. The shape of the shell can be related to the needs of the animal. The elongated, pointed terminal digitation is well adapted for pushing through soft but closely compacted mud, while the greater extent of the expanded lip and the lighter shell prevent it from sinking too far below the surface.

When *A. pes-pelecani* was placed on soft mud it moved about less easily than the other species, tending to flounder in it and being hampered by great accumulations of mud in the mantle cavity and on the foot. The animal made no attempt to burrow in the mud, but rather tended to raise the body as far as possible clear of the bottom. The animal was most clearly not adapted for life on such a bottom.

Examination of the genital organs of *A. serresiana* failed to reveal the presence of a brood-pouch for incubating the young, so it is probable that pelagic larvae are produced similar to those of *A. pes-pelecani* described by Lebour (1933). If this is so then the survival of the young of the two species, after they descend at metamorphosis from the surface waters, must depend on the type of bottom on which they fall (itself usually dependent on the depth). Young *A. pes-pelecani* which settle down in deep water will be unable to exist on the soft mud, and young *A. serresiana* will be similarly unable to burrow, and so find adequate protection, on stiff muddy gravel bottoms at moderate depths. In certain intermediate regions both species will be able to exist, though conditions will be ideal for neither and the population of both will be correspondingly sparse.

Both in the form and solidity of the shell and in the strength of the body the two species are clearly adapted for a similar mode of life on different

types of bottom and the fact that these occur at different depths explains the differences in the horizontal distribution. The reduced pigmentation of the body in *A. serresiana* is presumably the result of the reduced light in the greater depths where it lives.

DISCUSSION.

The genus Aporrhais consists of Gastropods adapted for burrowing in mud and collecting beneath the surface of this detritus of plant origin by means of an extensile proboscis. The manner in which they maintain contact with the water above represents a further adaptation of the proboscis and one which, so far as our present knowledge extends, appears to be unique amongst the Gastropoda. The mode of life resembles more that of a Lamellibranch than of a Gastropod, the majority of mud-living species of which are carnivorous, such as Buccinum, Murex or Nassa, which plough their way through the mud in the search for prey. It is, however, possible that Turritella, which as shown by Hunt (1925) has similar stomach contents, and just possibly Cerithium and Caecum, may prove to live in a somewhat similar manner to Aporrhais. The interesting freshwater genera, Chyta and Limnotrochus, from Lake Tanganyika have similar feeding and digestive organs (Digby, 1902), but nothing is known of their habits. They are certainly related to Aporrhais and to the Strombidae.

The characteristic expanded lip of the shell in the fully grown animal is not necessarily primitively an adaptation concerned with the burrowing habit. In the first place young specimens of *A. pes-pelecani* in which the terminal whorl has not yet been formed, and also older specimens in which the terminal whorl is present but the expanded lip has still to be formed, were both found capable of burrowing like the adults. These will also burrow, although with certain difficulty, when the terminal digitation has been broken off. In the second place a similar expanded lip occurs in the allied Strombidae—very well developed in Pterocera, less so in Strombus, but absent in Rosellaria—none of which live in the same manner. In Pterocera (Yonge, 1932) this flattening of the shell enables the animal to move about on the surface of the sand *without* sinking into this and to keep the right side up despite the ungainly, jerking movements referred to earlier in this paper. Strombus possesses somewhat similar habits ; those of Rosellaria are unknown to the author. It appears not impossible that the expanded lip of Aporrhais may originally have been evolved in connexion with a similar mode of life, but that the animals later took to life on mud instead of sand and then to burrowing in this with consequent changes in the form of the terminal digitation and in the breadth and flatness of the lip. There can be little doubt that both are of importance to the adult animals, the terminal digitations in

the manner described for the two species, and the horizontal shelf pro-
vided by the lip in the increased area over which the proboscis may
browse unimpeded and, in *A. serresiana*, possibly by the increased resist-
ance to sinking in the softer mud.

