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DEEP REEF RESEARCH WITH A SUBMERSIBLE;
LIVING PLEUROTOMARIAN SLIT-SHELLS.

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Deep Reef Research with a Submersible;
Living Pleurotomarian Slit-shells.

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An innovative programme using the submersible PC8-B has been in operation at the Discovery Bay Marine Laboratory, Jamaica, for the past two years. This facility is provided by Research Submersibles Ltd, Grand Cayman, through the Discovery Bay Research Foundation. The programme is unique in two important ways. First it provides observation, photographic, and collection capabilities to -244 m at extremely low cost (\$200/hr); secondly the programme allows intensive and repetitive studies of known sites over relatively long periods of time.

RSL also operates submersibles in the adventure/educational recreation market in Grand Cayman and the Turks and Caicos Islands. Research can be catered for at both these locations. All submersibles are equipped with a 91 cm domed anterior viewport and 9 smaller port-holes, a manipulator, external camera and strobe, and an array of powerful lights.

Eighteen different biology and geology projects have been initiated since the start of the programme. This paper describes the submersible operations and presents observations on living pleurotomarian slit-shells. The focus of the study is on gaining new information on an evolutionarily-ancient species, or so-called living fossil, with the view to explaining its persistence.

INTRODUCTION

The text of this paper is divided into two major sections:
1. The Submersible Research Programme at Discovery Bay Marine Laboratory, and
2. Living Pleurotomarian Slit-shells. The first part describes the submersible and mode of operation, and the environment in which it operates. In the second part data on live Entemnotrochus adansoniana biology and behavior is presented and discussed.

SUBMERSIBLE RESEARCH AT DISCOVERY BAY MARINE LABORATORY

The limitations of diving and remote sampling have left a significant gap in our understanding of marine biology and geology. While SCUBA diving has opened up the shallower environments to many scientists, the region

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below -60 m, though by far the greatest part of the oceans, has been largely inaccessible. For non-diving marine scientists all but the shallowest regions have been off-limits. One way to overcome these problems is to use a submersible. These vessels can provide direct, close range observation opportunities and manipulative ability. Excellent data on deep-water organisms and structures have been obtained in this way, but conventional operations are extremely expensive and this tool is therefore out of the reach of many. A new, more cost-effective method of operating submersibles has been in place at the Discovery Bay Marine Laboratory, Jamaica, since January 1984. It allows virtually anybody with an interest in underwater science the chance to view and work in the environment at close quarters.

Conventional submersible operations require a large and costly support system of a vessel to lift the sub in and out of the water, piloting and maintenance personnel. At DBML the overheads have been considerably reduced by operating from a shore-based support facility, using small tow boats to manoeuvre the submersible to the dive site.

The Submersible.

The submersible, PC8-B, has adapted well to her new role as research vessel after a safe career in North Sea oil exploration. This 2 - 3 m observation sub has a maximum working depth of -244 m. Standard features include a 91 cm diameter, domed, anterior viewport, 9 smaller portholes, and an array of 500 W lights. For research it can be fitted with one or two manipulator arms, collecting baskets, and a bulk-loading underwater camera with strobe mounted on a pan-and-tilt frame. Power is provided by banks of batteries carried in the pods below the pressure hull. The atmosphere within the hull is maintained at one bar, and life support for five days is carried. Routine maintenance, equipment exchange, camera loading, and battery charging take place at the shore base. PC8-B is lifted out of the water by crane in a sheltered lagoon, thus removing one of the greatest elements of danger to the submersible and crew: lifting in the open ocean.

Dive Procedure.

The key to this shore-based system is the topography of the north coast of Jamaica. The narrow Island Shelf allows easy access to the coral reefs throughout their depth range, and to the deep environments beyond. On a typical day's diving the submersible is loaded with the pilot, crew and equipment at a shallow water mooring behind the reef crest. After a safety check PC8-B is towed to the dive site, only a couple of hundred meters away. PC8-B submerges and radio communications are established. The sub completes its trim procedures in a sand channel on the terrace and then proceeds with the dive. Dive duration is typically between two and five hours. Radio checks are performed with the surface support boat at regular intervals.

Deep Environments.

