Aspects of the reproduction and life cycle of *Rhabdopleura compacta* (Hemichordata)

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Abstract

Rhabdopleura compacta Hincks is shown to be monoecious. It is suggested that the ovum is ovulated and extruded into the lumen of the coenecium via a temporary opening at the base of the metasome, and that the oviduct itself may serve only as a way for sperm to fertilise the ova internally. The zooids degenerate when reproducing sexually and when conditions are unfavourable. The larva and initial stages of astogeny are described. Some observations on seasonal variation in the colonies indicate that the dormant buds serve for storage of nutrients. Reproduction seems to occur throughout the year, but most actively in spring. Relationships with *Cephalodiscus* and the Bryozoa are briefly discussed.

Introduction

Little is known about the life cycle and reproduction of the 3 pterobranch genera: *Cephalodiscus*, *Rhabdopleura* and *Atubaria*. We are least ignorant of *Cephalodiscus* (Harmer, 1905; Andersson, 1907; Ridewood, 1907, 1918 a, b; Schepotieff, 1909; John, 1931), but much of the published work is descriptive and largely the result of examination of preserved material collected by expeditions, although some observations on living *Cephalodiscus* have been made by Andersson (1903, 1907) and Gilchrist (1915, 1917).

Much less is known about the life cycle and reproduction of *Rhabdopleura* (Dawydoff, 1948), despite the works of Lankester (1884) and Schepotieff (1907 a, b). This is due largely to the lack of observations on living animals, which have been difficult to procure within reach of laboratory facilities. Burdon-Jones (1954), however, working on *Rhabdopleura normani* in Norway, succeeded in keeping colonies alive in aquaria for 2 months while studying their temperature and salinity tolerances.

Least of all is known about *Atubaria*. It was initially described by Sato (1936) from Japanese waters. He failed to publish a description of internal structure, but this gap was filled by Komai (1949), using Sato's histological preparations.

In April 1967, *Rhabdopleura compacta* was found off Stoke Point in Devon (England), within easy reach of the Marine Biological Association's Laboratory at Plymouth (Stebbing, 1968, 1970). Since then, observations which clarify some aspects of the reproduction and life cycle of *Rhabdopleura*, have been made on living and preserved material.

The sexual condition of *Rhabdopleura*

Lankester (1884) was the first to describe the male gonads. He found a few zooids with testes, but none with ovaries. Vaney and Conte (1906) also found male zooids, but no females. As van der Horst (1936) has pointed out, they mistakenly thought that the buds forming at the base of the contractile stalk were ovaries and erroneously concluded, because they found such "ovaries" attached to male zooids, that *Rhabdopleura normani* was a hermaphrodite. True ovaries were first found and described by Schepotieff (1907 a), who showed that the sex of *Rhabdopleura* can be determined by microscopic examination of whole mounts. Mature female zooids can be recognised by the presence of large developing ova in their metacoels, and mature male zooids by the posteriorly pointed extension of the metasome, enclosing the posterior part of the testis.

Table 1. *Rhabdopleura compacta*. Data gathered from 3 collections, dredged at different times of year. Twenty colonies were used from each collection

| Characteristics	Collection date		
	November 1967	February 1968	April 1968
Number of zooidal tubes	178	160	137
Number of normal zooids	82	113	92
Number of degenerating zooids	30	12	16
% of zooidal tubes occupied by zooids	62	78	78
Numbers of embryos being incubated	3	4	15
Numbers of 1 zooid colonies	1	2	4
Numbers of normal buds	12	21	18
Numbers of dormant buds at each stage:			
Not capsulated	4	14	13
Capsulated and full of tissue	24	50	48
Capsulated and not full of tissue	50	4	5
Total numbers of dormant buds	78	68	66
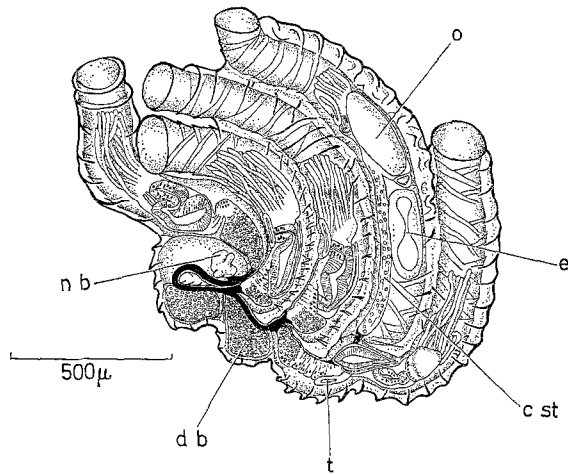
Fig. 1. *Rhabdopleura compacta*. Entire colony showing buds and zooids. Both male and female individuals are present in this colony. *c st* contractile stalk; *d b* dormant bud; *e* embryo; *n b* normal bud; *o* ovum; *t* testis

In 300 colonies examined by Schepotieff (1907 a), he found 25 with male zooids and only 3 with female zooids.

