Organisms associated with burrowing whelks of the genus *Bullia*

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Organisms found associated with the psammophilic neogastropod *Bullia* include hydroids, a boring sponge and algae which grow on, and burrow into, the shell. The shell may also be the recipient of the egg capsules of other species of gastropods. Peridinian ciliates are commonly found attached in some numbers to the tentacles and an occasional rotifer occurs on the soft parts of the animal. The gut is rich in bacteria, some of which are symbiotic. Digenetic trematode larvae are the most common internal parasites and larval cestodes also occur. Preliminary descriptions are given of two apparently new trematode larvae and of a cestode cysticercoid. A nematode worm is occasionally present in the gut. The absence of external parasites is noted and it is suggested that the shells of the whelk represent a refuge for smaller organisms or their eggs in an unstable environment lacking geological diversity.

Organismes wat in assosiasie met die sandbewonende *Bullia* (Neogastropoda) gevind word sluit hidroïede, 'n borende spons en alge wat op die oppervlakte en in die skulp groei in. Die skulp dien moontlik ook as 'n ontvanger van eierkapsules van ander Gastropoda spesies. Peridiniese siliate heg algemeen in redelike getalle aan die tentakels vas en Rotifera word af en toe op die sagte dele van die organisme aangetref. Die spysverteringskanaal is ryk aan bakterie, sommiges simbioties. Digenetiese Trematoda larwes is die mees algemene interne parasiete, en Cestoda larwes kom ook voor. Voorlopige beskrywings word gegee van twee klaarblyklik nuwe Trematoda larwes, asook van 'n Cestoda sistiserkus. 'n Nematood word ook soms in die spysverteringskanaal aangetref. Die afwesigheid van uitwendige parasiete word gemeld en daar word voorgestel dat die wulk skulp 'n veilige hawe aan kleiner organismes of hul eiers bied, in 'n onstabiele omgewing met min geologiese diversiteit.

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The genus *Bullia* (Prosobranchia: Neogastropoda) comprises over 25 species of small to medium-sized whelks, distributed from tropical west Africa around the southern African shore and along Indian Ocean coasts possibly as far east as Australasia (Cernohorsky 1984; Brown & McLachlan 1990). The biology of intertidal species has been summarized by Brown (1982) and Brown, Stenton-Dozey & Trueman (1989), while information on some subtidal species may be found in Brown (1961; 1982) and in Kilburn & Rippey (1982). All known species are psammophilic and all burrow into the substratum. Intertidal species surf up and down the shore in search of carrion. This communication brings together published and previously unpublished information on the organisms (other than predators) that have been found to be associated with these whelks. Preliminary descriptions of the larvae of two new species of Trematoda and a cestode are presented.

Biota associated with *Bullia*

1. Bacteria

While the body surfaces of the whelks appear to be remarkably free of bacteria, possibly indicating some bacteriolytic activity in the mucus, these prokaryotes are quite common on the shell and abundant in the gut of those species that have been examined in this regard (*B. digitalis, B. rhodostoma* and *B. tranquebarica*). A number of different bacterial types are found in the gut of *B. digitalis*, at least one of which is cellulolytic and assists the whelk in the digestion of algal material (Harris, da Silva, Bolton & Brown 1986). Ramesh & Venugopalal (1986) found luminous bacteria to be very common in the gut of *B. tranquebarica* (Röding) from the east coast of India; two bacterial species were present, *Vibrio harveyi* and *V. fischeri*, and both exhibited chitinolytic activity. Although much more abundant in the gut of *B. tranquebarica* than in the surrounding sea-water or sediment, the significance of these chitin-digesting bacteria in the life of the whelks is not clear.

2. Algae

Algae are commonly found growing on the shells of several South African species of *Bullia*, including *B. laevissima* (Brown 1961), *B. digitalis* (da Silva & Brown 1984; Harris *et al.* 1986) and *B. rhodostoma* (A. Hodgson, pers. comm.; Brown, unpubl.), although no epiphytic algae have been found associated with *B. tenuis* or *B. annulata*. The epiphytes are rocky-shore species and particularly forms such as *Hypnea spicifera* and *Codium duthieae*, which are common at the water's edge on rock inundated with sand (Brown, Wynberg & Harris 1991). Branch & Branch (1981) note that algae are more abundant on *Bullia rhodostoma* than on *B. digitalis* and this has been confirmed by subsequent observations (Brown, unpubl.). At the Strand in False Bay, numbers of *Bullia rhodostoma* were observed with the dorsal surface of the shell completely covered in a luxuriant growth of *Hypnea*, while the shells of *Bullia pura*, lower down the slope, were free of epiphytes (Brown, unpubl.). *Ulva* and *Enteromorpha* also occur regularly but less commonly in the western Cape, although in the eastern Province they may be prominent members of the epiphytic flora on the shells of *Bullia rhodostoma* (A. Hodgson, pers. comm.). The algae are normally extremely stunted compared with the same species growing on rocky substrata.

