ON THE BIOLOGY OF THE OPISTHOBRANCH
PLEUROBRANCHUS MEMBRANACEUS

By T. E. Thompson and D. J. Slinn

Marine Biological Station, Port Erin, Isle of Man

(Plate I and Text-figs. 1–8)

On 5 November 1958 our attention was drawn, by Mr A. K. Nagabhushanam, to the presence in Port Erin bay of large numbers of swimming gastropods. These gastropods proved on examination to be *Pleurobranchus membranaceus* (Montagu), a species generally believed to be exclusively benthic in habit. This paper is a report on this occurrence and on some aspects of the biology of *P. membranaceus*.

For 4 days these animals were abundant in the bay and hundreds could have been captured with a hand-net from the steps of the Raglan Pier. Only approximately forty specimens were taken, this number being ample for our purpose. Between 5 and 9 November, numbers were stranded on the beach by the receding tide. Although many local fishermen consented to look out for these easily recognizable animals, and the Port Erin research vessels were out each day, no record of their swimming outside the bay was obtained, although specimens were occasionally dredged. On 9 November they disappeared from the bay without trace, and otter trawl and D-net hauls in the bay yielded only two further specimens; none were found on frequent shore-collecting expeditions. However, on 2 December five more specimens were captured swimming near the Raglan Pier and occasional individuals were seen in the same place on 9 December. During the periods of their abundance it was ascertained that they swam during the hours of darkness as well as in daytime.

Hydrographic conditions were not unusual during this invasion; temperatures taken in Port Erin bay during November and December 1958 were only about 1° C above the grand monthly means (see Bowden, 1955), while the salinities of samples collected at a position 54° 05′ N., 4° 50′ W. (about 3 miles N. 65° W. of Port Erin and 3 miles N. 12° E. of Chicken Rock) were about 0·3‰ below the mean for the area.

A search of the literature brought to light only three references to swimming in *P. membranaceus*. Pruvot-Fol (1954) states that this species (referred to as *Oscanius tuberculatus*, pp. 220–2) 'nage avec des contorsions du pied', but gives no details. Garstang (1890, pp. 418–20) quotes observations made by A. R. Hunt on an invasion of Torbay by numbers of *P. membranaceus* in

December 1873 and January 1874; Hunt observed that the animal swims on its back, 'alternately flapping, with wave-like contractions from before backwards, the two halves of its broad foot. The mantle flaps assist also in the action.' Garstang (1890) also mentions that these animals can secrete a substance which will redden blue litmus and he states (without giving reasons) that this substance is sulphuric acid. Garstang (1892) mentions an invasion of Plymouth Sound in September 1892 by young *P. membranaceus*; numbers were seen on the night of 21 September swimming at the surface of the sea. Hartley (1940) states that Saltash was invaded by large numbers of pleurobranchids in October 1936, but he does not say whether these animals were swimming. Except that Yonge (1949, p. 252) mentions that *P. membranaceus* feeds on simple ascidians (also inferred by Hunt (1925)), this is all that is known of the natural history of the species.

Nomenclature of British animals referred to herein is according to the Plymouth Marine Fauna list (Marine Biological Association, 1957); in the case of foreign species, the name used by the author cited is employed.

Material for sectioning was fixed in Zenker's fluid (with or without acetic acid), cleared in amyl acetate (Barron, 1934) and embedded in Hance's rubber wax (Gurr). The stains employed were Heidenhain's alum haematoxylin, Mayer's haemalum and, as counterstains, eosin and alcian blue 8 GS (Steedman, 1950). Methods used in the investigation of the nature of the acid secretion will be described in context.

DESCRIPTION OF THE SPECIMENS

The external features and parts of the internal anatomy are shown in Textfigs. 1–6. Only those features which are not immediately apparent from these illustrations will be described. The description in the first instance will apply to animals which are creeping; the changes in form when swimming will be dealt with later.

External features

The lengths of the November specimens varied between $1\frac{1}{2}$ and $3\frac{1}{2}$ cm, measured while they were extended in creeping. Individuals of up to $4\frac{1}{2}$ cm in length were found in December. According to Pruvot-Fol (1954) adults may attain a length of 6 cm. In aquaria in the laboratory they spent by far the greater part of the time creeping and usually would swim only if disturbed.

Text-fig. 1A shows a specimen in the act of creeping on the bottom of a glass vessel in the typical gastropodan fashion. Noteworthy features are the anterior and posterior crenations in the mantle, the former giving rise to a wide temporary sheath for the rhinophoreal tentacles (Text-fig. 1A, *Ant.Cr.*), while the latter forms an exhalent aperture for the respiratory current (Textfig. 1A, *Post.Cr.*). In some individuals the posterior edges of the mantle