In colonies of *Rhabdopleura compacta* from Stoke Point, most zooids contained no gonads, and are therefore either immature or neuter. Nevertheless, sexual zooids are quite common (Table 1). In 20 colonies in which the sexes of all zooids could be differentiated, there were 114 neuter or immature zooids, 12 mature female zooids, and 11 mature male zooids. Six of these

colonies contained both male and female zooids (Fig. 1). One therefore finds a condition similar to that, for example, in Bryozoa, where both male and female individuals in a colony originate from the same genotype. Such animals are said to be monoecious. The situation in *Cephalodiscus* seems to be similar. Ridewood (1907) showed that buds of both sexes may be found developing from the stalk of the same parent zooid. Instead of being monoecious, there is also the possibility, suggested by Schepotieff (1907 a), that *Rhabdopleura* zooids may be protogynous or protandrous hermaphrodites. True hermaphroditism is impossible because, unlike *Cephalodiscus*, zooids of *Rhabdopleura* have only 1 gonad. Occasional individuals of *Cephalodiscus australiensis* (Johnston and Muirhead, 1951) and *C. nigrescens* (Ridewood, 1907) are known, which possess both an ovary and a testis.

Ovulation, incubation and problem of fertilization

As the stage at which fertilisation occurs is unknown, the progeny are here termed 'ova' until they are released from the parent zooid into the lumen of the coenoecium, whereupon they are termed 'embryos' until they acquire larval characteristics.

The embryos of *Rhabdopleura compacta* are found enclosed within the coenecium (Fig. 2 and Stebbing, 1970), like those of *Cephalodiscus* (Harmer, 1905; Ridewood, 1907, 1918 a, b; Gilchrist, 1915). They remain there while they develop into larvae. Usually 2 or 3, occasionally up to 5, embryos at various stages of development may be found in the tube of a parent
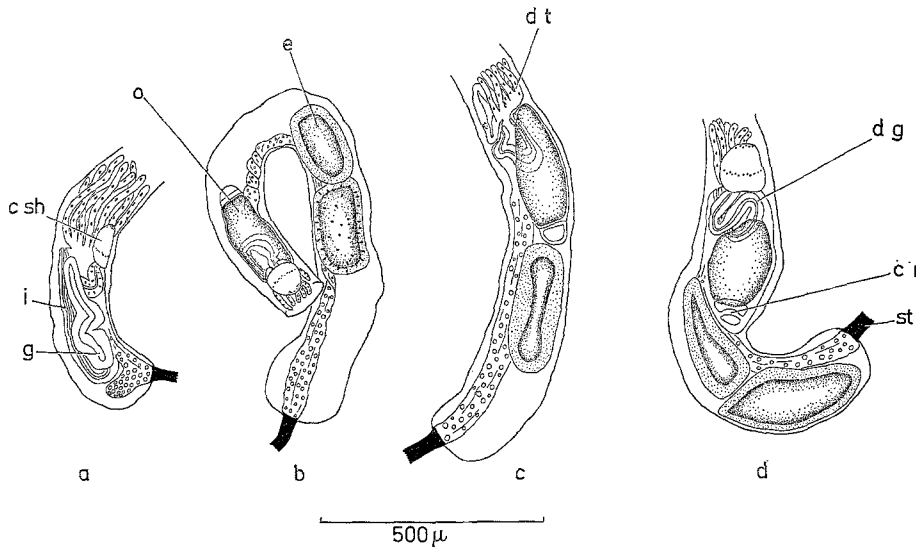