Epiphytic algae on *Bullia* shells face abrasion by sand as the whelks burrow but this may be partly offset by protection from grazers (see Bally, McQuaid & Brown 1984;

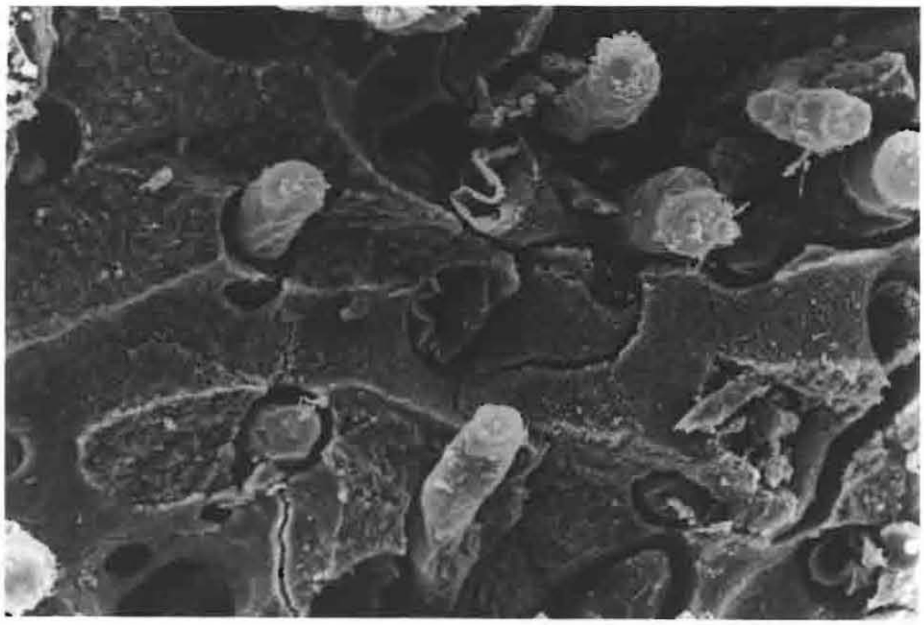

Figure 1 The alga *Eugomontia sacculata* in the outer prismatic layer of a fractured shell of *Bullia digitalis* (×850).

Brown *et al.* 1991). *Bullia* seldom burrows deeply and burial is normally shallow enough for the whelk's short siphon to extrude into the overlying water (Trueman & Brown 1992); sufficient light thus penetrates the sand to support algal growth (see Brown & McLachlan 1990).

The most common alga associated with *Bullia* in South Africa is not strictly epiphytic but is a green, filamentous, boring chlorophyte, the morphology of which corresponds to that of *Eugomontia sacculata* Kornm. (Harris *et al.* 1986). It occurs in the shells of both *Bullia digitalis* (Harris *et al.* 1986) and *B. rhodostoma* (Whittington-Jones 1992) but other species of *Bullia* have not been investigated in this regard. This alga bores into the outer prismatic layer of the shell, the filaments ramifying throughout that layer's crystalline matrix (Figure 1). The presence of this alga on *Bullia digitalis* is sometimes visually obscured by the brilliant colours of the shell. The alga appears to be important in the nutrition of the whelk (da Silva & Brown 1984; Harris *et al.* 1986), supplementing its essentially carnivorous diet, although whether the animal is an obligate omnivore is unknown.

3. Protozoa

Ciliates may sometimes be found in small numbers associated with irregularities in the shell and particularly in pits made by the boring sponge *Clione* (see below). The only species clearly having a relationship with the whelk, however, is a peridinian ciliate which attaches itself in rows to the soft parts of the animal and particularly to the tentacles of *Bullia digitalis* (Figure 2). Its presence is reported here for the first time but it has been noted on frequent occasions,