The powerful water currents through the mantle cavity due to the great
development of the gill, and the elaboration of the ciliary mechanisms
for disposing of sediment carried in with the respiratory current (the latter
better developed in *A. serresiana*) are both of them adaptations to the
mode of life. They have an added interest because they indicate the
manner in which ciliary feeding in Gastropods such as Crepidula (Orton,
1912) and *Vermetus novae-hollandiae* (Yonge, 1932) may have evolved.
The mechanism for rejection of large particles from the inhalent opening
may have become modified to form the food pouch in Crepidula, and the
rejection currents in the exhalent region to form the food channel. The
further flattening of the tips of the gill filaments and the appearance of
cilia carrying particles forwards in this region would convert the gill
into the food-collecting organ of Crepidula, or *Vermetus novae-hollandiae*.
It is hoped to develop this argument in more detail elsewhere.

The mode of feeding is very similar to that of Pterocera, the radula and
jaws having a similar selective action and the teeth of the radula being
few in number to permit of seizing instead of rasping. The form of the gut
is that of an herbivorous Gastropod, most notably in the presence of a
well-developed crystalline style and gastric shield which, as shown else-
where, occur in herbivorous Gastropoda which " feed by ciliary mechan-
isms, or by the slow but almost continuous action of a radula " (Yonge,
1932). It is certain that, if it is to obtain adequate supplies of vegetable
detritus having food value, Aporrhais must constantly be feeding. The
differences between Aporrhais and Pterocera consist in the presence
of a powerful cellulase in the latter—necessary because fresh algae, not
decomposing detritus, are swallowed intact and there is no means
of mechanical triturition—and the presence of an elaborate sorting
mechanism in the stomach of the former—the result of the varied size
of the particles collected by the proboscis and the necessity of ensuring
that only the smallest of these shall pass into the ducts of the digestive
diverticula for intracellular digestion. The remainder of the gut in
Aporrhais is concerned exclusively with the elaboration of faeces, of
profound importance, as Graham (1932) has emphasized in Patella, in
Gastropoda (and other Mollusca, Yonge, 1935) in which the anus opens
into the mantle cavity, fouling of which must be rigidly prevented.

NOTE ADDED IN PROOF. Since this paper appeared in proof, Mr. R.
Winckworth, in the course of a most helpful letter on the nomenclature
of the northern species of Aporrhais, has pointed out that Kobelt (1906,

p. 17) considered *A. serresianus*, described by Sars (1878, p. 198, pl. xii, fig. 7), to be merely a deep-water form of *A. pes-pelecani* and so re-named it *A. pes-pelecani sarsii*. The significant differences recorded in this paper between the form of the shell, the form and pigmentation of the exposed portions of the· body, and the reactions to different types of bottom, in *A. pes-pelecani* and *A. serresiana* lend little support to this view. Moreover, the fact that both were taken in the same haul of the dredge at intermediate depths, appears convincing evidence that *A. serresiana* is a true species.

SUMMARY.

1. *Aporrhais pes-pelecani* occurs on muddy gravel at moderate depths and is specialized for burrowing in this.

2. The mode of burrowing is described and also the formation of mucus-lined inhalent and exhalent openings by the proboscis.

3. There is a powerful respiratory current through the mantle cavity which also possesses three sets of ciliary currents for disposing of sediment carried in with this.

4. The animal is a specialized detritus feeder selecting only material of plant origin. The radula consists of one central and three lateral teeth on each side, an indication that it is used for seizing as opposed to scraping, *not* that the animal is carnivorous.

5. The stomach possesses a well-developed ciliary sorting mechanism. The large crystalline style and gastric shield indicate that the animal is herbivorous, but there is no cellulase.

6. The intestine is divided into three regions which are concerned exclusively with the gradual elaboration of the large elongated faecal pellets.

7. *A. serresiana* occurs in deeper water on a soft mud bottom. The differences in the form of the shell and the strength of the body between this species and *A. pes-pelecani* can all be correlated with the difference in habitat of the two species.

8. The form and the mode of life of both species are compared with those of the allied Strombidae of tropical coral reefs, and the ciliary mechanisms in the mantle cavity with those of ciliary feeding Gastropoda.

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