Fig. 2. *Rhabdopleura compacta*. Normal zooid (a) and female reproductive zooids (b), (c), (d) showing the way in which sexual zooids have ova in their metacoels and cap and ring structures at the posterior ends of the metasomes. Sexually reproductive zooids are always degenerate and often have embryos developing in their tubes. *c r* cap and ring structure; *c sh* cephalic shield; *d g* degenerate gut; *d t* degenerate tentacles; *e* embryo; *g* gut; *i* intestine; *o* ovum; *st* stolon

zooid at the same time; often a further ovum is present in the metacoel of the parent zooid. LANKESTER (1884), in his memoir on *Rhabdopleura normani*, illustrated a tube of what appears to be a mature zooid containing 6 oval bodies (his pl. xxxix, Fig. 2). These, as he suggested, are almost certainly embryos in various stages of development, for his figure clearly shows the peripheral layer of pigment bodies which are characteristic of late embryos of *Rhabdopleura* (see section on larvae).

The embryos are found between the metasome of the parent zooid and the septum, across the repent part of the tube. They are almost always found in a developmental sequence, the oldest embryos at the proximal or closed end of the tube, and the youngest distally (Fig. 2). The youngest embryos lack pigment bodies, are bright yellow in colour, and have a milky opacity. In time they become darker yellow, develop cilia and acquire the peripheral layer of elongated pigment bodies which the larvae possess.

Remarkably, it has been shown that the largest ova of *Rhabdopleura normani* (SCHEPOTIEFF, 1907a) are found furthest from the oviduct, and vice versa. The same appears to be true of *R. compacta*. The problems which follow are, first, to explain the manner in which ova ready to be released squeeze past the smaller ova to escape through the oviduct; second, to understand the manner in which an ovum, so large that it almost fills the metacoel, passes through the narrow oviduct; third, how these large, unciliated embryos, once free of the parent zooid, pass from the anteriorly situated oviduct, past the body, to a position in the tube posterior to the parent zooid.

When zooids containing large ova were examined closely, a tapered, ring-shaped structure bearing a cap was always observed at the posterior tip of the metasome (Fig. 2). The nature of this structure, and its occurrence solely in zooids containing large ova, suggest that it is involved in a process of extrusion of the ova from the metacoel. It appears possible that the cap breaks away from the metasome to allow the embryos to escape posteriorly into the tube of the zooid. The aperture thus created presumably then closes while another ovum develops.

The anomalous situation, noted in *Rhabdopleura*, whereby the largest unspawned ova lie furthest from the oviduct, exists also in *Cephalodiscus* (HARMER, 1905; RIDEWOOD, 1918b). MASTERMAN (1898) suggested that the ova of *Cephalodiscus dodecalophus* are set free by the death and disintegration of the parent zooid. Subsequently, GILCHRIST (1917) suggested that ovulation in *Cephalodiscus gilchristae* may involve the breaking away of the ovary (or part of it) from the body, without involving the death of the parent zooid.

Support for the occurrence of a mode of egg release other than via the oviduct is given by RIDEWOOD (1907). He illustrates an ovary of *Cephalodiscus nigrescens* with a tube at its posterior end as well as the

normal anteriorly situated oviduct. Although this tube ends blindly, he suggests that it looks like an oviduct.

If the manner of ovulation in *Rhabdopleura* is as suggested here, the oviduct seems to have no function except as a point of entry for spermatozoa to fertilise the ova internally. Internal fertilisation was also proposed by MASTERMAN (1898) for *Cephalodiscus dodecalophus* in conjunction with his hypothesis of ovulation by disintegration, mentioned above. Further support for this proposal is ANDERSSON's (1907) observation of sperm inside the ovary of *Cephalodiscus densus*. In both genera, internal fertilisation would seem compatible with the small numbers of ova produced.

Degeneration of zooids reproducing sexually

A peculiarity of mature male and female zooids of *Rhabdopleura compacta* is that they are morphologically different from other zooids (Fig. 2). The arms and tentacles of female zooids become much reduced in length, sometimes to such a degree that the tentacles do not extend beyond the anterior edge of the cephalic shield. The digestive tract also regresses until it is often compressed into the anterior third of the metacoel. Mature male zooids may also degenerate in a similar way, but to a lesser extent.

A similar condition has been recorded by VANEY and CONTE (1906). They found that sexually mature zooids of *Rhabdopleura normani* degenerate, principally by loss of tentacles and partial regression of the cephalic shield. HARMER (1905) recorded a similar state in *Cephalodiscus sibogae*, which may also be degeneration. Neuter zooids in this species have 4 pairs of tentaculate arms, but the sexually mature zooids have only 2 arms, which lack tentacles, and a vestigial digestive tract. The condition of the tentacles, arms, and gut, suggests that sexual zooids do not feed. In *Rhabdopleura*, zooids may be maintained by nutrients passing along the stolon from other zooids that have not degenerated, or from the dormant buds.