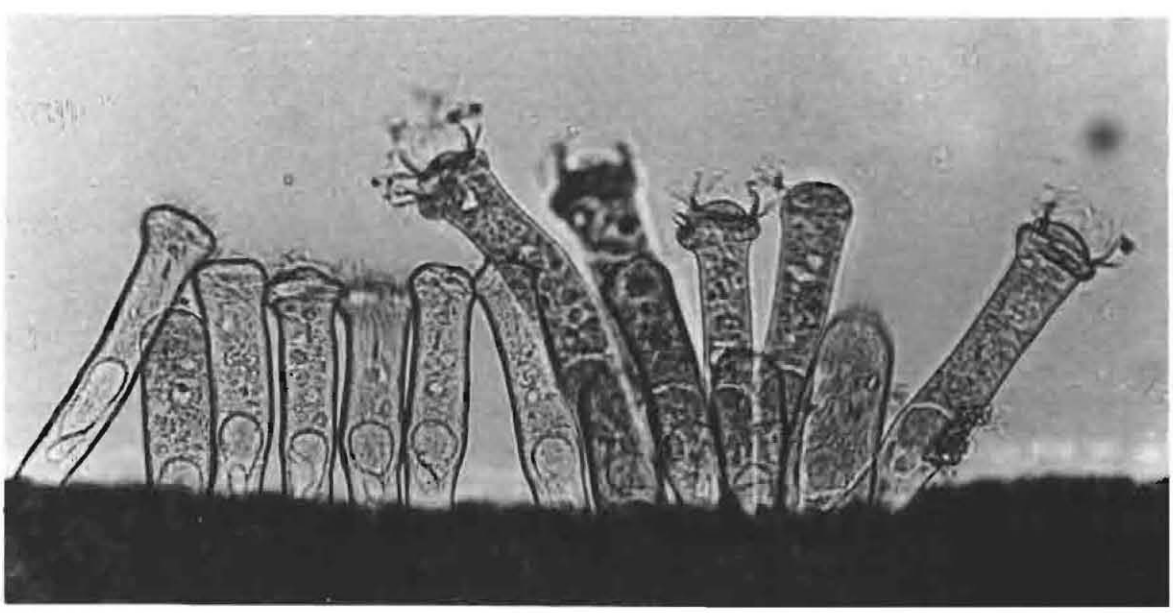

Figure 2 Peridinian ciliates attached to a tentacle of *Bullia digitalis*.

over a number of years, on Cape Peninsula whelks. Its presence on *B. digitalis* from eastern Cape beaches is confirmed by A.N. Hodgson (pers. comm.). An occasional ciliate discovered in the gut has probably been inadvertently ingested by the whelk.

4. Porifera

A boring sponge, *Clione* sp., is common in the shells of living *Bullia digitalis* and *B. rhodostoma*, and apparently less so in *B. laevissima* and *B. pura*. It has not been observed in *B. tenuis*. The sponge is found in pits up to 0,5 mm across and slightly less than that in depth (Figure 3). It tends to be much more common on the upper surface than on the lower surface of the shell. The sponges themselves harbour a protozoan fauna, notably of ciliates, together with an occasional, minute nematode worm. It is possible that, where the sponge is abundant (up to five per 10 mm^2 of shell surface), its excavations may weaken the shell of the whelk, making it more accessible to predatory fishes and crabs.

5. Cnidaria: Hydrozoa

Hydroids have not been found associated with any intertidal species of *Bullia*, presumably because they are susceptible to sand abrasion or cannot tolerate burial; it may be noted that hydroids are also extremely rare on South African rocky shores inundated by sand (Brown *et al.* 1991). However, subtidal species of *Bullia*, which tend not to bury themselves completely in the sand, sometimes have hydroids growing on the upper surface of the shell. Millard (1966) reported abundant colonies of the hydroid *Leuchartiara octona* (Fleming) (Pandeidae) growing on the shells of living *Bullia annulata* and several unidentified species have been found on the dorsal surfaces of the shells of subtidal *B. laevissima* (Brown, unpubl.). Brooks & Mariscal (1985) studied the protection afforded to hermit crabs by hydroid-colonized shells and it seems possible that similar protection from predators may in some cases be afforded to the original gastropod inhabitants of such shells.

6. Platyhelminthes: Trematoda

The common internal parasites of *Bullia* are larval digenean trematodes. Reimer (1976) described a metacercaria, *Gonocercella indica* from the Indian whelk, *Bullia melanoides*, while Brown (1971) noted the presence of larval digeneans in *B. digitalis* from the west coast of South Africa. Subsequently, Webb (1985) presented a thesis dealing with the parasites of *B. digitalis*, *B. rhodostoma* and *B. pura* in the western Cape Province of South Africa. He described digeneans of the families Zoogonidae, Ptychogonimidae, Microphallidae, Azygiidae and Allocreadoidea, all apparently new species, from *Bullia digitalis* and three species of metacercariae of the families Ptychogonimidae and Azygiidae from *Bullia pura*. The latter three species are not dealt with here, as their status is uncertain. A detailed study of *Cercaria hastata* Webb (Family Microphallidae) from *Bullia digitalis* has already been published (Webb 1991) and includes information on the prevalence of infection and possible effects on the host. It is probable that the cirolanid isopod *Eurydice longicornis* Studer is the second intermediate host of *Cercaria hastata*. The final host is almost certainly a vertebrate.

The following two species belong to the superfamily Allocreadoidea. This, in fact, tells one very little: La Rue (1957), in assigning the families Gorgoderidae, Gyliauchenidae, Troglotrematidae and Zoogonidae to this superfamily, expected that on further investigation their taxonomic status would require revision.