skirt may temporarily meet below this exhalent aperture, rendering it functionally a circular orifice (Text-fig. 1C). When the animal is at rest (Text-fig. 1B), with the foot contracted so that it does not project laterally
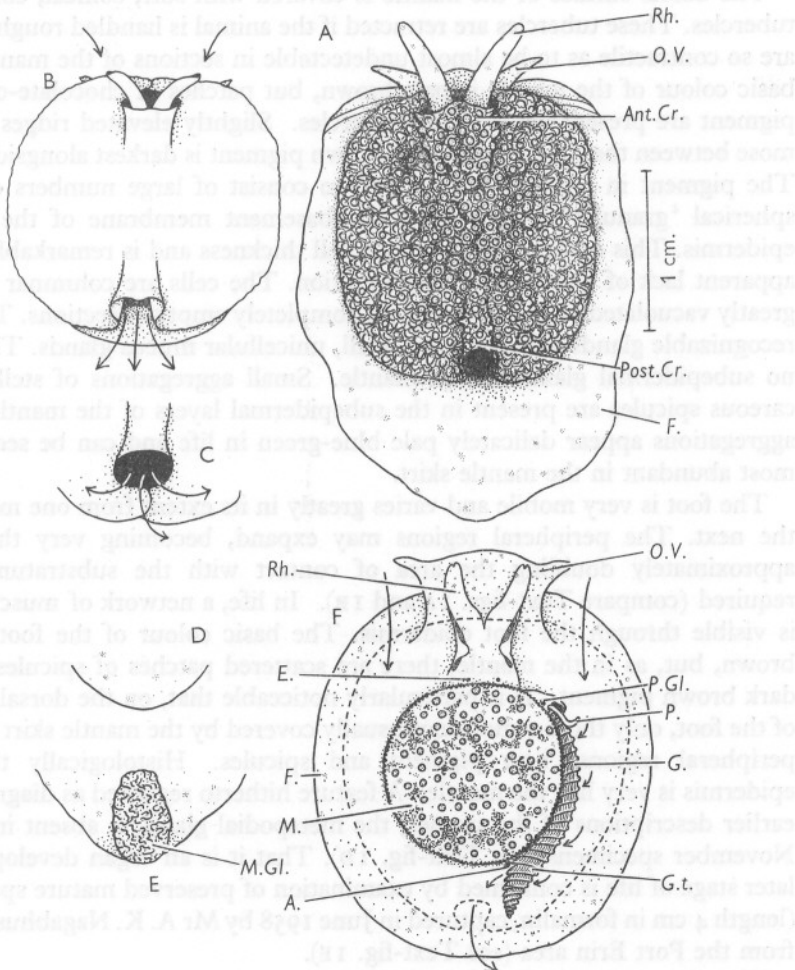
Text-fig. 1. External features of *P. membranaceus*, all drawings to the same scale: A, dorsal aspect of November specimen while creeping; B, dorsal aspect of November specimen while at rest; C, as for B, but showing alternative condition of posterior crenation; D, ventral aspect of tip of metapodium of November specimen; E, ventral aspect of tip of metapodium of mature specimen of June, 1958; F, dorsal aspect of November specimen with mantle skirt dissected away; the interrupted line represents the normal extent of the mantle skirt; the cut edge of the mantle is represented by a jagged line. The arrows in all cases show the direction in which ciliary currents impelled fine carmine particles. *A.*, anus; *Ant.Cr.*, anterior mantle crenation; *E.*, eye; *F.*, foot; *G.*, gill; *G.t.*, free tip of gill; *M.*, mantle; *M.Gl.*, metapodial gland; *O.V.*, oral veil; *P.*, penis; *Post.Cr.*, posterior mantle crenation; *P.Gl.*, prebranchial gland opening; *Rh.*, rhinophore.

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beyond the mantle skirt, this posterior crenation is relatively much wider than in the active animal. It is usually undetectable after death, which in part explains why it has not been described hitherto.

The dorsal surface of the mantle is covered with soft, conical, contractile tubercles. These tubercles are retracted if the animal is handled roughly; they are so contractile as to be almost undetectable in sections of the mantle. The basic colour of the mantle is pale brown, but patches of chocolate-coloured pigment are present between the tubercles. Slightly elevated ridges anastomose between the tubercles and the brown pigment is darkest alongside these. The pigment in sections can be seen to consist of large numbers of small spherical 'granules' lying against the basement membrane of the mantle epidermis. This epidermis is of single cell thickness and is remarkable for its apparent lack of histological differentiation. The cells are columnar and are greatly vacuolated so that they appear completely empty in sections. The only recognizable glands are scattered, small, unicellular mucus glands. There are no subepidermal glands in the mantle. Small aggregations of stellate calcareous spicules are present in the subepidermal layers of the mantle; these aggregations appear delicately pale blue-green in life and can be seen to be most abundant in the mantle skirt.

The foot is very mobile and varies greatly in its extent from one minute to the next. The peripheral regions may expand, becoming very thin, and approximately doubling the area of contact with the substratum when required (compare Text-figs. 1 A and 1 B). In life, a network of muscle fibres is visible through the foot epidermis. The basic colour of the foot is pale brown, but, as in the mantle, there are scattered patches of spicules and of dark brown pigment. It is particularly noticeable that, on the dorsal surface of the foot, only those regions not usually covered by the mantle skirt (i.e. the peripheral regions) bear pigment and spicules. Histologically the foot epidermis is very like the mantle. A feature hitherto regarded as diagnostic in earlier descriptions of the species, the metapodial gland, is absent in all the November specimens (see Text-fig. 1 D). That it is an organ developed at a later stage of life is confirmed by examination of preserved mature specimens (length 4 cm in formalin, captured in June 1958 by Mr A. K. Nagabhushanam) from the Port Erin area (see Text-fig. 1 E).

The rhinophores and oral tentacles bear patches of spicules and of brown pigment. The black-pigmented eyes (Text-fig. 1 F, E.), at the bases of the rhinophores, are hidden by the mantle when the animal is creeping.

The single gill is of the 'pectinate' type (Pelseneer, 1906) and is attached by its rachis to the lateral body wall on the right side along approximately three-quarters of its length. The free tip is muscular and mobile. The mantle skirt hides the gill from view when the animal is creeping. The respiratory currents set up by the cilia of the foot, mantle and gill lamellae are shown in Text-figs. 1 and 2. The respiratory chamber is elongated and tubular, bounded above by