The larva (Figs. 3a and b)

The terms dorsal, ventral, anterior and posterior used in this description are based on the orientation of the larva during locomotion.

BURDON-JONES (1954, 1964) noted that *Rhabdopleura* has free-swimming larvae, but did not describe them. Otherwise, the only published observations on the embryos or larvae have been a single record by SCHEPOTIEFF (1907a) and a drawing by LANKESTER (1884; his pl. xxxix, Fig. 2) of what he regarded as buds of exceptional form. He also considered the possibility that they were eggs, but in the light of the present observations, it now seems certain that they were embryos in a late stage of development.

The larva is ovoid in outline and almost radially symmetrical. When recently liberated it is an opaque

yellow colour. The peripheral layer contains many elongated dark bodies which have their longitudinal axes orientated radially. They are most numerous in the anterior quarter of the larva, but absent from a slightly flattened area along the ventral surface. There are also very small areas devoid of pigment bodies at the anterior and posterior extremities. Interspersed between the dark pigment bodies are green, multilobulate, pigment bodies such as those found in adult zooids (STEBBING, 1970). The larva is covered by a uniform layer of cilia which beat synchronously, enabling it to swim or crawl. Little internal structure can be seen in whole specimens because of the larva's opacity. Two days after being liberated, however, the larvae become less opaque and some internal structure can be made out (Fig. 3b). The posterior half of the

pyriform egg capsules attached by short flattened tubular stalks to the inside walls of the coenecium. The young larvae of *Cephalodiscus*, as described by ANDERSSON and GILCHRIST, are "planula-like" and seem very similar to those of *Rhabdopleura compacta*. Both have a peripheral layer of elongated and radially orientated pigment bodies, most numerous towards the anterior end, although absent from the anterior extremity. Both have a cavity in the anterior end, and a solid posterior end. SCHEPOTIEFF (1908) has described the larva of *Cephalodiscus indicus* at what appears to be a much later stage in development, for it has a much more differentiated structure. It is ciliated, and bears an apical tuft of elongated cilia around which is a ciliary ring. There is a mouth and anus with a partially formed gut connected to the former, but not the latter.

At the end opposite to the apical tuft is an internal sac with an opening to the exterior.

Some observations on living larvae

Late embryos of *Rhabdopleura compacta* have been observed through the transparent tubes of the parent zooids, while others which appeared to be nearing completion of their larval development have been squeezed out of the coenoecium in order to watch their behaviour. Unfortunately, it has not so far been possible to observe how they normally escape, nor have any of the larvae been observed to settle.
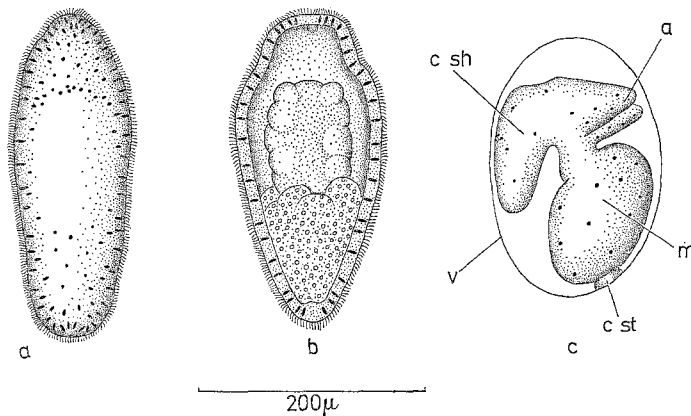

Fig. 3. *Rhabdopleura compacta*. Larva. (a) Surface view; (b) optical section; (c) early settled stage before tube secretion begins. The anterior ends point to the top of the page. *a* arms; *c sh* cephalic shield; *c st* contractile stalk; *m* metasome; *v* vesicle

larva is solid, while the anterior half contains a cavity which collapses when the larva is fixed in formol-calcium. No gut, mouth or anus can be discerned. It is thought that the larva must be lecithotrophic, as it appears to have no means of feeding and seems very yolky when first liberated.

