

## Statoblast morphology and systematics of the freshwater bryozoan *Hyalinella orbisperma* (Kellicott, 1882)

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The freshwater bryozoan *Hyalinella orbisperma* (Ectoprocta: Phylactolaemata), previously known only from Michigan, is added to the list of Canadian fauna from a specimen collected at Georgian Bay, Ontario. Floatoblasts match the appearance of those described from Michigan. The sessoblast of this species is recorded and illustrated for the first time. The case for other species with sessoblasts in the genus *Hyalinella* is extremely weak. Scanning electron microscopy of the floatoblast and sessoblast reveals a raised reticulation with interstitial tubercles covering the capsule periblast, suggesting a close phylogenetic relationship with certain *Plumatella* species. It is proposed that *H. orbisperma* be reassigned to the genus *Plumatella*.

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Le bryozoaire dulcicole *Hyalinella orbisperma* (Ectoprocta : Phylactolaemata), rencontré à ce jour seulement au Michigan, vient s'ajouter à la faune canadienne, puisqu'un spécimen a été trouvé dans la Baie Georgienne en Ontario. Les flotoblastes ont le même aspect que ceux qui ont été décrits chez les spécimens du Michigan. On trouvera ici une description illustrée inédite du sessoblaste de cette espèce. Les preuves de l'existence d'autres espèces à sessoblastes chez le genre *Hyalinella* sont très peu convaincantes. Le microscope électronique à balayage a permis de voir la réticulation en relief du flotoblaste et du sessoblaste; des tubercules interstitiels couvrent le périblaste capsulaire, ce qui reflète probablement un lien phylogénétique étroit avec certaines espèces de *Plumatella*. Nous croyons qu'*H. orbisperma* devrait être transféré au genre *Plumatella*.

[Traduit par la rédaction]

### Introduction

Like many aquatic invertebrates, the bryozoans (Ectoprocta) offer few reliable features by which species may be distinguished. For the class Phylactolaemata, taxonomists rely heavily on the morphology of encapsulated buds (statoblasts), which are a unique characteristic of this exclusively freshwater group of bryozoans. Statoblasts are sclerotized, dormant structures produced asexually by all phylactolaemate species, and can survive freezing, desiccation, and other environmental stresses (Bushnell and Rao 1974). A statoblast consists of a yolky germinal mass enclosed by two chitinous valves; the valves form an inner capsule surrounded by an outer periblast. Most bryozoans produce buoyant statoblasts (floatoblasts) with a peripheral annulus of gas-filled cells; they may also produce adherent, nonfloating statoblasts (sessoblasts), which are cemented through the colony wall to a firm substrate. The annulus of a sessoblast is reduced to a thin lamella. The surface patterning of the statoblast is often species-specific (Mundy 1980). These and other morphological characteristics of statoblasts are considered to be important diagnostic criteria in the identification of phylactolaemate bryozoan species, and have been used to elucidate their phylogenetic relationships (Lacourt 1968; Mukai 1990; Oda and Mukai 1985; Smith 1988; Toriumi 1956; Wood 1979).

*Hyalinella orbisperma* (Kellicott) (Phylactolaemata: Plumatellidae) is a freshwater bryozoan previously known only from

a few scattered ponds in Michigan (Bushnell 1965; Kellicott 1882). Kellicott (1882) provided a limited description of the new form, which he tentatively designated *Plumatella orbisperma*, and was undecided as to whether it represented a new species or simply a variety of either "*Plumatella arethusa*" (= *P. repens* (Linnaeus)) or "*Plumatella vesicularis*" (= *Hyalinella punctata* (Hancock)). In a detailed study of the Michigan freshwater bryozoans, Bushnell (1965) distinguished *P. orbisperma* from other *Plumatella* species primarily by the shape of the floatoblast, lack of a sessoblast, and certain colonial features, and reassigned the species to the genus *Hyalinella*. Lacourt (1968), apparently unaware of Bushnell's study, doubted the validity of *Hyalinella* (*Plumatella*) *orbisperma*, since the original description by Kellicott (1882) was inadequate and no specimens were known to exist. However, from an examination of Bushnell's specimens, Wiebach (1973) considered *H. orbisperma* to be a valid species.