The deep environments below the well-known shallow reefs of Discovery Bay received preliminary description in a group of papers resulting from the work of Lynton Land and others with the submersible Nekton Gamma, in 1972 (summarized by Lang, 1974). A near-vertical submarine cliff between -55 m and -130 m, cut during the Peistocene glaciations, is veneered with Holocene reef growth. The coral reef, dominated by Agaricia spp. near the top of the cliff,

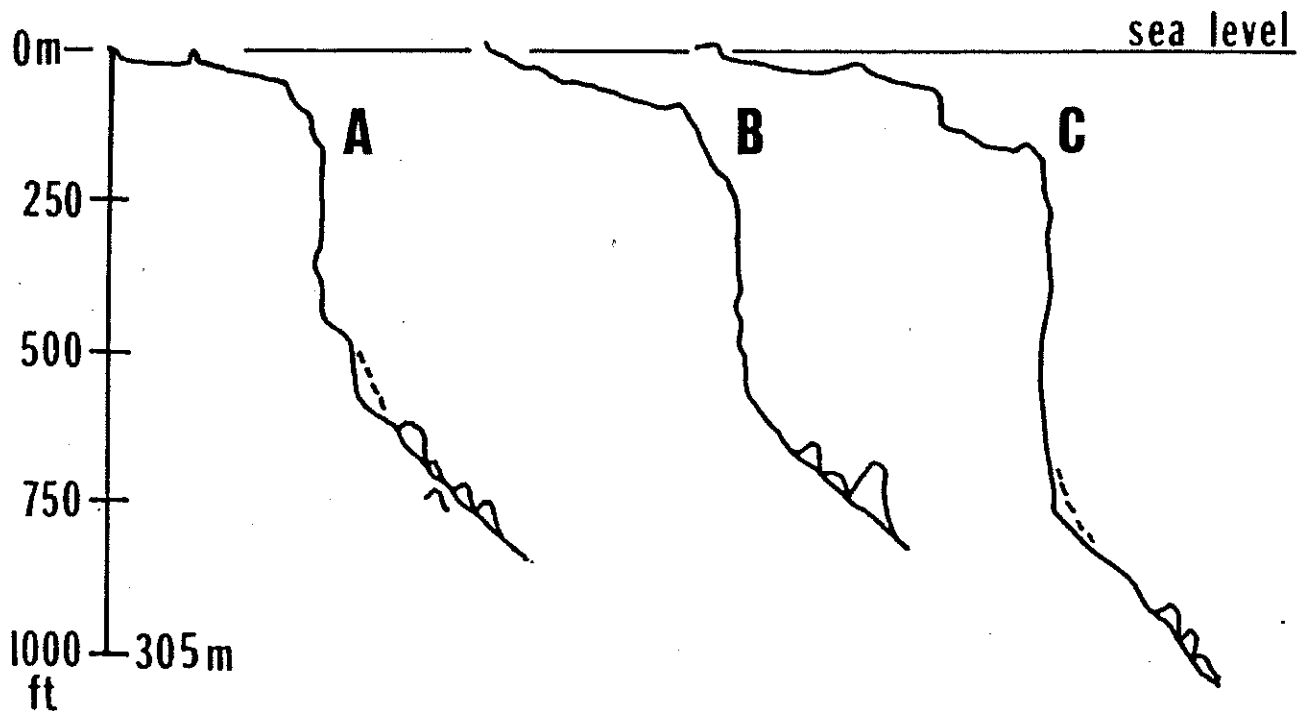


FIGURE 1. Reef profiles. A - Discovery Bay, north coast of Jamaica; B - Seven Mile Beach (southern end), west coast of Grand Cayman, C - Grace Bay, north coast of Providenciales, Turks and Caicos Islands.

gives way to sclerosponge reef by -90 m. At the foot of the cliff the island slope begins; unconsolidated talus succeeded by partly lithified slope, occasionally punctuated by massive outcrops of rock. By -230 m reef-derived sediments have largely given way to softer sediments of pelagic origin.

Since Research Submersibles has begun operations in Grand Cayman and Providenciales, Turks and Caicos, this scenario has been confirmed for the west and south-eastern shores of Grand Cayman, and the north shore of Provo. There are differences in the depth at which the slope begins and also in the angle of the slope itself (Figure 1.).

Scope of Research and Opportunities.