Embryos of *Rhabdopleura compacta* may perhaps differ from those of *R. normani* in one important way. SCHEPOTIEFF (1907a) found an 'egg', which was enclosed in a thin transparent covering, attached by a thin stalk-like appendage to the arms of a zooid of *R. normani*. This was only an isolated observation, however, and none of the many embryos seen in colonies of *R. compacta* were enclosed in a capsule or attached to anything by a stalk.

The embryos and larvae of *Cephalodiscus* have been described by ANDERSSON (1903, 1907), HARMER (1905), SCHEPOTIEFF (1908) and GILCHRIST (1915, 1917). The embryos of *Cephalodiscus gilchristae* are enclosed in

As the embryos are extruded from the parent zooid, they push the older ones deeper into the proximal part of the repent tube. It is common to find several embryos in any one tube, each at a different developmental stage (Figs. 2b, c, d). Those which lie furthest away from the orifice of the tube generally have most pigment spots, are least opaque, are ciliated and presumably the most advanced. In order to escape, each larva must find its way past the other developing embryos and the parent zooid; observations on living and preserved specimens provide evidence that this occurs. Occasionally a fully developed larva is found nearer the orifice than others at earlier developmental stages. Larvae have twice been found distal to the parent zooid. It appears that the larvae are highly plastic, and can squeeze past other stages occupying the same tube.

Larvae which were apparently fully developed were often seen to rotate slowly inside their parent's tubes. Each revolution took from 3 to 6 min. After larvae had been gently squeezed from their tubes with fine forceps, they sank to the bottom and began to crawl slowly

along using their cilia. Similar observations were made by Gilchrist (1915) on *Cephalodiscus* larvae. *Rhabdopleura compacta* normally crawled with their pigment-free area facing the substratum. Occasionally, they moved much more rapidly, skimming just above the substratum, and they then usually rotated about their longitudinal axes. Phases of skimming and crawling were initially interspersed with periods of spinning or pirouetting in a small area, on their posterior ends, with the longitudinal axis vertical, or nearly so; sometimes they would remain motionless in this position. Some larvae were also capable of quite vigorous longitudinal contractions, so that the usual ovoid shape became rounded.

Two larvae were kept alive for 50 h in the presence of a suitable settlement substratum (dead and separated valves of *Glycymeris glycymeris*). After 24 h they were seen to swim, as opposed to skimming over the substratum. They would crawl up the vertical sides of their container and launch themselves into mid-water. They would then swim unidirectionally for a few centimetres before their cilia stopped and they sank to the bottom.

As the larvae of *Rhabdopleura compacta* appear to be lecithotrophic, they probably do not remain free-living for long. Larvae 2 days old were already beginning to lose their yolky opacity, indicating that they were running short of food reserves and might soon settle and metamorphose.

criss-cross marking of repent tubes, and the erect tube is annularly segmented (Fig. 4a). By this time, the young zooid resembles the fully grown one more closely, as it has tentacles and a fully developed alimentary canal. Astogeny (the development of the colony by budding) commences in the primary zooid, when a small bud forms at the base of the contractile stalk and a septum is secreted separating a segment of the vesicle (Fig. 5a). The young zooid then breaks
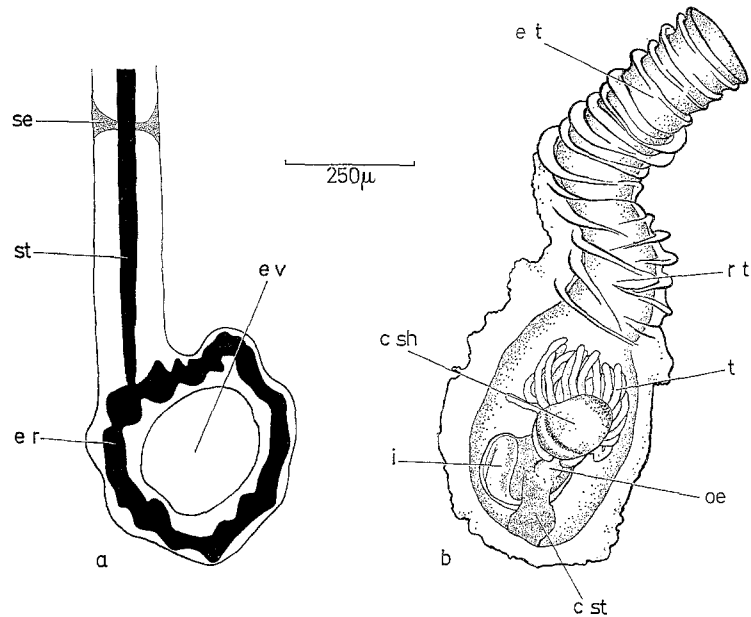