Recently, a review of bryozoans in the collection of the Royal Ontario Museum (ROM, Toronto, Ont.) revealed *H. orbisperma* from a specimen misidentified as *Plumatella fungosa* (Pallas), collected by A. G. Huntsman (date unknown) at Go Home Lake, Georgian Bay, Ontario. The species is thus added to the list of Canadian fauna. Based on other specimens obtained by Huntsman from the same location, the Georgian Bay specimen was probably collected around 1910. The specimen matches Bushnell's (1965) description quite closely, except for the presence of sessoblasts. In this study, the fine surface structure of both types of statoblasts in the Georgian Bay specimen was examined to evaluate the systematic position of *H. orbisperma* (Kellicott).

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## Materials and methods

The Georgian Bay *Hyalinella orbisperma* specimen (ROM No. K-13) is preserved in alcohol and consists of a small amount of fragmented colony on unidentified plant material. Statoblasts were examined and photographed in a Philips 500 scanning electron microscope. To conserve material for future examination, only a small number of statoblasts (6 floatoblasts and 3 sessoblasts) were extracted from the specimen. Prior to scanning electron microscopy (SEM) the statoblasts were dehydrated in an acetone series, subjected to critical-point drying with carbon dioxide (to prevent distortion of the capsule), and then sputter-coated in gold.

For comparative study, a specimen of *Hyalinella vaihiraie* was obtained from the Rogick collection (specimen No. 1) at the United States National Museum (USNM), and the statoblasts were examined following the procedure given above.

## Results and discussion

### Colony description of *Hyalinella orbisperma*

The Georgian Bay colony is recumbent and dichotomously branched. The ectocyst (in the preserved condition) is soft, translucent, swollen, without encrustation, and lacking the white spots that are often observed in *H. punctata*. Septation, keeling, and emargination are absent. Zooids are arranged both linearly and in clusters of 2–7 polypides. The polypide orifices are oriented vertically to the substrate. The polypides are retracted as a result of poor fixation, making tentacle counts impossible. Each zooid may contain 1 or 2 sessoblasts and an aggregation of 10–20 floatoblasts.

### Floatoblast morphology

The floatoblasts of the Georgian Bay specimen are circular in outline, or nearly so (mean length to width ratio = 1.11), biconvex, and generally symmetrical in lateral view, and have a thin annulus which widens slightly at the poles (Fig. 1). The ventral (deutoplasmic) capsule is pointedly convex, as was described for Michigan specimens (Bushnell 1965).

The floatoblast dimensions of the Georgian Bay specimen are slightly smaller than those given by Kellicott (1882) and Bushnell (1965), but the length to width ratios compare favorably (Table 1). White (1915) provides the only published records of bryozoans from Georgian Bay and briefly describes specimens identified as *P. fungosa* collected from pond weeds (*Pontederia* sp.). These had round statoblasts with a length to width ratio of 1.2, and may actually have been *H. orbisperma*.

Scanning electron microscopy of the floatoblast reveals a raised hexagonal reticulation on both valves which does not extend onto the annulus (Figs. 1, 2). A similar reticulation was illustrated in SEM photographs of *H. orbisperma* by Bushnell and Rao (1979) and Pennak (1989, p. 276). Prominent tubercles occur along the region where annulus and fenestra meet (Fig. 1); they become much less distinct toward the center of the fenestra and are absent from the rest of the annulus. A median cord between floatoblast valves is lacking, and the suture line is slightly serrated. The valves have begun to separate (Fig. 3), possibly due to the specimen's prolonged storage in alcohol.