the mantle and below by the foot. It is open anteriorly, lateral to the right rhinophore, and posteriorly, at the temporary exhalent aperture formed by the mantle crenation (Text-fig. 1A, *Post.Cr.*). Sections show the gill lamellae to bear large numbers of unicellular mucus glands, and the tubercles on the rachis (Text-fig. 2, *T.*) are rich in such glands, as well as being loaded with stellate spicules. Anterior to the gill is the opening of the pre-branchial gland
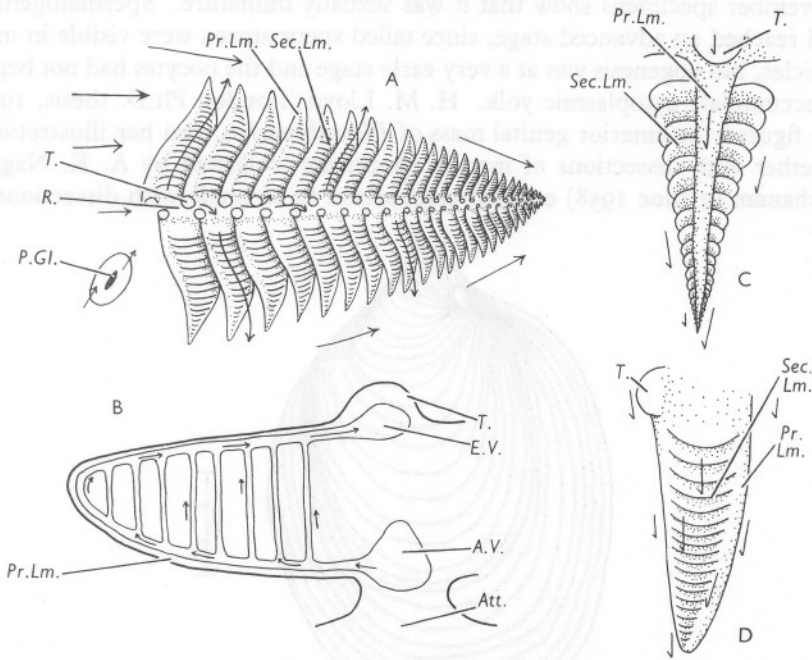

Text-fig. 2. The gill: A, gill dissected off and laid flat, the large arrow points towards the posterior of the animal; B, diagrammatic representation of the blood vessels in a gill pinnule, this is a simplified picture for there are in fact as many vertical vessels in the pinnule as there are secondary lamellae; C, single pinnule viewed from above; D, single pinnule viewed from the side. The arrows in A, C and D show the direction in which ciliary currents impelled fine carmine particles. In B they show the direction of the flow of blood in the branchial vessels. *Att.*, attachment of the gill rachis to the lateral body wall; *A.V.*, afferent vessel; *E.V.*, efferent vessel; *P.Gl.*, opening of prebranchial gland; *Pr.Lm.*, primary lamella; *R.*, rachis; *Sec.Lm.*, secondary lamella; *T.*, tubercle.

(the poison gland of Bourne (1885) or excretory organ of Bojanus (Vayssière, 1898; Abbott, 1949)), whose functions are not understood. Near the posterior extremity of the gill is the anal opening (Text-fig. 1F, *A.*). After feeding on *Ascidia* the faeces are very dark in colour and are expelled as elongated pellets, which, being on the 'downstream' side of the gill, present no problem in sanitation. Text-fig. 2B shows the blood supply of a gill pinnule. The course of the flow of blood in the gill can be seen readily if a dilute suspension of indian ink is injected into the haemocoel.

The ciliary currents over the rest of the body impel particles towards the posterior of the animal. No evidence of ciliary collection of food was obtained.

State of maturity

Microtome sections of the ovotestis of one of the larger (length $3\frac{1}{2}$ cm) November specimens show that it was sexually immature. Spermatogenesis had reached an advanced stage, since tailed spermatozoa were visible in male follicles, but oogenesis was at a very early stage and the oocytes had not begun to accumulate cytoplasmic yolk. H. M. Lloyd (London Ph.D. thesis, 1952) has figured the anterior genital mass of *Pleurobranchus*, and her illustrations, together with dissections of mature specimens (collected by A. K. Nagab-hushanam in June 1958) enabled comparison to be made with dissections of
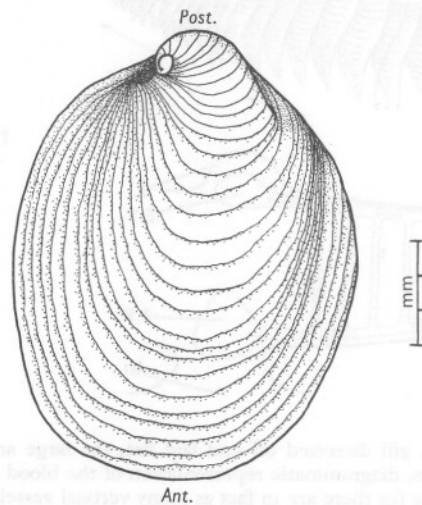
Text-fig. 3. The shell; dorsal aspect.

the sexual organs of our November specimens. This showed clearly that the genital mass of our specimens was in all respects in a rudimentary condition, although all the organs were present. The *external* genitalia, however, have all the appearance of maturity and the penis is long, and, in life, very mobile. This emphasizes the danger of judging a gastropod mature merely because the externally visible genital organs have the appearance of full development.

None of our specimens was observed to copulate or lay eggs either in the sea or in the laboratory.

FEEDING BEHAVIOUR

Specimens killed immediately after capture while swimming had no recognizable matter in the stomach. A little white flocculent matter of unknown nature was all that could be found. This white matter was certainly not composed of any of the usual planktonic organisms.

In the laboratory they fed readily on both compound and simple ascidians. Starved animals will, when creeping on the meniscus of the water, extrude the proboscis, and observations on such animals, together with those on specimens actually feeding, go to make up the ensuing description.

Yonge's (1949, p. 252) account of the patience of *P. membranaceus*, awaiting the relaxation of the siphons of the ascidian before shooting in the proboscis, could not be confirmed. *P. membranaceus*, like most opisthobranchs, is a voracious feeder, dealing with its prey with scant ceremony and considerable mechanical efficiency. No constant region of the prey is attacked.