Fig. 4. *Rhabdopleura.* Primary zooid. (a) *R. normani* (after Schepotieff, 1907b); (b) *R. compacta. c sh* cephalic shield; *c st* contractile stalk; *e r* embryonal ring of stolon; *e t* erect tube; *e v* embryonal vesicle; *i* intestine; *oe* oesophagus; *r t* repent tube; *se* septum; *st* stolon; *t* tentacle

Primary zooids and early astogeny

Many specimens of very recently settled *Rhabdopleura compacta*, which were found on shells dredged in April 1968, provided examples of the earliest stages in colony formation.

Recently settled larvae encapsulate themselves completely in a vesicle which appears to be constructed of the same substance as the coenecium. The vesicle is ovoid, except that it is flattened on the side next to the substratum. In what appear to be the youngest vesicles, the developing zooid is an amorphous mass of tissue, speckled by pigment bodies and attached posteriorly to one end of the vesicle. In slightly older specimens, the rudiments of a cephalic shield, arm buds and a contractile stalk become differentiated from the metasome (Fig. 3c). The next stage is the breakdown of the anterior wall of the vesicle and the secretion of the tube. The first few segments have the characteristic
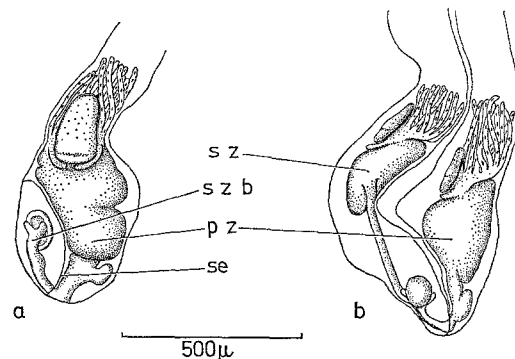

Fig. 5. *Rhabdopleura compacta.* Two young colonies in the early stages of astogeny. *p z* primary zooid; *se* septum; *s z* second zooid; *s z b* second zooid as bud

down the wall of the vesicle and begins to secrete its own tube. Subsequently, the new zooid, as well as the primary zooid, produces buds (Fig. 5b) which also

become new zooids. Thus astogeny proceeds by the asexual replication of zooids.

SCHEPOTIEFF (1907b) has described the origin of *Rhabdopleura normani* colonies, although he found only 11 examples among the 300 colonies he examined. The colony originates by one or more outgrowths from a ring of stolon, which is enclosed in a similarly shaped part of the repent coenecium (Fig. 4b). SCHEPOTIEFF found that the "embryonal vesicle" and the "embryonal ring" were always empty. Unless he misinterpreted the evidence from his specimens, it is clear that the colonies of *R. normani* and *R. compacta* originate in different ways. No specimens of *R. compacta* examined resemble those figured by SCHEPOTIEFF (1907b; his pl. 21, Figs. 11 to 15 and pl. 23, Figs. 21 and 24).
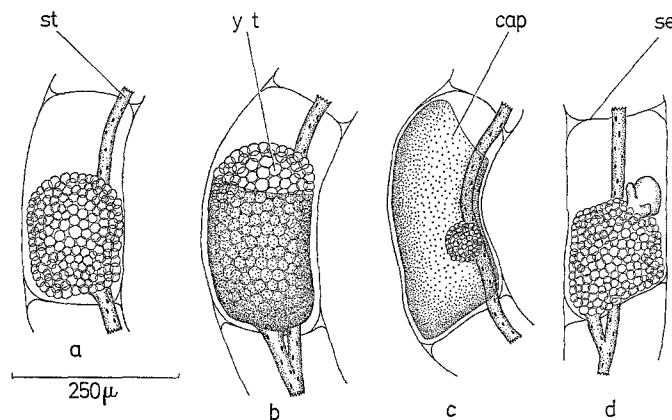

Fig. 6. *Rhabdopleura compacta*. Dormant buds at different stages (see text). The capsule has been omitted on (d). *ca* capsule; *se* septum; *st* stolon; *y t* yolky tissue

The buds

The majority of buds in *Rhabdopleura compacta* are of 2 types (STEBBING, 1970): first, those that, whilst still very small, show the rudiments of arms and cephalic shields and presumably develop into zooids without delay, contributing to the growth of the colony. Second, those that form ovoid or spherical masses with apparently no differentiation of tissues or organs; these are termed "dormant buds". Both types are formed at the base of the contractile stalk of the zooid and subsequently become enclosed in a chamber of the repent coenecium by the secretion of a septum across the tube.

