A Note on the Habits and Nutrition of *Solemya parkinsoni* (Protobranchia: Bivalvia)

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With two plates (figs. 1 and 2)

SUMMARY

Adult specimens of *Solemya parkinsoni* Smith, embedded in mud at a depth of 50 cm or more, were collected near low water (spring tide). The animal burrows with the anterior end downwards and does not maintain an opening to the surface. An inhalant current is drawn into the mantle cavity anteriorly on each side of the foot, while an exhalant current leaves by the single, posteriorly situated aperture. This is probably a respiratory current, bottom material entering the mantle cavity as a result of the muscular activity of the mantle and foot.

The course of the alimentary canal is described, and the problem of feeding and nutrition correlated with the extreme reduction of the gut exhibited by *S. parkinsoni* discussed. It is suggested that an initial breakdown of organic material may take place in the mantle cavity.

INTRODUCTION

LIVING specimens of *Solemya parkinsoni* Smith were collected during a brief visit to the Marine Biological Station, Portobello, New Zealand. The intention was to investigate the gut and to compare the results with those obtained from similar studies on members of the Nuculidae (Owen, 1956) and Ledidae. This was not possible in the time available. Previous workers (Pelseneer, 1891; Stempell, 1899; Yonge, 1939) have remarked that the gut of *Solemya* is noteworthy for its small size but this does not prepare one for the extreme reduction of all parts of the gut exhibited by *S. parkinsoni*, particularly since the gut in the Nuculidae and Ledidae is rather large. Fig. 1, A, B represents cross-sections of corresponding regions of the stomach of *Nucula sulcata* (shell size, 2·0 × 1·5 cm) and *S. parkinsoni* (7·5 × 3·0 cm) and illustrate the exceptionally small size of the gut in the latter. This is further emphasized by the fact that a first attempt to expose the stomach and intestine failed, the anterior aorta where it passes through the gonadial tissue being dissected by mistake (see fig. 3); the intestine in this region is less than half the diameter of the aorta. It is therefore pertinent to inquire what part the reduced gut plays in the nutrition of a rather bulky and potentially active animal. Owing to the difficulty of obtaining living specimens, the enigma presented by the gut of *S. parkinsoni* was not solved, but it is thought worth while to give a brief account of observations on preserved material. Observations on the habits of the living animal made during the brief visit to Portobello are also included, since previous accounts of the mode of burrowing and the position of the inhalant current vary.

OBSERVATIONS ON THE LIVING ANIMAL

Observations on the habits of *Solemya* have been made by Drew (1900), Morse (1913), and Yonge (1939). According to Morse, specimens of *S. velum* and *S. borealis* frequently burrow with the anterior end downwards, while Drew (1900) reported that '*Solemya* lives in rather hard mud, and, I think, keeps its burrow more or less open'. Yonge (1939), on the contrary, found that *S. togata* always burrowed with the anterior end downwards, and on no occasion was there any indication of an opening to the surface. Specimens of *S. parkinsoni* embedded in sandy mud at a depth of 50 cm or more were obtained near low water (spring tide); a few small specimens were found nearer the surface. The surface of the substrate was searched carefully for any indication of the presence of *S. parkinsoni*, but without success, and specimens were obtained by random digging in the area. Attempts were also made to determine the orientation of the animal within the substrate. A number of specimens were obtained with the foot cut off, but the remainder of the animal undamaged. On these occasions, the animal was invariably thrown out on to the discarded heap of mud while the severed portion of the foot remained in the substrate. This suggests that the animal lay either horizontally or vertically, but with the foot extending downwards. The latter would appear more likely and this is supported by other observations and by information subsequently received from Dr. Batham at Portobello.