Text-fig. 6A shows the alimentary canal dissected out entire. A conspicuous feature is the great development of the oral canal to form a long introvert. By turning the oral canal inside out, a highly mobile proboscis, up to a centimetre in length, is extruded through the mouth. Patches of brown pigment on the inside in the retracted state are external when the proboscis is extruded. The tip of the extended proboscis is formed by the muscular buccal sphincter (Text-figs. 4A and 6C, *B.Sph.*), through which the radula and jaws can be protruded. The buccal armature is shown in Text-fig. 5. Text-fig. 4A shows the phases of action through which the radula and jaws pass during rasping. During the first phase (Text-fig. 4A_1) the radula is expanded and bulged out through the buccal sphincter, whose aperture dilates. As it makes its effective stroke (in the direction indicated by arrows in Text-fig. 4A_1) and is withdrawn, the two halves of the radula are brought together. The effect is to carry particles caught on the radular teeth upwards and inwards. While the radula is halfway through its effective stroke, the extrusion of the jaws through the buccal sphincter marks the beginning of the second phase (Text-fig. 4A_2). The jaws then make a short upward stroke; this it is inferred pushes further matter on to the radular teeth and the radula is then withdrawn into the buccal mass, followed by the jaws. The third phase (Text-fig. 4A_3) is a brief resting period with the buccal sphincter contracted and the buccal armature withdrawn before the next cycle of action begins. Each cycle occupies between one and two seconds.

Extrusion of the proboscis is brought about by the action of the buccal mass protractor muscle (Text-fig. 6B, *B.M.Prot.M.*), aided by the extrinsic musculature of the buccal mass and also, no doubt, by pressure changes in the haemocoel. Its withdrawal is accomplished by a pair of stout buccal mass retractor muscles (Text-fig. 6A–C, *B.M.Ret.M.*), running from the buccal mass to the posterior body wall. Anatomical features associated with the

great development of the oral canal are the relatively great length of the cerebro-buccal connectives (Text-fig. 6A, *R.C.-B.C.*), of the salivary gland ducts (Text-fig. 6A, *Sal.D.*) (the salivary glands themselves lying attached to the anterior face of the digestive gland) and the extreme extensibility of the oesophagus.
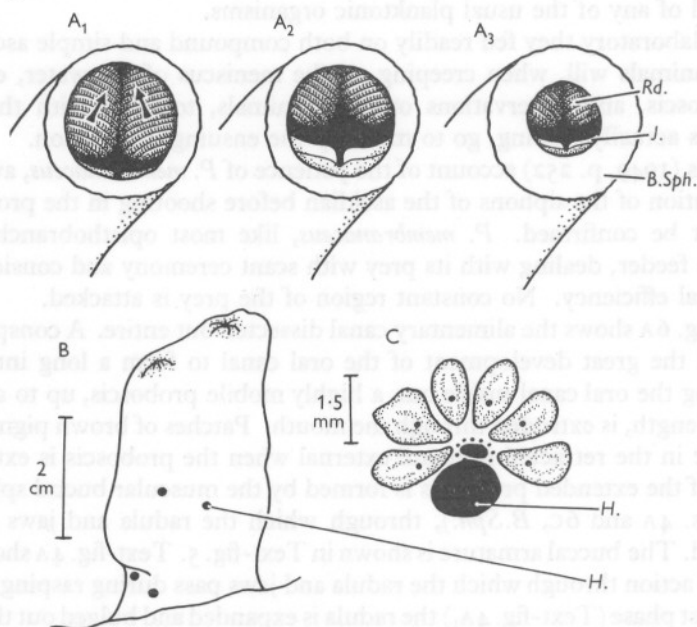
Text-fig. 4. The feeding mechanism: A, three phases of action of the radula and jaws at the tip of the extruded proboscis (see text for explanation); B, *Ascidia mentula* attacked by *Pleurobranchus*; C, *Botryllus schlosseri* attacked by *Pleurobranchus*. *B.Sph.*, buccal sphincter; *H.*, hole drilled by *Pleurobranchus*; *J.*, jaw; *Rd.*, radula.
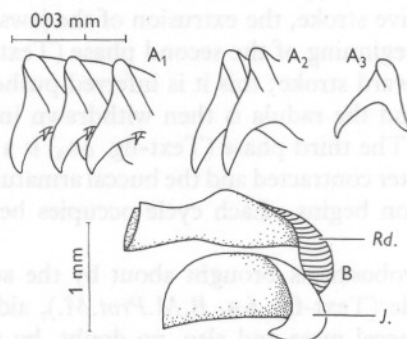
Text-fig. 5. The buccal armature: A, radular teeth, showing teeth from centre of radula (A₁), more lateral teeth (A₂) and a tooth from the extreme edge (A₃); B, radula and jaws dissected out entire seen from lateral aspect, with anterior to the right of the page, dorsal to the top. *J.*, jaws; *Rd.*, radula.
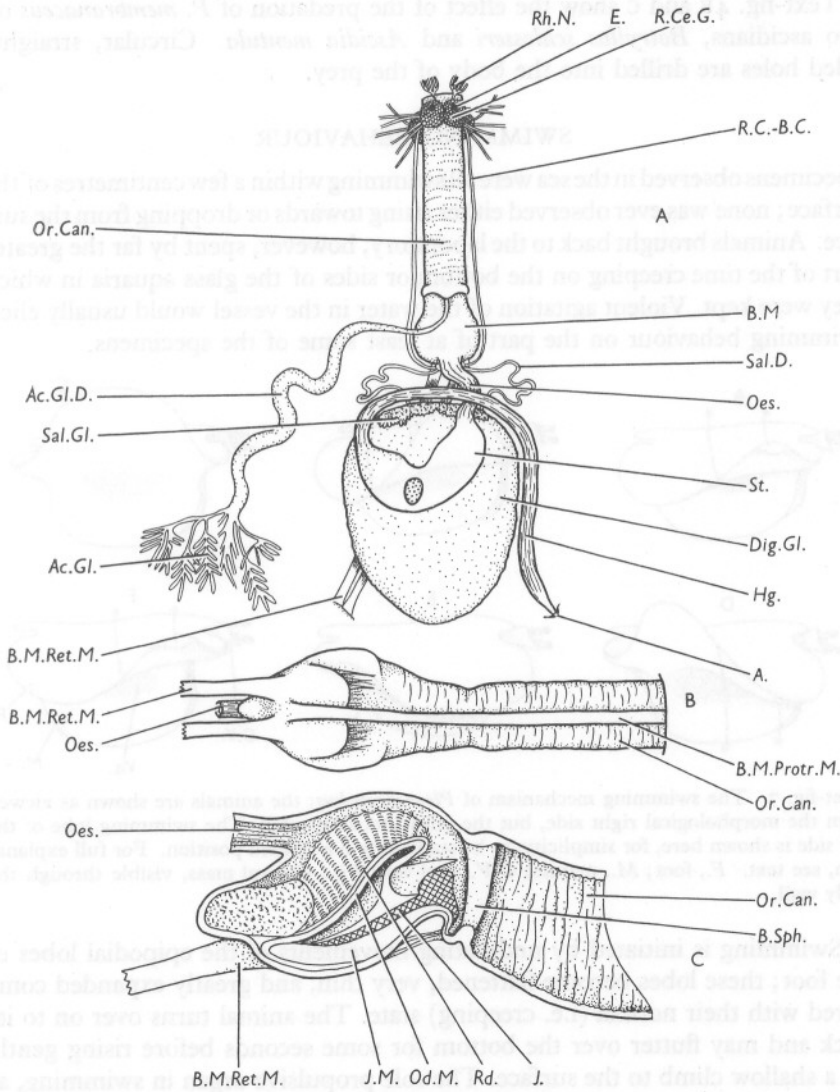
Text-fig. 6. The alimentary canal: A, alimentary canal dissected out entire from dorsal aspect with buccal mass retracted; B, ventral view of retracted buccal mass; C, left sagittal half of retracted buccal mass, cut surfaces left blank. *A.*, anus; *Ac.Gl.*, acid gland; *Ac.Gl.D.*, acid gland duct; *B.M.*, buccal mass; *B.M.Protr.M.*, buccal mass protractor muscle; *B.M. Ret.M.*, buccal mass retractor muscle; *Dig.Gl.*, digestive gland; *Hg.*, hindgut; *J.*, jaw; *J.M.*, jaw muscle; *Oes.*, oesophagus; *Od.M.*, odontophore muscle; *Or.Can.*, oral canal; *R.C.-B.C.*, right cerebro-buccal connective; *R.Ce.G.*, right cerebro-pleural ganglion; *Rd.*, radular membrane; *Rh.N.*, nerves to rhinophores; *Sal.D.*, duct of salivary gland; *Sal.Gl.*, salivary gland; *St.*, stomach.