The dormant buds consist of a yolky mass flecked with pigment spots in the peripheral layer. At first these buds are naked (although, of course, each is enclosed in a chamber of the coenecium; Fig. 6a), but in time they become enclosed in a capsule which is presumably secreted by the bud. Secretion of the capsule proceeds from the point where the bud is attached to the stolon towards its distal end, so that the capsule remains open-ended for some time (Fig. 6b). Subse-

quently, the contents of the capsule shrink from its walls, until only a small spherical mass of tissue remains (Fig. 6c).

Dormant buds in *Rhabdopleura normani* were termed "hybernacula" by LANKESTER (1884), although he did not otherwise suggest that they had any connection with overwintering. He thought them to be normal buds whose development had become arrested. SCHEPOTIEFF (1907b) called them "sterile buds", presumably because he thought that they did not develop into zooids like normal buds. This is certainly not so in *R. compacta*, where dormant buds are capable of developing into zooids (Fig. 6d). SCHEPOTIEFF noticed that these buds were especially numerous in autumn and suggested that they were connected with over-wintering. He also suggested that the "black crust" or capsule enclosing the buds had a protective function.

A third type of bud, called a "regeneration bud" by SCHEPOTIEFF (1907b), also occurs in *Rhabdopleura compacta*. It differs in appearance from a normal bud only in that it develops in the tubes of adult zooids that have degenerated.

Aquarium observations and the degeneration of non-sexual zooids

Colonies were kept in aquaria from November 1967 and April 1968 (when they were dredged off Stoke Point) until June 1969. Attempts to feed them on unialgal cultures of several species failed. Subsequently, the zooids died and decomposed, or slowly degenerated. However, even in May 1969, a few degenerate zooids were still living. They had no tentacles and their arms were much reduced in length; their metasomes had shrunk and their cephalic shields were also much smaller. Dormant bud capsules containing living tissue were less rare than zooids but, in those that contained some living tissue, the proportion of space taken up was much less than before. In most cases the living tissue had disappeared.

There is evidence that degeneration and regeneration of non-sexual zooids occurs when *Rhabdopleura* is in its normal habitat. SCHEPOTIEFF (1907b) showed that regeneration of a zooid could occur from the stump of the contractile stalk when, he believed, the zooid had become detached accidentally. Similar regeneration buds have been found in *Rhabdopleura compacta* (see section on buds). VANEY and CONTE (1906) realised that complete degeneration of non-sexual zooids occurred, but did not separate it, in their discussion, from the partial degeneration of sexual zooids. The cause and result are probably different in the two cases. They observed that, in the degenerating non-sexual

zooids, a brown body is formed comparable to that found in degenerating zooids of marine Bryozoa. Similar brown bodies were found in *R. compacta*, and this character has been the one used to recognise degenerating zooids in the collection of the data in Table 1.

Another feature of zooids that are degenerating is that they often secrete a septum between themselves and the open, distal end of their tubes. Similar behaviour has been described in *Cephalodiscus nigrescens* (RIDEWOOD, 1907), *C. solidus* and *C. densus* (RIDEWOOD, 1918a, b).

Marked changes in the width of adjacent annuli on erect tubes of *Rhabdopleura compacta* appear to reflect the stage in their secretion at which degeneration and subsequent regeneration of zooids occurred. This might be expected, as the cephalic shield, which secretes the annuli, also degenerates and regenerates. Often a number of annuli of normal width are succeeded distally by much narrower annuli, which gradually increase in size towards the tube orifice. The point at which the change in width of adjacent annuli occurs appears to be the stage at which cessation of tube secretion and degeneration of the zooid begins. The narrow annuli were probably secreted by the regenerating zooid before it regained its full size. The increase in annulus width towards the orifice would reflect the growth of the zooid.

Seasonal variations

Collections of *Rhabdopleura compacta* were made at Plymouth in April and November 1967, and February and April 1968. To give some record of seasonal variations, 20 colonies in which the components could be counted under a low power microscope were examined from each of 3 collections (Table 1).