Cercaria bulliae (*Cercaria Y* of Webb's thesis), also from *Bullia digitalis*, is a tailless, pharyngeate, distome Xiphidiocercaria. No description of it has yet been published. Its sporocysts form a yellowish mass concentrated in the tissues

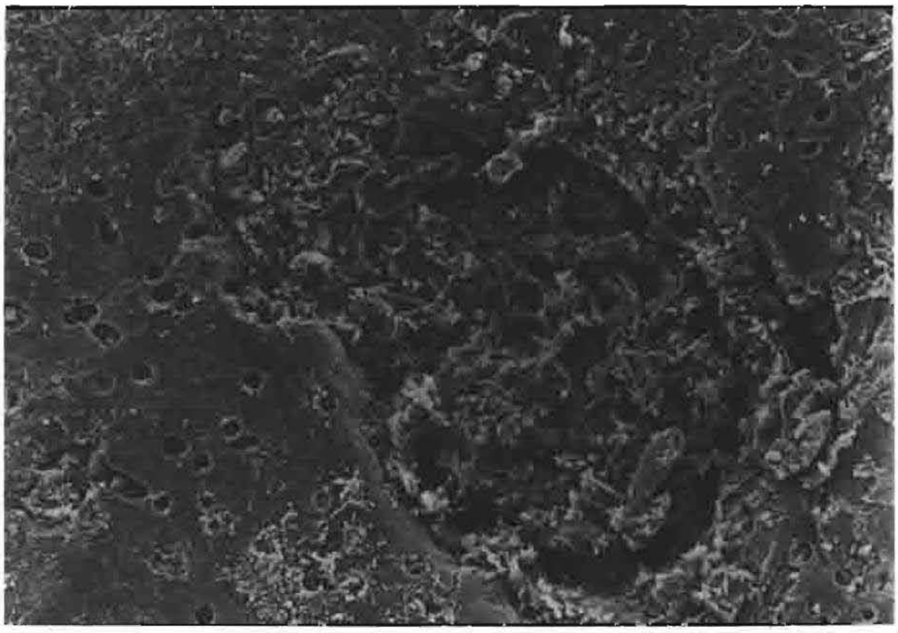

Figure 3 Cavity in the shell of *Bullia digitalis*, left by the boring sponge *Clione* sp. The smaller holes were made by the alga *Eugomontia sacculata* (×600).

immediately surrounding the whelk's alimentary canal. Individual (daughter) sporocysts are opaque and spherical or ellipsoid. They have no birth pore. Light microscopy failed to distinguish tegumental structures and intravital stains revealed no contained germinal material. All cercariae in each sporocyst were at the same stage of development. The sporocyst failed to exhibit any signs of mobility and no excretory structures were discernible. Mean sporocyst length was 511 μm, with a range of 364–607 μm (n = 10). Mean width was 427 μm, with a range of 340–535 μm. The sporocysts held, on average, five cercariae, the minimum being three, the maximum eight.

The tegument of the cercaria (Figure 4) is covered with backward-facing, triangular spines, each about 2 μm long, arranged in staggered transverse rows. The distance between rows is about 4 μm. The stylet is conical and very stout. It flares slightly at the base, which has a serrated circumference and is embedded in the sucker musculature. There is a shoulder half-way along the stylet, which then proceeds to a sharp point. The stylet is held parallel to the long axis of the body. On either side of the point lie openings of the penetration glands. The subterminal oral sucker is longer than broad. There is a short prepharynx, followed by an oval pharynx, which is about half the length of the oral sucker. The oesophagus runs back to the ventral sucker, where it bifurcates to form two short caecae.

There are four pairs of penetration glands, which start just anterior to the ventral sucker and lead forward in two bundles of ducts. The ducts thicken just behind the oral sucker, then each bundle bifurcates. The oval orifices of the penetration glands appear longitudinally divided; this division is more marked when nile blue sulphate is applied. The inner pair of glands stain less heavily than the outer pair. (Nile blue is toxic to the cercariae.)

The cercaria has some 25 gland cells distributed throughout the body. Nile blue sulphate renders these purple. The muscular ventral sucker is broader than long and is about twice the size of the oral sucker. The bladder, an irregular but entire bag with a thick, muscular wall, lies behind the ventral sucker. There are seven pairs of flame cells but the excretory ducts were not visible. Four pairs of flame cells occupy positions anterior to the ventral sucker; three pairs lie posterior to it. The excretory pore is terminal. Mean cercarial length (n = 10) is 689 μm, with a range of 446–859 μm. Mean width is 56 μm, with a range of 49–73 μm.

Prevalence of infection, estimated from the entire population range of *Bullia digitalis*, by *Cercaria bulliae* was 1,18% on Fish Hoek beach and 3,04% at Mnandi (both in