Text-fig. 4B and C show the effect of the predation of *P. membranaceus* on two ascidians, *Botryllus schlosseri* and *Ascidia mentula*. Circular, straight-sided holes are drilled into the body of the prey.

SWIMMING BEHAVIOUR

Specimens observed in the sea were all swimming within a few centimetres of the surface; none was ever observed either rising towards or dropping from the surface. Animals brought back to the laboratory, however, spent by far the greater part of the time creeping on the bottom or sides of the glass aquaria in which they were kept. Violent agitation of the water in the vessel would usually elicit swimming behaviour on the part of at least some of the specimens.
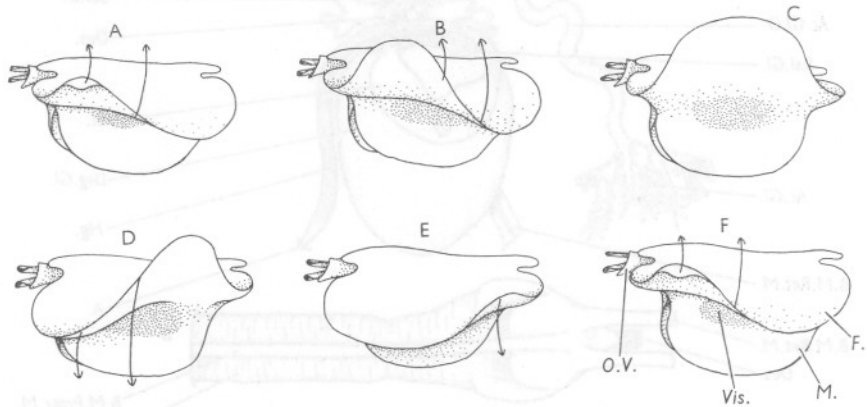

Text-fig. 7. The swimming mechanism of *Pleurobranchus*: the animals are shown as viewed from the morphological right side, but the gill is not illustrated. The swimming lobe of the left side is shown here, for simplicity, to be stationary in a relaxed position. For full explanation, see text. *F.*, foot; *M.*, mantle; *O.V.*, oral veil; *Vis.*, visceral mass, visible through the body wall.

Swimming is initiated by undulating movements of the epipodial lobes of the foot; these lobes become flattened, very thin, and greatly expanded compared with their normal (i.e. creeping) state. The animal turns over on to its back and may flutter over the bottom for some seconds before rising gently on a shallow climb to the surface. The sole propulsive organ in swimming, as in creeping, is the foot. The mantle is reflected away from the broad epipodial lobes; posteriorly the edges of the mantle skirt touch, forming a keel at the rear. The most striking feature of the swimming movements of the foot is the fact that the two lobes are not synchronous in action; that of one side under-