Colonies appeared to be in a much more thriving condition in February and April 1968 than in November 1967. A larger proportion of the zooidal tubes were occupied, while dormant buds were being secreted and existing ones filled their enclosing capsules with "yolky tissue". In November, however, the tissue inside many of the capsules had shrunk or disappeared. It appears that the major role of dormant buds is to store nutrients when food is plentiful, and to maintain the colony when food is less abundant. Degenerating zooids were most common in November. At such times of apparent scarcity it seems that food reserves contained in the dormant buds may maintain the colony in a viable condition, and the fact that so many of the dormant bud capsules were then practically empty suggests that some demand had already been made on this store. Some colonies at that time had no zooids left at all, but some dormant buds usually remained which were probably capable of developing into new zooids when conditions became favourable.

Each of the collections also included examples of zooids containing ova, embryos being incubated in their parental tubes, and primary zooids. Embryos and primary zooids were most numerous in the April collection, but it appears that *R. compacta* is capable of successful sexual reproduction throughout the year.

Phylogenetic considerations

The close relationship between *Rhabdopleura* and *Cephalodiscus* is well established (M'INTOSH, 1882; HARMER, 1905; RIDEWOOD, 1907). The present work shows that there are additional similarities between the 2 genera. First, the larva of *Rhabdopleura compacta* is very similar to that of *Cephalodiscus gilchristae* (GILCHRIST, 1915), both in appearance and behaviour. Second, the present observations on *R. compacta* and those by VANEY and CONTE (1906) on *R. normani* seem to explain the condition reported by HARMER (1905) in sexual zooids of *C. sibogae*. These had arms devoid of tentacles and a vestigial gut, as though they had undergone degeneration, just like the same structure in *Rhabdopleura*. Finally, the method of ovulation and fertilization proposed here for *Rhabdopleura* may well apply to *Cephalodiscus* too, for that would explain the difficulties to which attention was drawn by MASTERMAN (1898) and GILCHRIST (1915, 1917).

Some new features of the pterobranchs revealed by this study resemble conditions seen in the Bryozoa. It is interesting to recall that the discoverers of *Rhabdopleura normani* (ALLMAN, 1869) considered it to be a bryozoan. Not until 24 years later was it placed in the Hemichordata by FOWLER (1892). However, more recently, DAWYDOFF (1948) has shown that the pterobranchs have important features in common with the Bryozoa. These features may be summarised as follows: first, the similarity of the arms and tentacles of pterobranchs with the lophophore of Bryozoa (especially in the Phylactolaemata); second, the occurrence in both groups of a U-shaped alimentary canal; third, the similarity in appearance and disposition of the pterobranch protosome and the epistome of phylactolaemotous Bryozoa; finally, several striking similarities of a bryozoan larva (*Bugula* sp.) with the larva of *Cephalodiscus* (BRAEM, 1911). DAWYDOFF might have added to this list the similar position of the main nerve ganglion in both groups.

During this investigation of *Rhabdopleura compacta*, some more characteristics of possible phylogenetic significance, common to both pterobranchs and Bryozoa, have become apparent. First, the formation of "brown bodies" in degenerating zooids of *R. compacta* and *R. normani* (VANEY and CONTE, 1906); second, the occurrence of a monoecious sexual condition in both groups and, finally, the ability of zooids to degenerate during sexual reproduction or when conditions are unfavourable. Although these may be regarded as some evidence of affinity, they are also features that one

might expect to find associated with sessile, colonial, tubicolous animals, so should not be stressed unduly.

Summary

1. The sexual condition of *Rhabdopleura* is discussed and *R. compacta* HINCKS is shown to be monoecious.

2. Fertilisation, ovulation, incubation and liberation of the larvae are considered. It appears that fertilisation is internal and that the ova are released from the parent by a temporary opening at the base of the metasome.

3. Zooids are shown to degenerate when reproducing sexually. The manner and extent of their degeneration is described.

4. Some observations are given on the behaviour of living larvae and the larva is described.

5. The earliest settled stages and the early astogeny of the colony are described.

6. The different types of buds are ennumerated and dormant buds at different stages are described. They appear to serve for storing nutrients.

7. A study of seasonal variation shows that *Rhabdopleura* is in breeding condition for most of the year.

8. Some previously unnoted similarities are given between *Rhabdopleura* and *Cephalodiscus* and a closer relationship between pterobranchs and the Bryozoa is suggested.

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