Further observations on the burrowing activities of *S. parkinsoni* were made in the laboratory, and the sequence of burrowing is essentially similar to that described for *S. togata* by Yonge (1939). This is illustrated in fig. 1, C–E, where the ability of the terminal region of the foot to expand, and so obtain a purchase in the substrate, is clearly shown (see also fig. 2, D). Morse (1913), in support of his contention that *S. velum* frequently burrowed posterior end downwards, described how specimens placed on the sand with the ventral side uppermost protruded the foot ventrally and arched anteriorly to press against the substrate, thus lifting the anterior end of the shell and depressing the posterior end. Similar movements were observed in the laboratory with *S. parkinsoni* (fig. 2, D), but the posterior end of the animal was depressed only when the foot failed to penetrate the substrate sufficiently to provide the necessary purchase to draw the anterior end of the animal into the substrate. There seems little doubt that *S. parkinsoni* normally burrows obliquely into the substrate with the anterior end downwards (fig. 1, E) and, moreover, does not maintain an opening to the surface. Swimming of *Solemya*, described by Drew (1900), was observed on one occasion and is spectacular. As one observer commented, 'It exhibits the sort of speed that in molluscs one normally associates with cephalopods'. That swimming is a normal feature of the behaviour of *Solemya*, however, is unlikely (Yonge, 1939).

FIG. 1 (plate). A and B, sections of the stomachs of *N. sulcata* and *S. parkinsoni* respectively, photographed at the same magnification.
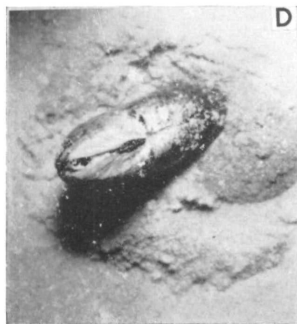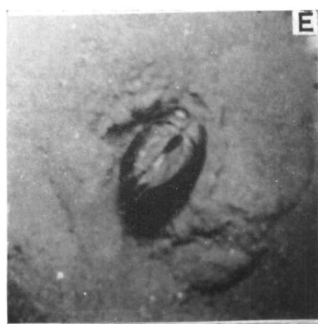
C–E, a specimen of *S. parkinsoni* burrowing into sandy mud.
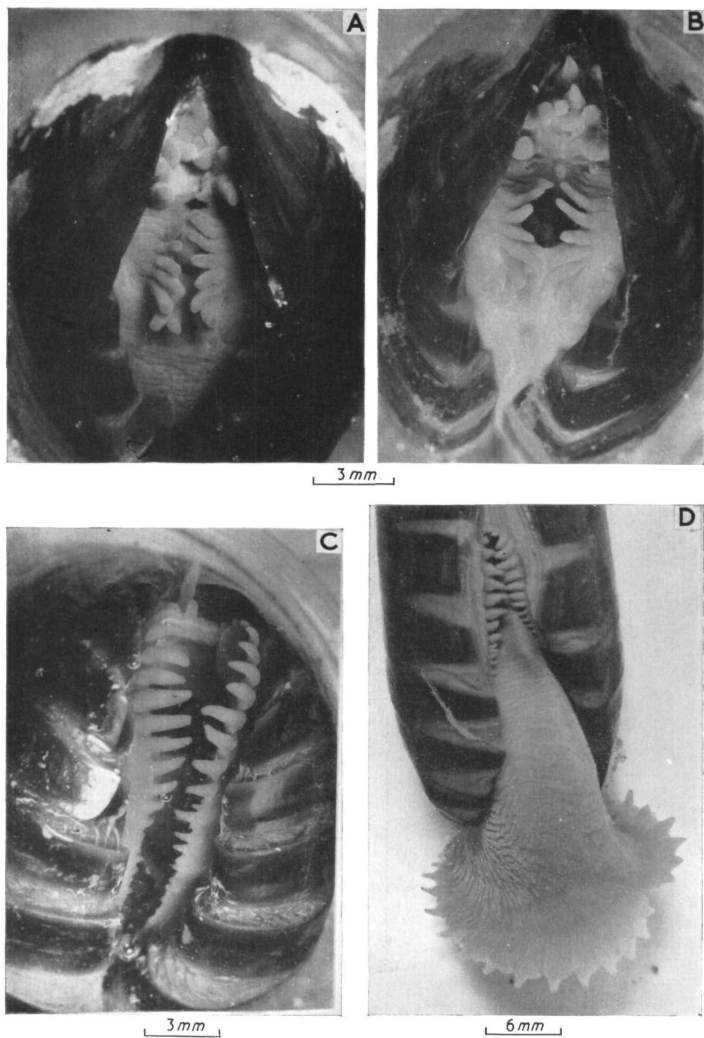
aorta

