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Swimming zooids: an unusual dispersal strategy in the ctenostome bryozoan, *Hislopia*

T. WOOD, P. ANURAKPONGSATORN & J. MAHUJCHARIYAWONG

A b s t r a c t : *Hislopia* is the genus of a common ctenostome bryozoan in fresh waters. Six species have been described, mostly from tropical regions of the world. A new species, not yet described, is now reported from two small reservoirs in Prachin Buri Province, east central Thailand. A unique feature of this species is the production of special lateral buds that project obliquely away from the substratum. As the buds develop, their connection to the parent zooid becomes narrow and fragile. A small, thumb-like projection appears at a point slightly proximal to the orifice. Once development of the new zooid is complete, its connection to the parent colony breaks and the zooid swims away propelled by the beating cilia of its extended lophophore. This nautizoid feeds as it swims, but the duration of its free existence is unknown. The thumb-like projection and the proximal end of the nautizoid both have adhesive properties and adhere easily to any solid surface. Upon settling, the thumb-like projection elongates rapidly, becoming a true adventitious bud. Preliminary data from laboratory-reared colonies suggest that the special nautizoid buds may form at any point around the margin of a parental zooid, even in the absence of a functioning polypide. As many as five nautizoids may develop simultaneously from a single zooid, and a parental zooid can produce both adventitious and nautizoid buds at the same time.

K e y w o r d s : Bryozoa, Ctenostomata, *Hislopia*, Thailand, dispersal, reproduction.

Introduction

Dispersal is essential to the survival of all species. It is probably the most important life history trait relating to species persistence and evolution (RONCE et al. 2001). All organisms have one or more specific strategies to expand their range and promote gene flow. For most animals this involves walking, swimming, or flying. Plants typically have seeds or spores adapted for transport by wind, water currents, or by animals. In freshwater bryozoans dispersal is normally achieved by the drifting of planktonic larvae or by the release of tiny dormant statoblasts.

However, one bryozoan species in Thailand has developed a means of dispersal which we believe to be unique: the sessile colony produces actively swimming zooids. The bryozoan is an undescribed member of the ctenostome genus *Hislopia* CARTER 1858. *Hislopia* species occur worldwide in tropical and subtropical fresh waters. Colonies are flat, encrusting, and uncalcified, with uniserial, branching lines of zooids spreading across the substratum. Seven species are recognized on the basis of features such as the

degree of branching and the dimensional proportions of the zooid, stomach and gizzard (D'HONDT 1983). The taxonomic reliability of these features has never been seriously questioned, and beyond this shaky framework very little is known about the entire group.

In the new Thai species zooids are relatively large and elongate, tapering at each end. One of every three or four zooids in series generates a lateral branch which grows nearly perpendicular to the first. The lophophore of each zooid bears 13 tentacles. However, it is the swimming zooids, or "nautizooids," that present the most unusual feature of the species. This paper describes the formation and behavior of these nautizooids. The new *Hislopia* species itself will be more fully described and named in a separate paper.

Materials and methods

The bryozoans were collected during March, 2005 from two irrigation reservoirs in Prachin Buri Province, east central Thailand: Huay Chan Reservoir (13°59.2'N, 102°26.8'E) and Tah Krabak Reservoir (13°58.6'N, 102°15.4'E). The colonies occurred on wood, plastic, and stone substrata in water less than one meter deep. Taken to Bangkok for closer study, pieces of plastic substratum with their attached bryozoans were glued inside inverted plastic petri dishes and suspended in a fish culture pond on the Bangkok campus of Kasetsart University. Eventually the colonies grew onto the dishes and could be maintained in the laboratory using the methods of WOOD (1996).

Results

As in several other *Hislopia* species, the first adventitious bud of a new zooid is normally the distal one, advancing the serial progression of zooids in a straight line. These buds are entirely recumbent, adhering to the substratum throughout their length. In rapidly growing colonies a new bud often appears before the parental zooid is fully formed (Fig. 1). Lateral buds may develop later, normally at a specific location near the wide midpoint of the zooid. A single zooid may produce one or (rarely) two lateral buds.