From the inception of the Submersible Research Programme at Discovery Bay Marine Laboratory it has provided opportunities for studies on : social behavior of deep reef fishes, marine endolithic fungi, sclerosponge reproduction, sedimentation rates, wall biota, reproduction in deep water echinoderms, ultrastructure of deep corals, *Madracis* taxonomy, distribution and behavior of echinoderms, behavior and feeding in stalked crinoids, and ecology and biology of live slit-shells.*

Research Submersibles Ltd operates similar submersibles with depth capabilities to -304 m in the recreation market in Cayman and Turks and Caicos. These submersibles can be leased for research at very competitive rates.

* Enquiries and reservation for space in the 1986 programme should be addressed to: Dr Jeremy Woodley, DBML, P O Box 35, Discovery Bay, St Ann, Jamaica.

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Limited shore laboratory facilities are available. RSL can also provide submersibles of equal or greater depth range for sale or lease to research institutions.

LIVING PLEUROTOMARIAN SLIT-SHELLS

Introduction.

Entemnotrochus adansoniana Crosse and Fischer 1861, is the largest living Caribbean slit-shell, and was the second discovery by Western science of living members of a family of molluscs (Pleurotomariidae) whose geological history extends back to the Cambrian (Bayer, 1963). The primitive condition of the soft parts of the animal, with paired mantle organs provides as much interest for the malacologist as the long fossil record of the distinctive shell.

Specimens of E. adansoniana have been observed on the wall and slope at Discovery Bay prior to this report; in 1972 from the submersible Nekton Gamma (Yonge, 1973). Yonge's (1973) personal observation of one individual at -160 m alongside a sponge was of "the foot partly expanded and the slit clearly lined with tissue, but the epipodium with its tentacles withdrawn." Little else is known of the live animals, except observations by Roper and Young in Deep Rover in 1968 off the Bahamas (Robertson, R. pers comm) and RSL's dives in Cayman and the Turks and Caicos indicate that slit-shells are a common component of the mobile invertebrate fauna in the deep Caribbean.

In the nine months between August 1984 and April 1985 five live individuals and the empty shells of four dead animals were observed and collected from the island slope off Discovery Bay between -150 m and -240m. None of the dead shells were occupied by hermit crabs although large crabs do occupy milk and queen conch shells at these depths. Three full-sized live adults (diameter 120 mm +), and two juveniles (diameters 70 mm and 25 mm) were collected. In this article I report observations on the orientation of the body to the shell in life, respiratory currents, and deposition and form of faeces.

Life Position of Body.

Figure 2 illustrates various positions adopted in the aquarium by the first adult snail collected. The figure is drawn from photographs. The positions shown in Fig. 2 Band D have been documented for adults in the field on the slope where a thin layer of sediment cloaks the hard substrate. Position Fig. 2 A has been observed in the juveniles on the vertical surfaces of the rocky outcrops between -213 m and -244 m, and in adults on vertical and overhanging surfaces on the wall in Grand Cayman. At all times the foot is wrapped closely around the base of the shell and the head is held under the leading edge of the shell, and is not protruded from the aperture. The snails can crawl with equal facility on surfaces at any angle. When removed from the substrate E. adansoniana can retract as it is beginning to do in Fig. 2 C, until the entire body is withdrawn into the shell and the operculum has closed against the inner surfaces about one half turn back from the aperture, ie. behind the rear of the slit.

Respiratory Currents.

Figure 3 A shows the slit with the typical positions of the inhalent and exhalent apertures in the mantle lining. The siphons are separated by the pressing together of the edges of the mantle along the length of the slit. The position and length of the inhalent aperture can be varied by the animal and more than one is sometimes created (Figure 3 B). Lengths of 1 to 4 cm have been