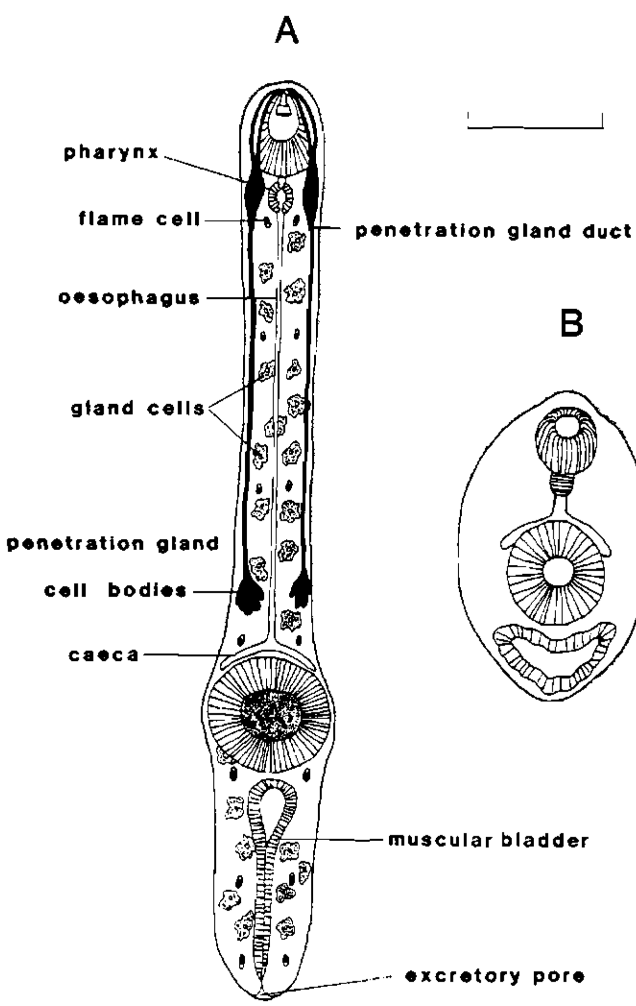

Figure 4 *Cercaria bulliae*. A. extended; B. contracted. Scale bar = 100 μm.

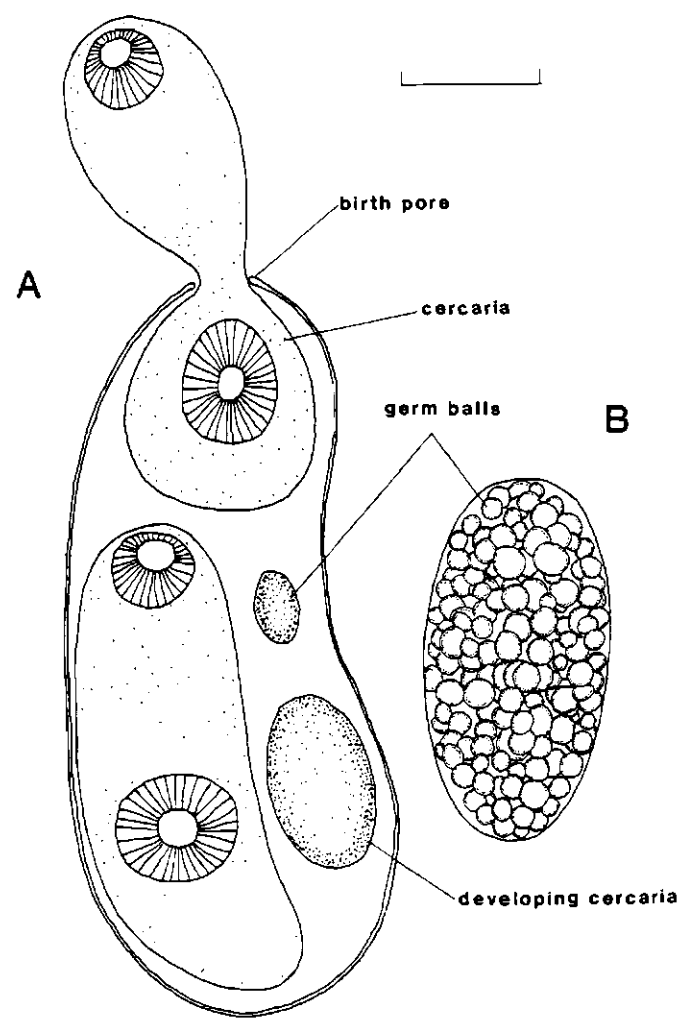

Figure 5 *Cercaria hapax*. A. escaping from a mature sporocyst; B. an immature sporocyst. Scale bar = 100 μm.