gut

0·5 mm

2 cm
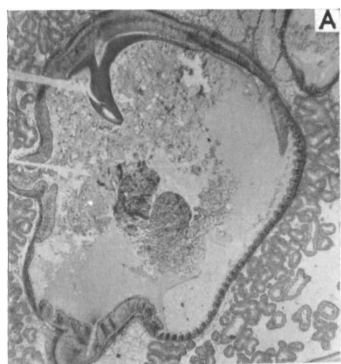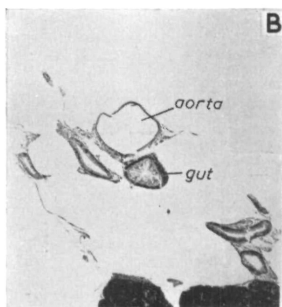
2 cm

Fig. 1

G. OWEN

FIG. 2

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The single posterior aperture of *Solemya* received considerable attention from earlier workers, many of whom (Deshayes, 1845–8; Stempell, 1899; Morse, 1913) described it as an anal-branchial siphon. Both Kellog (1892) and Morse (1919) described changes in the form of the opening and noted how, on occasions, it is partly divided into dorsal and ventral regions, which, they suggested, may represent exhalant and inhalant apertures respectively. Orton (1913), on the contrary, states that the inhalant current is drawn in anteriorly, dorsally at the base of the foot, while Yonge (1939), owing to the small size of the specimens of *S. togata* examined, found exact determination of the inhalant current difficult. He suggested that the arrangement of the gills and the shape and habits of *Solemya* all indicate the presence of an anterior inhalant current. The partial division of the posterior aperture was observed in *S. parkinsoni* (fig. 2, A, B), the lateral margins being drawn together so that the tentacles in this region interlock and divide the aperture into a small dorsal opening at the base of the dorsal series of tentacles and a larger ventral one. Nevertheless, an exhalant current only was observed in this region, sometimes issuing from both dorsal and ventral regions of the aperture, and on occasions from one portion only, the other being partially closed. An inhalant current is drawn in on each side of the foot through both the antero-dorsal and postero-ventral regions of the pedal gape (fig. 3) between the interlocking tentacles borne by the mantle margins of these regions (fig. 2, C, D). Thus in *Solemya*, as in *Nucula* (Yonge, 1939), water is taken into the mantle cavity anteriorly and from beneath the surface of the substratum.

The Alimentary Canal

The gut of *S. parkinsoni* follows more or less the course described by Yonge (1939), although the relative reduction of all parts of the gut would appear more extreme than in the much smaller *S. togata*. A small tubular oesophagus passes posteriorly between the anterior retractor muscles of the foot (fig. 3). At the posterior margin of these muscles there is a slight dilation associated with the entry of the ducts, one on each side, from the digestive diverticula; this represents the stomach (fig. 4). The diverticula comprise a small number of distinct, elongated tubules arranged on each side of the stomach and having a brownish-green colour in fresh material; numerous rather stout muscle fibres are inserted on to the distal ends of the tubules. Posteriorly to the stomach, the gut is continued as a slender greenish thread which swings slightly to the left of the mid-line and extends postero-ventrally into the gonadial tissue which forms the bulk of the visceral mass (fig. 3). Near the posterior margin of the visceral mass, the intestine bends sharply to run dorsally before penetrating the wall of the visceral mass. It then extends

Fig. 2 (plate). Photographs of a living specimen of *S. parkinsoni*.

A and B, the posterior aperture.

C, the antero-dorsal inhalant region of the pedal gape.

D, the foot extended with the terminal region expanded. The postero-ventral inhalant region of the pedal gape is shown.

posteriorly as the rectum along the floor of the ventricle and of the posterior aortic bulb before opening at the anus on the postero-ventral face of the posterior adductor muscle.