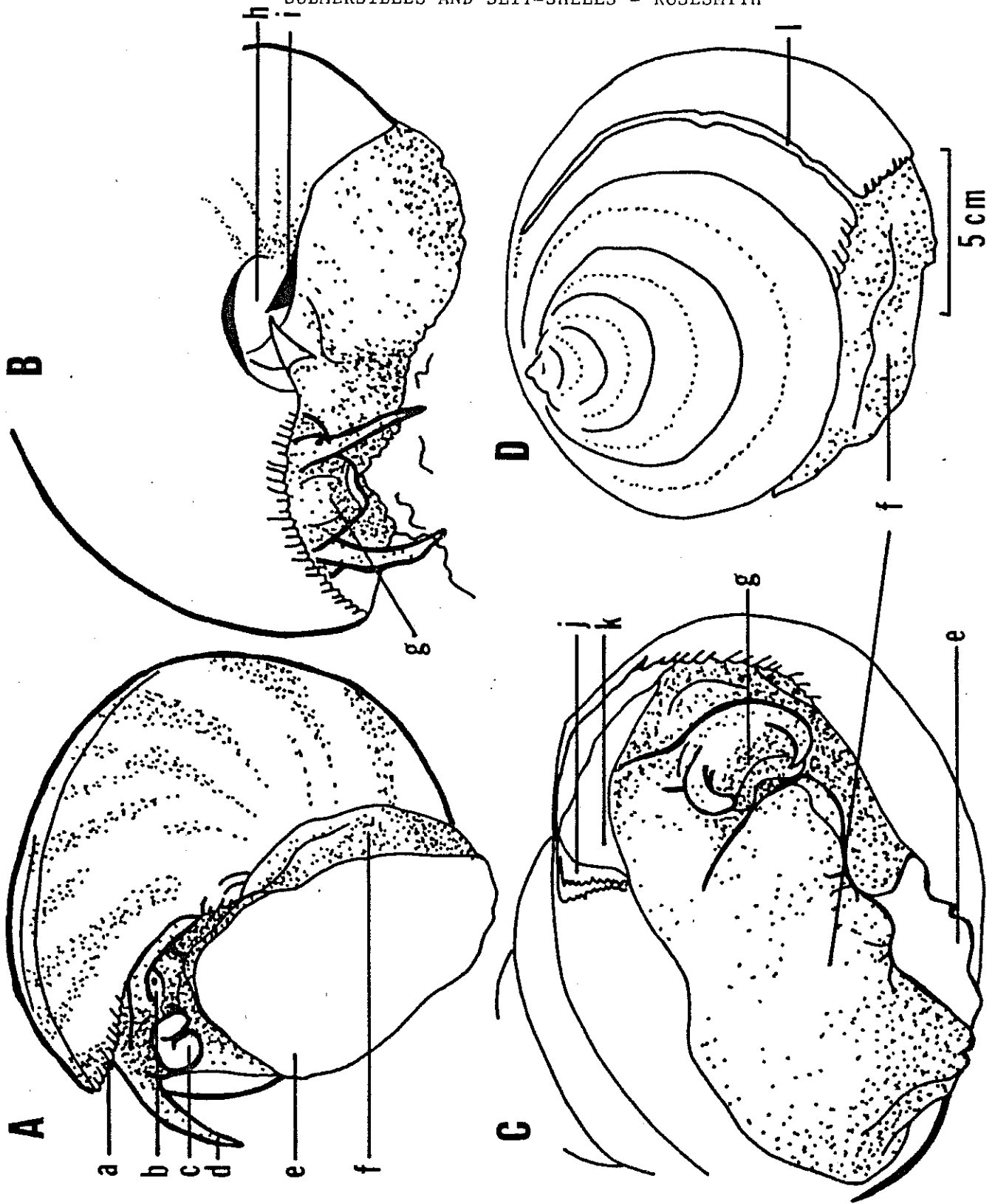


FIGURE 2. Life positions of *Entemnotrochus adansoniana*.*
 A - crawling up side of aquarium, sole of foot pressed to glass, snout and tentacles exploring surface.
 B - animal pushing sediment in front of foot and testing it with lips of the snout.

* Key follows literature cited.