EXPLANATION OF PLATE I

Photographs taken through the side of a glass vessel of swimming *Pleurobranchus membranaceus*, viewed from the anterior; by electronic flash. ×2. *F.*, foot; *M*, mantle; *R.*, rhinophore.
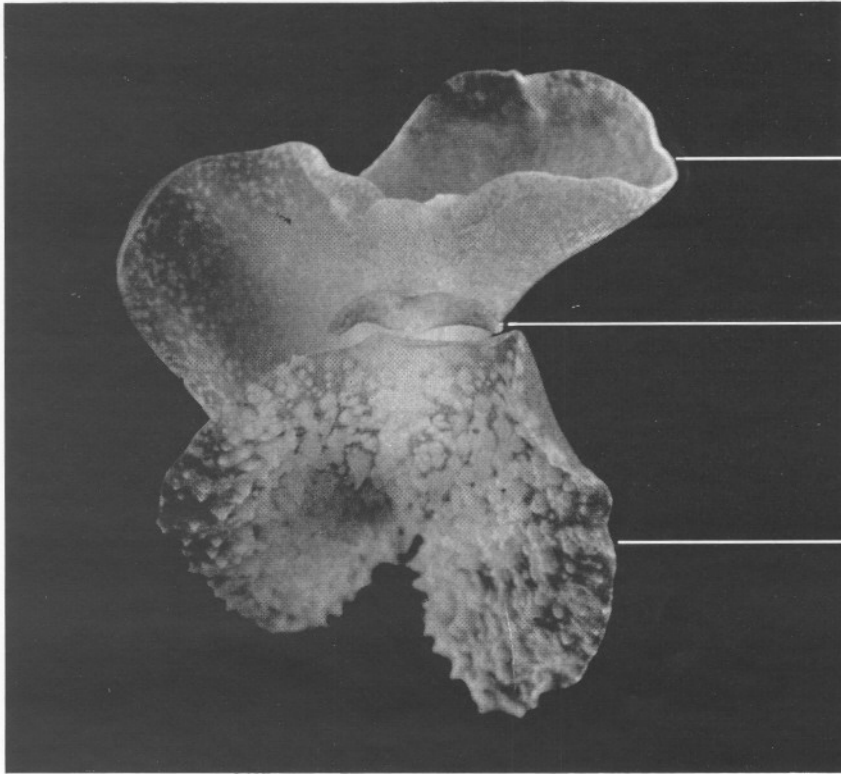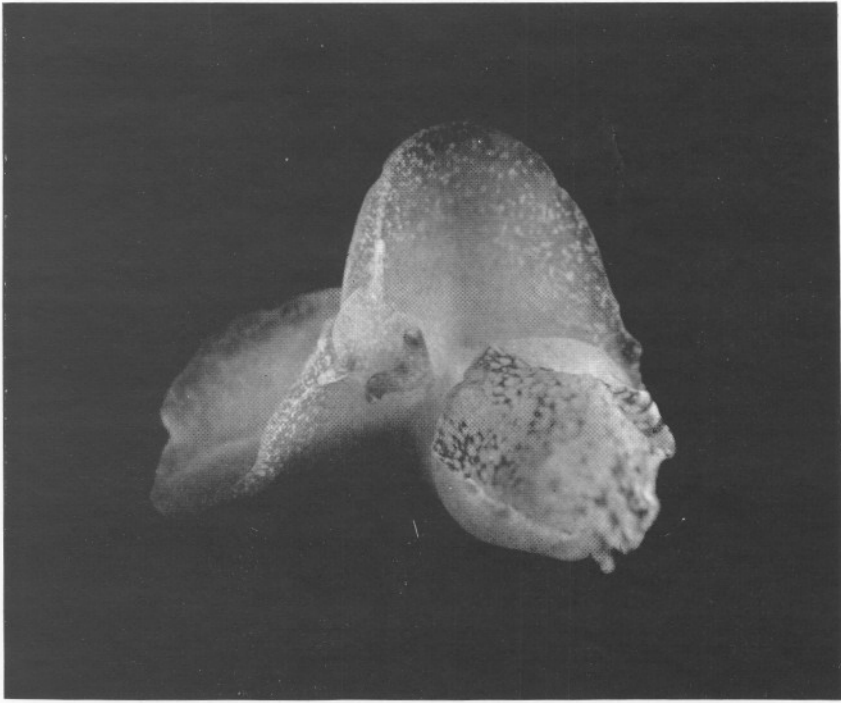
goes its recovery stroke at the precise time when the other is in the phase of effective beat. This causes a high degree of instability in progression: the roll to either side is approximately 45° and so a movement through about 90° occurs between each pair of strokes. The anterior and posterior extremities of the foot are deeply notched (see Text-fig. 7), marking the line of discontinuity of action of the two lateral halves of the foot.

The cycle of activity through which each epipodial lobe passes may be best explained by reference to the figures. Text-fig. 7A shows the lobe at the commencement of the recovery stroke; this is initiated anteriorly, a wave of action passing back (Text-fig. 7B) until the whole lobe is poised above the animal (Text-fig. 7C). The effective stroke again begins anteriorly (Text-fig. 7D), passing backwards; the result is quite a powerful beat, providing a lifting component, with the thinner trailing margin of the lobe helping to provide a posterior component resulting in a small amount of forward progression (Text-fig. 7E). These swimming movements are not unlike those of a skate, except that, as stated above, the two swimming lobes act asynchronously in *Pleurobranchus*, and the wave of action in this gastropod is of relatively greater magnitude.

The mantle, reflected away from the body, provides no protection for the gill during swimming; this organ is widely exposed at each recovery stroke of the right epipodial lobe. This contrasts with the behaviour of the animal when creeping, with the gill completely enclosed from view in a furrow between the mantle skirt and the foot. While the animal is swimming the mantle acts as a double keel, counteracting to some extent the rolling and yawing consequent on the nature of the mode of progression.

Counts of from 55 to 60 strokes per minute (of each epipodial lobe) were made with animals in sea water at 15° C, in the laboratory.

While in the sea the animals did not appear to be swimming in any particular direction, and were completely at the mercy of the currents. *P. membranaceus* at this stage of its life cycle is more planktonic than pelagic.

ACID SECRETION

The opportunity was taken to re-investigate the statement of Garstang (1890) that *P. membranaceus* rendered itself distasteful to predators by the secretion of sulphuric acid. It is clear that Garstang was referring to previous work by some other naturalist, but we have been unable to trace the original source.

Preliminary tests were made by applying pH papers to the mantle and foot of a roughly stimulated animal. Blue litmus immediately turned red at the point of contact, and Johnson's pH papers indicated a pH in the region of 1. Repeated stimulation (with a glass rod) of a small area of the mantle soon brought about local exhaustion of the capacity to produce this acid. The secretion does not seem to be produced continuously, but only when the

animal is abruptly disturbed; pH papers resting lightly on the mantle of a creeping specimen exhibited no colour change.