The floatoblasts of *H. orbisperma* and *H. punctata* differ greatly in shape and surface detail. The length to width ratios reported for *H. orbisperma* floatoblasts (1.07–1.11; Table 1) do not overlap those reported for *H. punctata*, which vary from 1.31 to 1.77 (Massard and Geimer 1991). Bushnell (1965) noted that the larger, broader floatoblasts of *H. punctata* have a proportionately greater float area than the smaller, rounder floatoblasts of *H. orbisperma*. In the Georgian Bay

TABLE 1. Dimensions ( $\mu\text{m}$ ) of floatoblast of *Hyalinella orbisperma*

	This study	Bushnell 1965	Kellicott 1882
No. of measurements	6	156	—
Total length	320–336 (332)	300–370 (340)	343
Total width	288–304 (300)	280–350 (310)	320
Mean L/W	1.11	1.08	1.07
Dorsal fenestra			
Length	192–240 (213)	225	
Width	192–208 (203)	215	
L/W	1.05	1.05	
Ventral fenestra			
Length	240–272 (257)	250	
Width	224–256 (232)	240	
L/W	1.11	1.04	

NOTE: Numbers in parentheses are mean values. L/W is the length to width ratio.

specimen, the maximum width of the annulus is less than 18% of the length of the floatoblast (Table 1). Bushnell (1965) also emphasized that although both floatoblast capsules of *H. punctata* are convex, they are not as inflated as those of *H. orbisperma*, and the ventral capsule is not pointed. In both species, the suture line between the floatoblast valves is serrated, but the discontinuous medial rib (a linear arrangement of sutural knobs) described for *H. punctata* (Bushnell and Rao 1979; Massard and Geimer 1991) is absent in *H. orbisperma*. Finally, the fenestra of *H. punctata* floatoblasts bears generally larger tubercles than that of *H. orbisperma*, without any raised reticulation (Bushnell and Rao 1979; Geimer and Massard 1986; Massard and Geimer 1991).