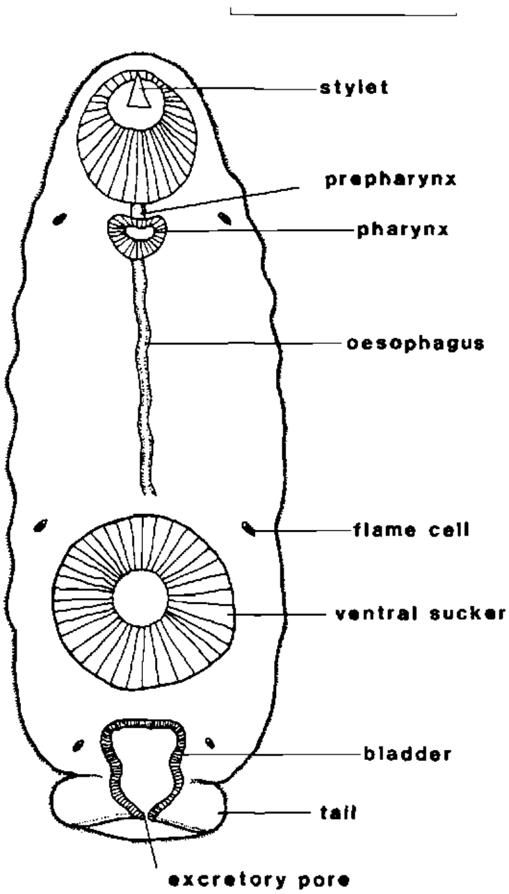

Figure 6 *Cercaria hapax* in ventral view, showing internal structure. Scale bar = 100 μm.

False Bay), but only 0,7% at Hout Bay, on the Cape Peninsula's west coast (Webb 1985). Although the cercaria is highly contractile and capable of vigorous movement, often using the ventral sucker as a holdfast, it cannot swim. Thus the second intermediate host would have to approach a *Bullia* closely for transmission to occur. The presence of a stylet and penetration glands suggests an arthropod intermediate host. On the other hand, the observed ability of the cercaria to encyst without use of its penetration apparatus could imply that the life-cycle is telescoped, the parasite going directly to its final host, probably a predatory fish.

Cercaria hapax (Family Zoogonidae) (*Cercaria X* of Webb's thesis) was found only once during the examination of over 3 000 *Bullia digitalis*, the infected individual coming from Melkbosstrand, on South Africa's west coast. Sporocysts of *Cercaria hapax* (Figure 5) were found in the tissue underlying the columnar epithelium of the whelk's gut. This sac-like sporocyst is covered by a smooth tegument and it exhibits a birth pore. Mean length was 551 μm, with a range of 388–778 μm, while the mean width was 227 μm, with a range of 194–267 μm (n = 10). Each sporocyst usually contained only one, and at most two, mature cercariae, others being in various states of immaturity.

The cercaria of *C. hapax* (Figures 6 & 7) has a distinctive tail, developed as a holdfast. This has a sucker-like appearance but during contortions of the body it may be reduced or elongated into a pointed termination to the body. The ellipsoidal oral sucker opens subterminally (Figures 6 & 7B) and the base of the stylet is embedded in its musculature. There are no penetration glands associated with the simple, conical stylet, which is held at 45° to the long axis of the body (Figure 5A). The tegument is heavily armed with spines; both the tegument and its spines take up neutral red strongly, with the production of much stained mucus. There are three widely-spaced pairs of flame cells. The mean length of the cercaria is 348 μm (200–648 μm), mean width 120 μm (40,5–162 μm) (n = 10). The cercaria does not swim but the body is highly contractile and variable in shape. The tail holdfast is often employed in locomotion but neither the oral nor ventral suckers are used.

The cercaria bears a strong resemblance to *Zoogonoides viviparus* (Dawes 1946) and may very possibly be assigned to the same genus. Previous zoogonid infestations have been reported from South Africa by Fantham (1938) and Bray (1985), the former in the Hottentot fish *Spondyliosoma blochii*. The stylet of *Cercaria hapax* suggests an arthropod as second intermediate host but the absence of penetration glands and the profuse mucus production from the tegument's cystogenous glands may imply encystment and ingestion directly by a final, vertebrate host.

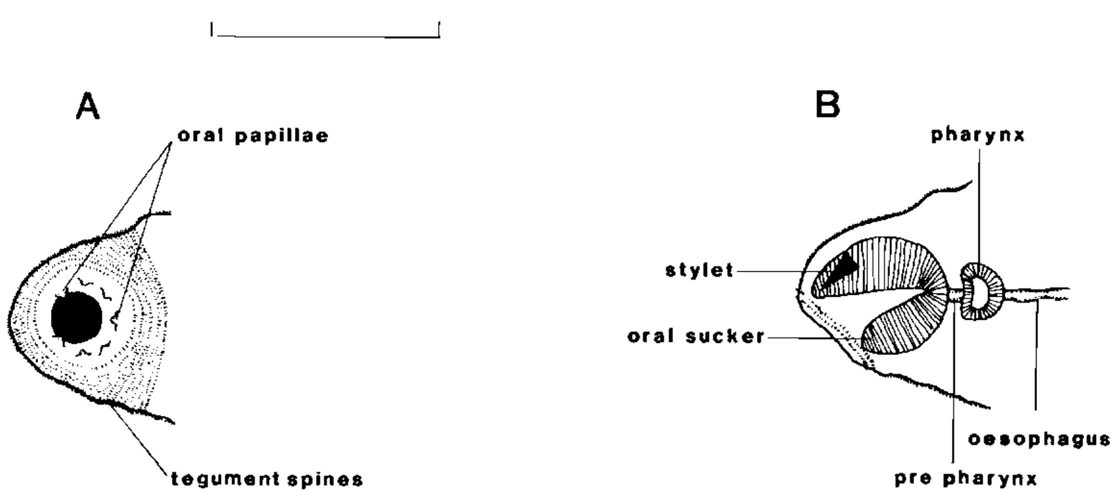

Figure 7 *Cercaria hapax*. A. external features of anterior end; B. sagittal section of anterior end. Scale bar = 100μm.