By contrast, nautizooid buds seem to occur in no particular location along the margin of the parental zooid. Unlike the slender adventitious buds, the nautizooid buds are bulbous (Fig. 2). They grow not along the substratum but obliquely away from it. In laboratory culture the young polypides develop rapidly, becoming fully functional within three days at 27° C (Fig. 3, 5). In laboratory culture, an adventitious bud normally requires one or two days longer than this. A single zooid may produce up to five nautizooid buds simultaneously (Fig 4). Nautizooids will even develop from aberrant parental zooids in which a feeding polypide has never formed.

Detachment of the nautizooid from the parental colony is a spontaneous event that requires no external action. However, any disturbance to a large colony, such as placing it gently in a dish under the microscope, is usually enough to launch dozens of nautizooids freely into the water (Fig 6). With lophophores extended the free-swimming zooids travel at a speed of about 0.8 mm per second.

Morphologically the nautizooid is very similar to other feeding zooids within the bryozoan colony. The polypides are essentially identical in size, digestive anatomy, and number of tentacles. However, the first adventitious bud of the nautizooid appears not at the

distal end, but at a point just proximal and ventral to the orifice. Its adhesive properties enable this finger-like projection to adhere to any firm surface. A second adhesive zone develops at the proximal end where the nautizoid was originally attached to the parental zooid.

When a swimming nautizoid encounters a firm substratum the lophophore flattens itself against the surface, tentacles splayed, cilia continuing to beat. It may release this hold by quickly withdrawing the lophophore, then drifting away and re-deploying the ciliated tentacles. Alternately, when the lophophore is pressed against the substrate with beating cilia, the nautizoid may flex the region just below the lophophore to bring the two adhesive pads into direct contact with the substratum. This action amounts to permanent settling. Within a few hours the adventitious bud lengthens along the substratum, solidifying its hold and eventually producing a new feeding zooid.

Discussion

The most common freshwater ctenostome in Thailand *Hislopia mayalensis*, routinely produces planktotrophic cyphonautes larvae in abundance throughout the year. These larvae are weak swimmers, and the evidence so far indicates that initial mortality is high. The duration of the larval phase has not yet been determined, but the larvae normally grow to nearly 15 times their original size before they settle.

In terms of dispersal, a nautizoid of this new *Hislopia* species is the functional equivalent of a planktotrophic cyphonautes larva. Unlike sexually produced larvae, however, nautizoids are formed from asexual buds of the parent colony and are therefore virtual clones. Also, nautizoids seem prepared to settle at any time, while *Hislopia* larvae have an obligate period of growth and development before they are capable of settling successfully.

Cyphonautes larvae in the new *Hislopia* species have not yet been observed. However, a colony occupying 1 cm³ of substratum at Huay Chan Reservoir is capable of releasing at least 10-14 nautizoids per day. Survivorship in the laboratory is high among those zooids settling on suitable substrate. When protected from predation, nearly all are successful in forming colonies of 5 zooids or more.

So far, the new *Hislopia* species has been found only in the still, shallow water of two reservoirs in Thailand. The more common species, *H. malayensis*, occurs in a wide range of habitats, especially flowing waters. It is tempting to speculate that nautizoids represent an adaptation to habitats where there is little opportunity for passive dispersal on water currents.

There are no published reports of free-swimming zooids in any other bryozoan species. However, BUSHNELL (pers. com.) reported observing leptoblast ancestrulae of the phylactolaemate *Plumatella casmiana* propelled through the water in a deliberate fashion by the cilia of their lophophores. Leptoblasts are the weakly buoyant statoblasts found only in this species. They germinate almost immediately upon release from the colony (WOOD 1989). Since this method of self-locomotion has apparently not been noticed by other workers, it may occur only under unusual circumstances. However, whether or not leptoblast zooids are self-propelled, they would still function somewhat like nautizoids by quickly expanding the size and local reach of the population through asexual propagation.

The discovery of nautizooids in the new *Hislopia* species raises many questions. Under what conditions are they produced? How do they orient in their environment? What is the duration of their free existence, and what is their practical range? Do they exercise any selection of their final substratum? It is expected that future studies will clarify the ecology of nautizooids and their role in the life cycle of the species.