The oesophagus, like the rest of the gut, is lined by a well-developed ciliated epithelium which attains a height of 40 to 50 μ. The diameter of the oesophagus is approximately 180 μ, while the stomach immediately before the entry of the ducts from the digestive diverticula is triangular in outline and
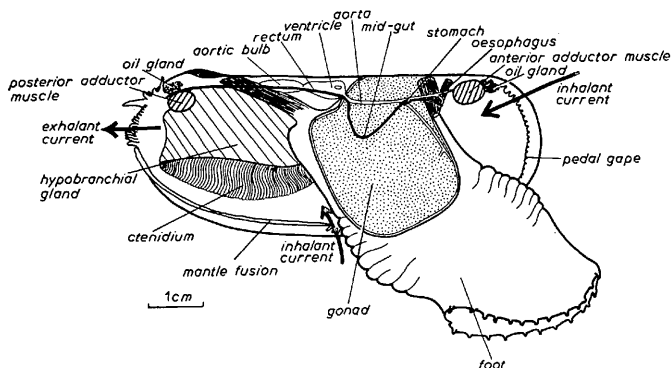

FIG. 3. The alimentary canal (solid black line) of *S. parkinsoni* viewed from the right side. Arrows indicate the inhalant and exhalant currents.

measures 300 by 250 μ; the adjacent aorta has a diameter of over 500 μ (fig. 1, B). Muscle-fibres, which form a rather thin layer round the oesophagus, are well developed in the region of the stomach and form a layer 30 μ thick. Despite the small size of the stomach in *S. parkinsoni*, all the essential features of the bivalve stomach would appear to be present. Immediately posterior to the laterally situated slit-like apertures of the ducts from the digestive diverticula, the lateral and dorsal walls of the stomach are covered by a cuticular structure, ∩-shaped in section, which can be removed intact from the stomach; it is presumably homologous with the extensive cuticular region of the stomach in the Nuculidae (Owen, 1956). Sections of the stomach reveal the presence of a small caecum which curves slightly to the left and corresponds with the dorsal hood of other bivalves. It is not visible in dissections. This region of the stomach is followed by one possessing a typical style-sac ciliation with a shallow groove—the intestinal groove—extending the length of the right wall. The style sac tapers into the intestine, which has a diameter of approximately 150 μ, and is surrounded by a layer of circular muscle-fibres some 5 to 6 μ thick. The gut extends to the anus with little change.

The digestive diverticula comprise a small number of finger-like tubules on each side of the stomach (fig. 4). The lumina of the proximal regions are

lined by a ciliated epithelium which rests on a thick basement membrane underlain by well-developed muscle fibres. This region is similar to the ducts of the diverticula of other bivalves (Owen, 1955). Unfortunately, fixation of the distal regions of the tubules was poor, but cilia are undoubtedly present, while many of the cells contain numerous coloured inclusions.
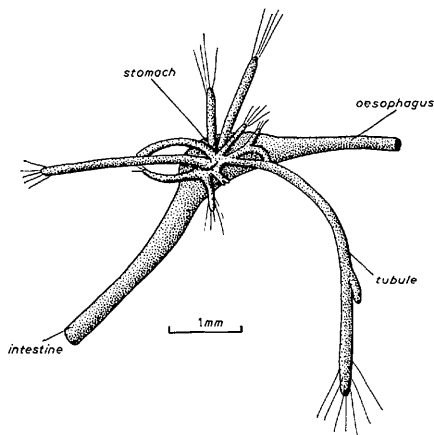

FIG. 4. The stomach and digestive diverticula of *S. parkinsoni* viewed from the right side.

DISCUSSION

Members of the three families of the Protobranchia—the Nuculidae, Ledidae, and Solemyidae—are deposit feeders. In the Nuculidae and Ledidae, the large palp proboscides extend between the valve margins and actively collect the bottom deposits. In the more specialized Ledidae, the palp proboscides are the sole food-collecting organs, while in the Nuculidae the part played by the small ctenidia is slight and probably incidental (Yonge, 1939). Selection of the collected material is exercised by the ridged surfaces of the palp lamellae, but in both families the stomach is large and invariably contains a high proportion of inorganic material, features characteristic of deposit feeders. In the Solemyidae the palp proboscides are smaller and it is the muscular activity of the mantle and possibly of the foot, correlated with the flexibility of the shell (Beedham & Owen, 1960), that results in large quantities of bottom material entering the mantle cavity (Yonge, 1939). According to Morse (1913), Orton (1913), and Yonge (1939), the sole food-collecting organs are the greatly enlarged ctenidia, and in this context the observations of Morse are of interest. 'The gills, however, are the food accumulators from which as we have seen the palp-appendages [palp proboscides] collect material