FIGURE 2. continued -

- C - response to being detached from bottom, head contracting and lateral surfaces of foot curling in around the sole of the foot, dorsal surface of foot still pressed to bottom of shell, and mantle still spread against inside of aperture.
 - D - view from above showing normal position of foot, wrapped around side and bottom of shell. Head/snout not visible below leading edge of shell.
- Illustrations drawn from photographs.

recorded. The single exhalent aperture is always at the rear of the slit but varies in length (1.5 - 2.5 cm) from time to time. The direction of the currents were demonstrated in still and flowing water using carmine and fluorescein dyes. No inhalent currents could be detected on either side of the head nor anywhere around the aperture of the shell. (Figure 3 C)

Damage to the slit of the larger juvenile allowed the disposition of the ctenidia to be observed more closely. The pair of gills lie to the lower side of the slit. They do not appear to be symmetrically disposed on either side as in the Scissurellidae (Yonge, 1947). The free tips of the gills very mobile and extend forward to the region where the inhalent aperture is positioned. Although preliminary observations on the flow of currents through the gills were made on this snail the results were not conclusive and are not reported here. The absence of the upper edge of the slit can be expected to distort the currents which might normally impinge on the inner surface during their passage through the mantle cavity. It is intended to repeat this procedure experimentally and replace the removed shell with transparent plastic windows in order to mimic the intact mollusc more closely.

Faeces and Deposition.

One Entemnotrochus adansoniana was observed depositing faeces in situ in the early afternoon. Seven pellets had already been deposited on the substrate below the rear of the slit and an eighth was extruded and deposited while observations were in progress, from the extreme rear of the slit, through the exhalent aperture. This confirms Yonge's (1947) speculation that the anus opens at the rear of the slit. The anterior inhalent aperture was open throughout this time. This individual was observed on five dives between 9 February and 11 March 1985, at depths between -157 m and -161.5 m. Maximum horizontal distance travelled was not recorded.

Figure 4 illustrates a faecal pellet collected in the aquarium on the third day after the snail was collected. As in the in situ example the pellets are extruded and then break off at the slit when the other end touches the substrate. This process is enhanced by a contraction of the shell muscle as supposed by Yonge (1947). The "seam" running down the side of the pellet is not always as distinct, and appears to be moulded by the mantle edges as the pellet passes diagonally through the slit.

The faeces are composed of sediment and organic particles bound together by a mucus sheath, a tube of finer particles enclosing the coarser material. Among the particles from faeces collected shortly after capture of the snails have been identified: sponge spicules, foraminifera, shell, bryozoan, and echinoderm spine fragments, calcareous flakes and occasionally whole veligers with the body intact, in addition to sand grains.