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Author's addresses: Timothy S. WOOD
Department of Biological Sciences
Wright State University
3640 Colonel Glenn Highway
Dayton, OH 45435 USA
E-mail: tim.wood@wright.edu

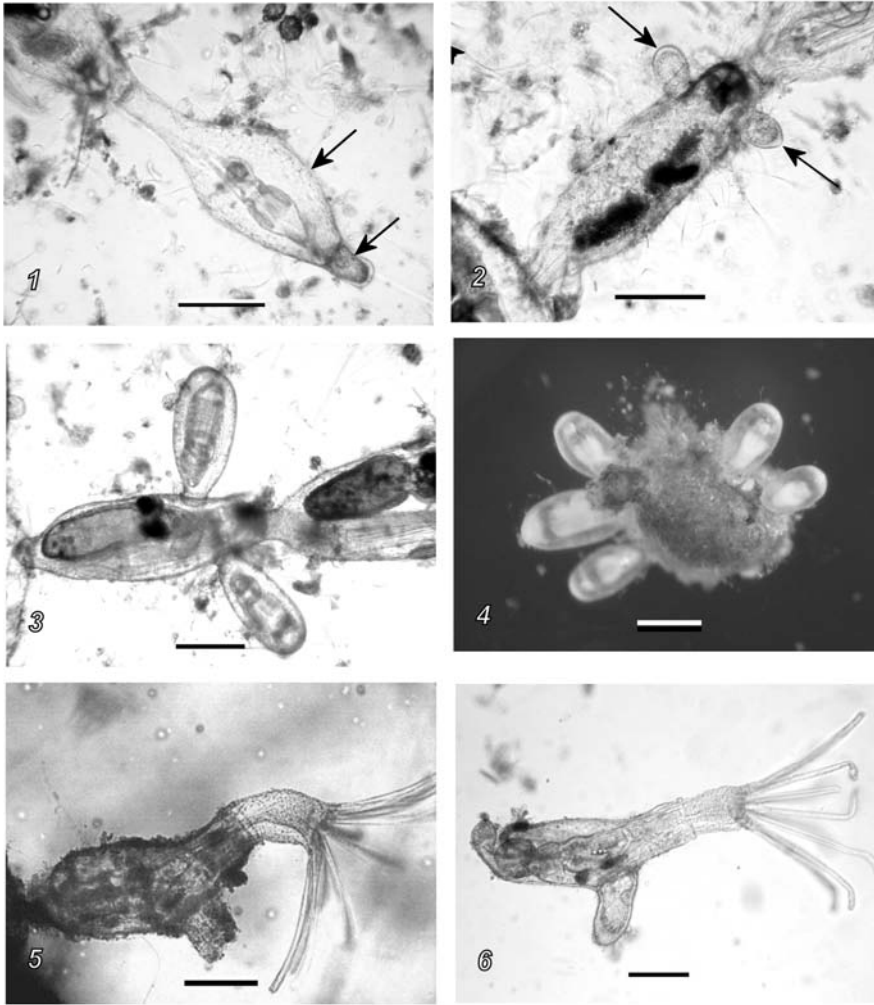


Fig. 1-6: (1) Two normal, developing adventitious buds in series (arrows) of the undescribed Thai *Hislopia*, Scale bar = 0.25 mm. (2) *Hislopia* zooid with two young nautizoid buds (arrows). Scale bar = 0.25 mm. (3) *Hislopia* zooid with two nautizoid buds almost ready for release. Scale bar = 0.25 mm. (4) Single *Hislopia* zooid dissected from a colony, with five nautizoid buds distributed in seemingly random locations around the margin. Scale bar = 0.25 mm. (5) Nautizoid bud, already feeding, ready to break away from the colony. Scale bar = 0.25 mm. (6) Free-swimming nautizoid. Scale bar = 0.25 mm.

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Autor(en)/Author(s): Wood Timothy S., Anurakpongsatorn P., Mahujchariyawong J.

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