for nutrition . . . the continual ingestion of food is indicated by the great quantity of excreta which is voided.' These observations do not suggest the extreme reduction of the gut exhibited by *S. parkinsoni*, and it is probable that Morse confused the mucus-bound material extruded from the mantle cavity (i.e. pseudofaeces) with true faecal material.

A more detailed analysis of the ciliary currents of the ctenidia and palps of *Solemya* has been presented by Yonge (1939). While Stempell (1899) suggested that the small size of the gut of *S. togata* was correlated with the high organic content of the substratum in which the animal lives, Yonge (1939) considered more significant the rigorous sorting of particles by the ctenidia and palps which results in only the finest particles entering the mouth. The frontal cilia of the ctenidial filaments convey fine particles to the inner margins of the ctenidia, where a weak anteriorly directed current conveys them towards the labial palps; large masses of material are conveyed posteriorly over the surface of the ctenidia and rejected. Ciliary currents over the inner and, in this case, smooth surfaces of the palp proboscides are directed into a narrow groove bounded by richly ciliated ridges representing reduced palp lamellae. Ciliary currents in the depth of the groove are directed towards the mouth while those over the ridges beat actively out of the groove and towards the rejection tracts of the foot. Thus according to Yonge only the very finest particles in the depth of the groove reach the mouth. Certainly, observations on the contents of the gut of freshly collected specimens of *S. parkinsoni* support the view that very little particulate material enters the gut, despite the presence of large quantities of bottom material in the mantle cavity. It is, therefore, difficult to appreciate how an animal which attains the bulk of *S. parkinsoni* can obtain sufficient nutriment by either intracellular, or for that matter, extracellular processes within the limits of such a reduced gut.

A possible explanation of the extreme reduction of the gut is suggested by observations on specimens of *S. parkinsoni* collected at Portobello, New Zealand. Two small specimens were left overnight in sea-water containing starch, iron saccharate, and titanium dioxide. They were fixed in Bouin's fluid and subsequently serially sectioned. Considerable quantities of starch, iron, and titanium dioxide were present in the mantle cavity but no trace of these substances was discovered either in the lumen of the gut or in any of the tissues. It is interesting to note, however, that the periodic acid/Schiff test and the iodine test revealed that the starch was undoubtedly undergoing a preliminary breakdown within the mantle cavity. While little value can be placed on the results obtained, and various explanations can be given for the observed breakdown of starch, there exists the possibility that digestion of organic material may take place in the mantle cavity of *Solemya*, and it is the products of this digestion that are ingested at the mouth. The ciliary currents of the ctenidia and palps would appear to prevent particulate material entering the gut. Morse (1913) has described the palp proboscides as long, semi-tubular structures with enlarged ends. Such structures, possessing the ciliation described by Yonge, would be admirably suited for collecting the products of

any digestion which may occur in the anterior half of the mantle cavity; the ciliary currents of the reduced palp lamellae would serve to remove particulate material carried in the current created by the proboscides. The ctenidia could then be regarded as retaining, to a large extent, their primitive function of respiration. Their large size would be an adaptation to the specialized mode of life of *Solemya*, which lives buried in the substrate (40 to 60 cm deep in the case of *S. parkinsoni*) without direct contact with the water above.

There remains the question of the source of any enzymes which may be present in the mantle cavity. The characteristic glands present in the epithelium of the foot are worthy of further investigation in this respect. They are unlike any seen elsewhere in the Bivalvia and are present in both *S. togata* and *S. parkinsoni*, but are not found in members of the Nuculidae. It must be emphasized that the above hypothesis may be far removed from the true explanation of the extreme reduction of the gut exhibited by an animal which is an undoubted deposit feeder, and further investigation of the processes of feeding and digestion in the Solemyidae is desirable.

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