Some simple qualitative tests were then made in order to identify the anions present. To obtain samples of the acid secretion, the animal was passed rapidly through three changes of distilled water and excess water removed with filter paper. It was then placed in a Petri dish and the mantle stimulated with a glass rod. A few drops of distilled water were placed on it and then immediately drawn off with a fine pipette. Drops of this fluid were then tested for anions (see, for example, Belcher & Wilson, 1946). Chloride and sulphate were found to be present, but nitrite, nitrate and such organic radicals as oxalate, tartrate and citrate were not detected.

Gravimetric methods were used in an attempt to determine the sulphate: chloride ratio of the acid secretion, although the very small quantities of material available for testing rendered the results variable. Several animals were passed quickly through three changes of distilled water and then roughly stimulated with a glass rod. After stimulation the animals were washed in a minimum amount of distilled water, and determinations carried out on the combined washings (about 1–2 ml.).

Tests for proteins, with such coagulating reagents as mercuric chloride, ethyl alcohol and concentrated nitric acid were negative. Therefore it was assumed that proteins were not present in sufficient quantities to interfere with the gravimetric determinations.

Sulphate and chloride were precipitated as barium sulphate and silver chloride respectively, according to the procedure recommended by Vogel (1951). To reduce the effects of co-precipitation of the sulphates of sodium and potassium, this precipitation was carried out in the presence of picric acid. Precipitates were separated from the fluid by means of a centrifuge. The results of four separate determinations varied rather widely, giving a mean SO_4'':Cl' ratio of 0.75 ± 0.19:1. Two determinations carried out on local sea water using the same technique gave ratios of 0.13:1 and 0.14:1, compared with a mean value of 0.13991:1 found by Bather & Riley (1954) for the sulphate-chlorinity ratio of Irish Sea water. This fairly close agreement suggests that the technique used to obtain the fluid is the cause of the variation in our results, rather than the method of analysis.

Thus, when disturbed, *Pleurobranchus* produces an acid fluid of approximately pH 1, in which sulphate and chloride are the only anions present in appreciable amounts. The proportion of sulphate to chloride is much greater than in sea water. No analyses were made of the internal body fluids of *Pleurobranchus* due to the uncertainty of knowing whether a sample was contaminated with acid fluid from the epidermis or the acid gland. Robertson (1949) has given figures for the ionic composition of the body fluid of *P. membranaceus*, and he found the sulphate:chloride ratio to be about 0.143:1, only slightly above that of sea water.

Sites of production of the acid secretion

The general body surface. As mentioned above, the mantle and foot are both able to produce the acid fluid. The histological structure of the epidermis in *Pleurobranchus* is apparently simple and is quite unlike that of a dorid nudibranch (Thompson, 1958), in which large numbers of unicellular and multicellular epidermal and subepidermal glands open to the surface all over the mantle and its tubercles. In *Pleurobranchus* there are no subepidermal glands associated with the mantle or foot; there are only scattered small unicellular mucus glands of the usual type associated with ciliated epithelia.
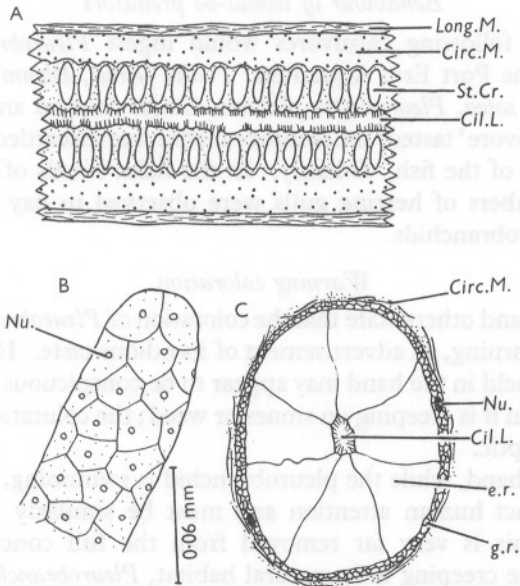
Text-fig. 8. The acid gland: A, diagrammatic longitudinal section through the acid gland duct; B, branch of the acid gland, stained intra-vitally with methylene blue; C, transverse section through a branch of the acid gland, fixed Zenker-without-acetic, stained Heidenhain's alum haematoxylin. *Cil.L.*, ciliated central lumen; *Circ.M.*, circular muscle fibres; *e.r.*, empty region; *g.r.*, granular region; *Long.M.*, longitudinal muscle fibres; *Nu.*, nucleus; *St.Cr.*, storage crypts.

The acid gland (Text-fig. 6A, *Ac.Gl.*, and Text-fig. 8). This is a large, ramifying gland, communicating with the roof of the buccal mass by a stout duct. Tests performed on extracts of this gland showed that it produced a strongly acid fluid. Text-fig. 8B shows an ultimate branch of the gland and Text-fig. 8C a section through such a branch. The gland cells (see Text-fig. 8C) have the same appearance in sections as the cells of the mantle and foot epidermis. The main duct (Text-fig. 6A, *Ac.Gl.D.*, and Text-fig. 8A) has two muscle layers and huge numbers of crypts opening off the central ciliated lumen. It is inferred that the secretion of the gland cells is stored in this

spongy duct, to be expelled rapidly when required, by contraction of the muscle layers.

To summarize: acid secretions are produced by the mantle and foot epidermis and by the ramifying median buccal gland (therefore called the 'acid gland'). The primary characteristic of the cells responsible for the secretions is a striking histological anonymity. They appear completely empty in sections; this, it is interesting to note, contrasts with the appearance of mammalian oxyntic cells, whose function is believed to be the secretion of hydrochloric acid (see Carleton & Leach, 1949).

Behaviour of would-be predators

None of the following carnivores would ingest *Pleurobranchus* in tests carried out at the Port Erin Aquarium: *Tealia felina*, *Blennius pholis*, *Pholis gunnellus*, *Solea solea*, *Pleuronectes platessa*, *Gadus calarias* and *G. virens*. In all cases the carnivore 'tasted' the pleurobranchid, but discarded it immediately, and, in the case of the fish, violently. In the field, shoals of coalfish (*Gadus virens*) and numbers of herring gulls were observed to pay no attention to swimming pleurobranchids.