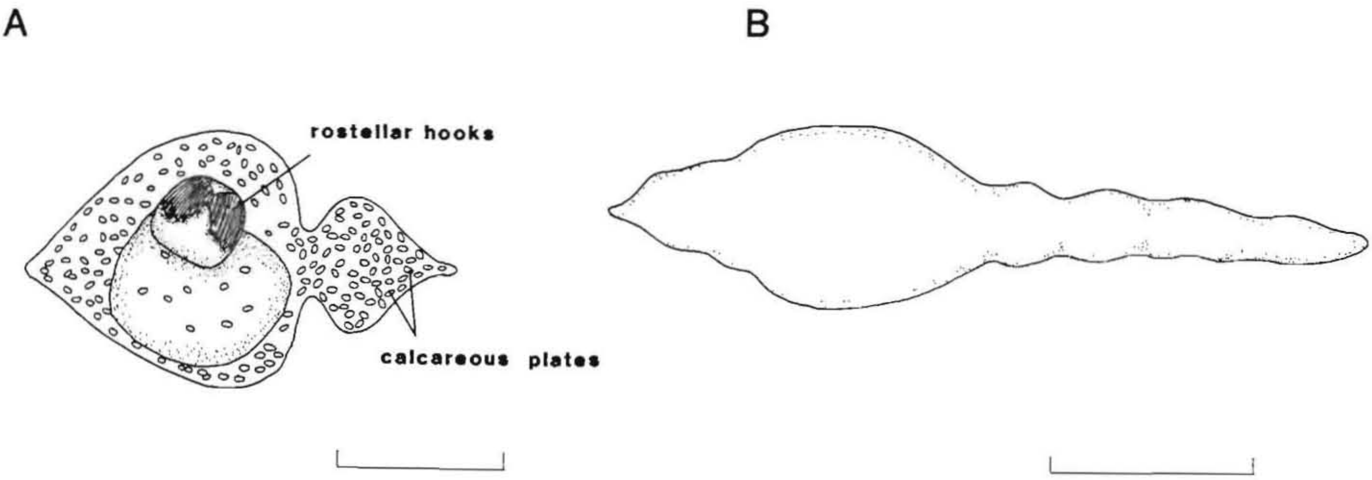

Figure 8 *Echinobothrium* cyst. A. freshly removed from a *Bullia digitalis*; B. after one hour. Scale bars = 400 μm.

Compared with *Bullia digitalis*, Webb (1985) found trematode parasites to be uncommon in *Bullia rhodostoma* from western Cape beaches and Whittington-Jones (1992) reports them as being rare in populations of the same species in the eastern Cape.

7. Platyhelminthes: Cestoda

Anantaraman (1963) described a cysticercoid larva of *Echinobothrium* sp. (Order Diphyllidea) from the Indian whelk *Bullia melanoides* and gave an estimate of its prevalence, while Reimer (1975) described the cysticercoids of *Echinobothrium lateroporum* Subhapradha and *Polypocephalus* sp. (Order Trypanorhyncha), from the same species of *Bullia*. Webb (1985) discovered a cysticercoid of *Echinobothrium* sp. in both *Bullia digitalis* and *B. pura* from Mnandi beach in False Bay, near Cape Town.

The cysts of this *Echinobothrium* sp. lie quiescently in the host viscera and are often obscured by tissue. Up to three cysts were found per host but more usually there was only one. The cyst is a pale spheroid (Figure 8A) containing a distinctive formation of pink to red rostellar hooks belonging to a single, non-inverted larva. When dissected out, the cyst elongates, appearing vermiform at maximum extension (Figure 8B). Mean length of the cysticercoid was 954 μm (769–1134 μm), mean width 432 μm (364 to 527 μm) (n = 9).

The cysticercoid wall comprises a thick, muscular inner layer and a thin tegument. The host envelops this with an epithelial layer several cells thick. Oval, plate-like, calcareous bodies lie densely packed in the cyst fluid. Each body has bevelled edges and is dotted with small nodules on the faces. At the base of the scolex, two bothria arise and wrap, leaf-like, around the neck. They are capable of an undulating, wave-like motion and are covered over the outer surface and edges with small spines. The bothria contain numerous flame cells. The neck leads to an undeveloped strobilus. The crown of large rostellar hooks (Figure 9) is divided into two similar groups, each numbering between 19 and 22. Two groups of five to six small hooks occur between them. The large hooks alternate in length and each has a flat, mattock-like proximal anchor. Small ones either taper to a point or broaden to a flat or curved proximal anchor. The hooks are set on a curved, muscular pad. Two excretory ducts arise indistinctly in the neck and run almost to the scolex before recurving and becoming indistinct near their origin.