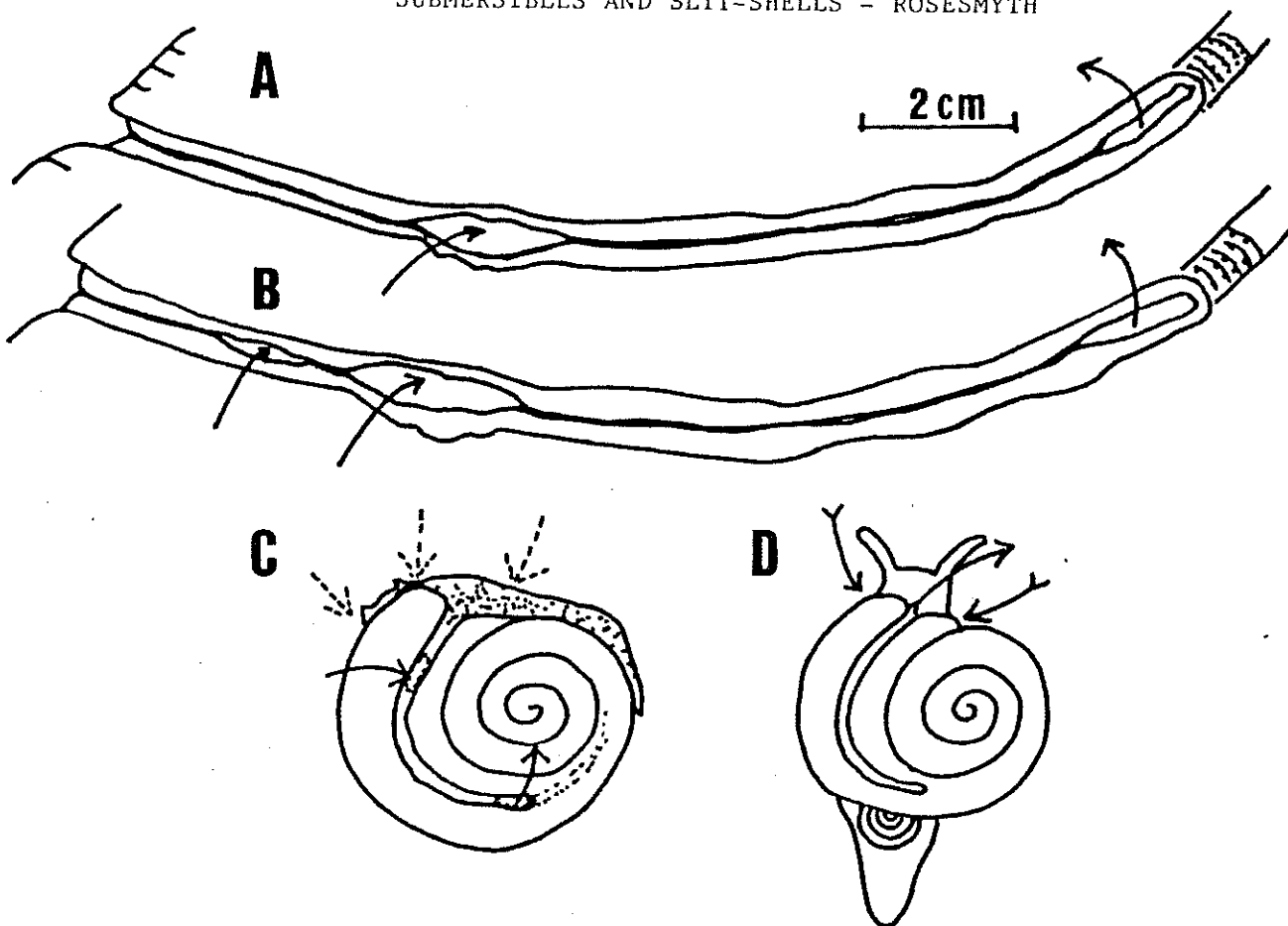


FIGURE 3. A and B - views of the slit showing inhalent and exhalent siphons in mantle tissue. C - true orientation of body to shell. D - original assumed orientation from Yonge (1947) based on Woodward (1901). Solid arrows - true currents, dotted arrows - points where no currents could be detected, feathered arrows in D - assumed directions of currents.

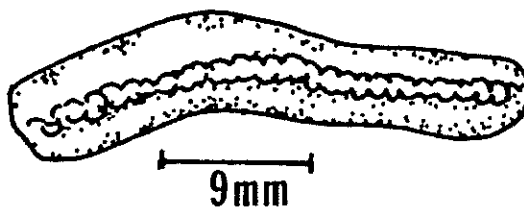


FIGURE 4. Faecal pellet deposited third day after adult Entemnotrochus adansoniana was collected.

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In the aquarium faeces were deposited overnight for two to three weeks after the slit-shell was collected, but got progressively thinner until no more were produced. Macro algae, sponges, zoanthids, ground gastropod tissue, coral plates with tissue on the surface and encrusting sponges and bryozoa underneath were all rejected as food sources. When slope sediments were introduced thin mucus strings with small blobs of matter at intervals began to be produced again. The last adult collected was photographed six weeks after collection scrapping algae from the walls of the aquarium. I was unable to make further observations after this unusual event.

Discussion.

These observations on live Entemnotrochus adansoniana are of a preliminary nature, yet they provide many new insights into the biology of the animal, and confirm or deny some of the hypotheses concerned with the disposition of the body and contents of the mantle cavity. This new data may help to clarify the position of the pleurotomarians in the evolution of the prosobranchs. The following points can be made: 1. Professor Yonge's (1973) observations at Discovery Bay are confirmed. E. adansoniana naturally does not expand the body greatly around the shell. 2. The respiratory current patterns in E. adansoniana are unlike those in any other archaeogastropod with slits or apertures in the shell. In Haliotis, Diodora, Emarginula, and Puncturella, the marginal slit or shell aperture exists solely for permitting the exhalent current, with waste products from the anus and renal pores, to pass out clear of the head (Yonge, 1947). In E. adansoniana the slit also functions to support the inhalent siphon, which can be controlled in both location and size by the animal. This facility, in conjunction with the blockage of the aperture by the head and lateral walls of the foot, prevents fouling of the mantle cavity. Yonge's (1947) conclusion that water is drawn into the mantle cavity on either side of the head as in Haliotis is not valid. His opinion that live animals must be examined is fully supported. Figure 3 C and D illustrate the differences in the true disposition of the body and that concluded from examinations of fixed material. 3. Data from the faecal pellets and responses to offered food items suggest that E. adansoniana is a deposit feeder, if not exclusively. R. Roberston (pers comm) has tabulated published data which shows that pleurotomarians are omnivorous and even carnivorous.