Warning coloration

Cooke (1895) and others state that the coloration of *Pleurobranchus membranaceus* acts as a warning, an advertisement of its odious taste. However, while a *Pleurobranchus* held in the hand may appear to be conspicuous, this is certainly not the case when it is creeping on stones or weed; the coloration of the mantle is efficiently cryptic.

On the other hand, while the pleurobranchid is swimming, the movements of the foot attract human attention and must be similarly obvious to fish. Nevertheless, this is very far removed from the full concept of warning coloration. While creeping in its natural habitat, *Pleurobranchus* is effectively camouflaged; while swimming it does not advertise its presence by striking coloration, but neither does it make the least effort at concealment.

DISCUSSION

Swimming is a well-documented phenomenon in gastropods; it is widespread in the group and the possession of a swimming mechanism can be only warily accepted as evidence of close relationship. The means by which swimming is effected are as follows. (1) By lateral waves passing backwards along the whole body, e.g. the nudibranchs *Dendronotus giganteus* and *Melibe leonina* (Agersborg, 1922), *Scyllaea pelagica* (Collingwood, 1881), *Phyllirhoe* and *Cephalopyge* (Morton, 1958b). The waves pass down each side alternately, and the mechanism may be assisted either by the presence of an oar-like tail, as in *Lomanotus* (Trinchese, quoted by Colgan, 1908), or vertical undulations of the head, as in *Plocamopherus* (Lowe, quoted by Alder & Hancock, 1845–55). (2) By

vertical waves passing backwards along the mantle skirt, e.g. some tropical dorid nudibranchs (personal communication from J. S. Colman). (3) By movements of expanded lobes of the foot, as in most swimming gastropods. The action may resemble (as Morton, 1958*a*, points out) in essence either sculling, e.g. *Clione* (Morton, 1958*a*), Heteropoda (Morton, 1958*b*), or rowing (or even 'flying'), in which the lateral halves of the foot may either beat synchronously, e.g. *Akera* (Morton & Holme, 1955), *Gastropteron* (Morton, 1958*b*), *Limacina* (Morton, 1954), or beat asynchronously, e.g. *Pleurobranchus membranaceus*.

The majority of these gastropods spend most of their lives swimming; this is plainly not the case in *Pleurobranchus*, which has only occasionally been seen swimming. Pelagic seasonal swarming is a familiar phenomenon in marine animals and it is usually associated with feeding, reproduction or dispersal. None of these fits the facts concerning *P. membranaceus*, for this species apparently does not feed while swimming, is sexually immature during the requisite phase and already has (in the shape of a pelagic veliger phase) a dispersal mechanism of the usual molluscan type. The only other suggestion which we can advance at present is that this is a phenomenon similar to the much-debated inshore migrations of nudibranchs, namely, a means of bringing about aggregation for reproduction at a much later date. However, since it is unlikely that drifting in the surface layers of the sea will bring about any such aggregation, and since the existence of migrations in nudibranchs is denied by several authorities (a summary has been given by M. C. Miller, Liverpool Ph. D. thesis, 1958), this hypothesis is of questionable value. The true explanation will only be obtained when more facts concerning the natural history of *P. membranaceus* are discovered.

This report would be incomplete without some comments regarding the systematic position of the pleurobranchids. It is known that in the nervous system, the reproductive system,[1] the alimentary canal (with its 'holohepatic' arrangement—see Text-fig. 6), and features of the development (compare the mode of formation of the adult mantle in the metamorphosing larvae of *Berthellina* (Gohar & Abul-Ela, 1957) and *Adalaria* (Thompson, 1958)), the pleurobranchids are closely related to the dorid nudibranchs. This was recognized by Thiele (1931) who placed the pleurobranchids in the suborder Notaspidea, which, together with the suborder Nudibranchia, made up his order Acoela. In support of this is the arrangement of the exhalent respiratory aperture, formed by a temporary crenation in the mantle skirt (see Text-fig. 1 A, *Post.Cr.*), rendering the anus in *Pleurobranchus* in the same position *functionally* as that of the dorid nudibranchs. A simple change in the position of the gill would turn the pleurobranchid into a dorid. A homology of the dorid branchial circlet with the 'tectibranch' gill was first suggested by Evans (1914). In addition the way in which the mantle skirt encloses the basal parts

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[1] H. M. Lloyd, London Ph.D. thesis, 1952.

of the rhinophoreal tentacles in *Pleurobranchus* (see Text-fig. 1 A, *Ant.Cr.*) is strikingly similar to a developmental stage of the dorid *Adalaria* (Thompson, 1958); in *Adalaria* the anteriorly extending mantle fold during metamorphosis encircles and isolates the developing rhinophores. *Pleurobranchus* clearly shows an evolutionary stage in the production of the dorid rhinophore, which in the adult dorid appears to arise from the mantle.

Note added in proof

Specimens dredged and trawled during the spring and summer of 1959 were, through the kindness of Mr P. J. Miller and Mr R. G. Hartnoll, made available to us. Specimens of up to 7 cm long were collected during April and May and these deposited spawn masses in captivity. The ability to swim if abruptly disturbed is possessed even by the largest individuals. No specimens were found on the shore during 1959. None was dredged or trawled after the end of May; the inference is that *Pleurobranchus membranaceus* has an annual life cycle (like that of many dorid nudibranchs), the adults dying at the close of the breeding season.

SUMMARY

An account is given of an invasion of Port Erin bay by large numbers of swimming *Pleurobranchus membranaceus* (Montagu).

Descriptions are given of the external features of the specimens, the state of maturity, feeding behaviour and swimming behaviour.

The sites of production and the nature of the acid secretions are described.

Thiele's placing of the pleurobranchids close to the dorid nudibranchs is discussed and additional evidence to support this view is furnished.

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