Of the 150 individuals of *Bullia pura* examined from Mnandi beach, 63 contained cysticercoids, giving a prevalence of 42%. On the other hand, only two individuals of *B. digitalis* were infested out of a total of 494, a prevalence of 0,4%. Adults of *Echinobothrium* species have been found in many selachian fishes, including rays (see Williams & Campbell 1980) and it seems probable that the *Echinobothrium* from Mnandi has such a final host. This report of the genus from South Africa fills a void between India and the North Atlantic and suggests that *Echinobothrium* has a world-wide distribution.

Nematoda

An occasional nematode worm has been found in the alimentary canals of both *Bullia digitalis* (Brown 1971) and *B. rhodostoma* (Whittington-Jones 1992). Whether these are parasitic or have simply been ingested by the whelk is unclear, although Whittington-Jones (1992) felt that some of those he observed were actively parasitizing the host. In any case they appear to be rare and were not found at all by

Figure 9 Cysticercoid of *Echinobothrium* sp.: details of hooks.

Webb (1985). Tiny nematodes are also sometimes associated with the boring sponge, *Clione* (Brown, unpub.).

9. Rotifera

Rotifers are quite commonly found attached to the soft parts, and less commonly to the edge of shell, of *Bullia digitalis* and *Bullia pura* (Brown & Webb 1986). Several have also been found attached to *B. laevissima* and *B. annulata* (Brown, unpub.). Rotifers are also not uncommon in the surrounding sand (Brown & McLachlan 1990) and may, perhaps, inadvertently attach themselves to a whelk on occasion, instead of to a sand grain.

10. Mollusca: Gastropoda

A number of individuals of *B. laevissima*, dredged in Algoa Bay, were found to have numerous egg cases of a marginellid prosobranch attached to their shells (Brown 1982). Each case contained a single embryo, almost ready to hatch. *B. laevissima* tend not to bury themselves completely (Brown 1961) and thus present a relatively stable substratum for the attachment of egg cases of other species.

11. Crustacea: Cirripedia

Barnacles are certainly not commonly associated with *Bullia* shells, either because most species, at least, cannot tolerate burial (Brown *et al.* 1991) or because the larvae tend to be very discriminating, settling only in areas that have previously been colonized by the same species. Nevertheless, once established, the barnacle may flourish indefinitely. It must certainly have a markedly negative effect on the burrowing performance of the whelk.

12. Crustacea: Anomura

Bullia shells are in much demand by psammophilic hermit crabs. Indeed, in some localities along the South African coast, such as the beach at Uilkraalsmond (Brown, unpub.), *Bullia* shells provide the only suitable accommodation for a vast population of these Crustacea. Competition among hermit crabs for gastropod shells is well documented (see Abrams 1987); less well known is aggressive behaviour on the part of the crab towards the living gastropod inhabiting the shell. Barnard (1963) observed a hermit crab and a living whelk inhabiting the same shell and Brown (unpub.) has observed a similar relationship between a *Diogenes brevirostris* and a *Bullia digitalis* at Uilkraalsmond.

Discussion and Conclusions

While Webb (1985) undertook a rigorous study of the parasites of *Bullia* in the western Cape Province of South Africa, no other populations of the genus have been accorded such investigation, either for parasites or for other associated organisms. Most observations have been casual and haphazard. Nevertheless, putting all the scattered evidence together, one is struck by the apparent total absence of external parasites infecting members of the genus and the fact that the body surfaces are also virtually free of bacteria. One might put this down to some noxious property of the skin or mucus were it not for the fact that peridinean ciliates and an occasional rotifer are found attached to the soft parts. These are clearly not parasitic, however. The possibility remains that the mucus has bacteriolytic activity.

The apparent absence of external parasites is not reflected in a paucity of internal parasites; infestation may be intense and a number of species, particularly of trematodes, may be present in a single individual. Not all species or populations are equally infected, however, and *B. rhodostoma* appears to be far less infested than *B. digitalis* (Webb 1985; Whittington-Jones 1992).

Sandy substrata present unstable environments, lacking geological diversity. A more stable surface, such as may be provided by a protruding rock, for example, thus presents a refuge to many organisms. The refuge is likely to be temporary only, however, with the possibility that the object will, sooner or later, be covered by sand. In such circumstances, the shells of subtidal *Bullia* species may present a unique opportunity for colonization, as in quiet water these animals tend not to bury themselves completely in the sand and rise quickly to the surface if sand covers them. Not only does current evidence show that such an opportunity is, in fact, exploited by epibiotic forms but that the shells may also be the recipients of the egg cases of other gastropod species. Even intertidal *Bullia* species, which do bury themselves completely, act as refuges for epiphytes, peridinian ciliates and other organisms which can tolerate repeated sand inundation.

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