The sum of these conclusions is that Entemnotrochus adansoniana is not a hapless, primitive living fossil, its large gill structure in danger of being clogged at every step. E. adansoniana displays modifications to the postulated primitive organization of the mantle organs which allows it greater latitude in habitat choice and behavior. Yonge (1947) noted that all the living zygobranchs that had been examined to that time were specialized in some way. This new data demonstrates that a modern pleurotomarian is also specialized, or at least does not conform to the postulated primitive organization. However, Entemnotrochus has the longest, narrowest slit of the living pleurotomarians. Mikadotrochus and Perotrochus have shorter and wider slits (Bayer, 1965), and could possibly have different current patterns.

As more information is gathered on the so-called living fossils of the deep sea it is becoming clearer that the popular conception of these animals as being handicapped by depth, and apparent rarity is mainly founded on our limitations and not those of the animals. Although pleurotomarian shells have remained virtually unchanged since the earliest fossils the very persistence of some species should indicate that the organism has adapted in some ways to be

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able to survive to the present, and not merely through retreating to refuge habitats.

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Key to FIGURE 2.

- a - lower edge of shell aperture.
- b - eye.
- c - lips of snout.
- d - tentacle.
- e - sole of foot.
- f - lateral surface of foot.
- g - snout.
- h - umbilicus.
- i - operculum.
- j - limit of inner shell nacre.
- k - mantle.
- l - slit.

ADDITIONAL NOTES ON SLIT-SHELLS

Observations by R. M. Linsley, Department of Geology, Colgate University, Hamilton, New York 13346.

In June 1985 I had the opportunity to examine a live slit-shell courtesy of the Submersible Research Programme, Discovery Bay Marine Laboratory, and recorded the following observations.

It has long been a presumption among neontologists and palaeontologists alike (Yonge, 1947; Morton and Yonge, 1964; Knight, 1952; Linsley, 1977) that primitive gastropods with two gills would possess two inhalent currents, one for each of the gills. It was therefore a surprise to find that Entemnotrochus adansoniana had only a single inhalent stream. The slit of E. adansoniana is a very narrow, deep slit extending about one half a revolution (140 degrees) back from the aperture. During its active life the slit is entirely sealed by mantle flaps which extend to either side of the slit. The mantle flaps are muscular and can be pulled back to form openings at the mantle margins anywhere along the length of the slit. Normally there are two openings in the slit. One, an inhalent opening, is located about 40 mm from the apertural margin and the exhalent opening is located at the adapertural end of the slit. However, the placement of these openings, in particular the inhalent opening, is variable and the inhalent opening was observed in one instance to have moved deep in the slit so that it was no more than 50 mm from the exhalent opening. Observations made in flume tank did not indicate that the position of the inhalent opening varied relative to directional currents.

Observations of the currents were made using fluorescein dye. The time of passage through the mantle cavity varied from 25 s to 59 s between introduction of the dye to the inhalent opening and its reappearance at the exhalent opening. It was not determined what caused the variation in residence time in the mantle cavity. The dye exited the exhalent opening in a fine stream suggesting laminar flow throughout the mantle cavity. In contrast, the exhalent stream from the neogastropod Fasciolaria tulipa resembles a cloud, suggesting that water flow through its mantle was turbulent rather than laminar. Possibly the distinctive and limiting feature of the bipectinate gills of the Archaeogastropoda is that they have characteristics which can only tolerate laminar flow while the monopectinate gills of the Caenogastropoda can accomodate turbulent flow. This would suggest that the replacement of the Archaeogastropoda, which dominated Palaeozoic Seas, by the Caenogastropoda of the Mesozoic and Caenozoic Seas, may be somewhat analogous to the replacement of the laminar flow brachiopods by the turbulent flow bivalves.

Thanks are due to J D Woodley of DBML for use of the flume tank, and M LaBarbera for discussions on flow characteristics.

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