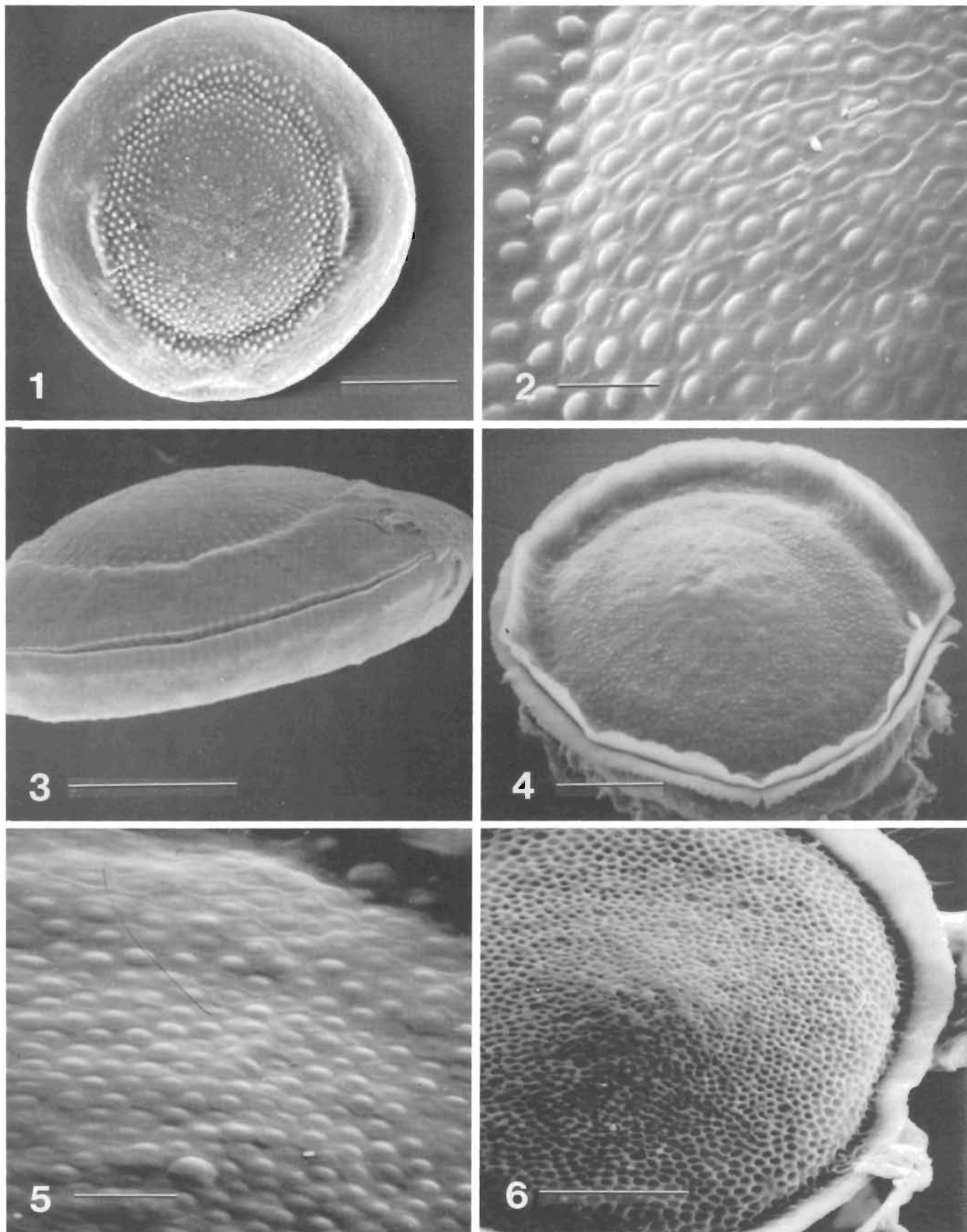
### Sessoblast morphology

The sessoblast of *H. orbisperma* (Fig. 4) is described here for the first time. It is circular in outline. The lengths and widths ( $\mu\text{m}$ ) of three sessoblasts are  $528 \times 410$ ,  $544 \times 430$ , and  $576 \times 448$ , with a mean length to width ratio of 1.2. The lamella is reticulated and its edges are serrate. Tubercles on the frontal periblast are small and low, disappearing toward the center but extending onto the lamella. Tubercles near the lamella are enclosed in a raised reticulation that is very faint but otherwise identical with that which appears on the floatoblast.

### The sessoblast problem in *Hyalinella*

The existence of a sessoblast in *Hyalinella* has been questioned, since Jullien's (1885) original description of the genus precluded sessoblasts. Toriumi (1956), noting the overlap in colonial morphology between specimens of *Plumatella* and *Hyalinella*, suggested that the difference between the two genera is the absence of a sessoblast in the latter. However, Lacourt (1968) expanded the definition of the genus *Hyalinella* to include certain species with sessoblasts. In his revision of *Hyalinella*, Wiebach (1973) accepted the validity of four species previously reported to produce sessoblasts: *H. punctata*, *H. africana* Wiebach, *H. indica* (Annandale), and *H. minuta* (Toriumi).

A brief review of each of these species reveals considerable uncertainty on the issue of sessoblasts in *Hyalinella*. Annandale (1915) found no sessoblasts in the type material of *H. indica*. Lacourt (1968) described sessoblasts from a specimen that he identified as *H. indica* (No. SMF-836 in the Senckenberg Museum, Frankfurt), but the same specimen is considered by Wiebach (1973) to be a species of *Plumatella*.



FIGS. 1–5. Scanning electron micrographs of *Hyalinella orbisperma* statoblasts. Fig. 1. Dorsal (cystigenic) surface of a floatoblast. Scale bar = 100  $\mu\text{m}$ . Fig. 2. Detail of the floatoblast surface, showing reticulation and tubercles. Scale bar = 20  $\mu\text{m}$ . Fig. 3. Suture zone of a floatoblast. Scale bar = 100  $\mu\text{m}$ . Fig. 4. Frontal view of a sessoblast. Scale bar = 100  $\mu\text{m}$ . Fig. 5. Detail of a frontal sessoblast valve, showing the surface pattern. Scale bar = 20  $\mu\text{m}$ . Fig. 6. Sessoblast of *Hyalinella vaihiriae*, frontal view. Scale bar = 100  $\mu\text{m}$ .

In his original work on *H. minuta*, Toriumi (1941a, 1955) confirmed the absence of sessoblasts. Later, he reported collecting colonies with a few sessoblasts, allowing that these may be formed in a "special case" (Toriumi 1972). These sessoblasts were never described, and no specimens are known to exist. Furthermore, Rao (1973) did not find sessoblasts in any of the Indian specimens of *H. minuta* that he had examined. Until more convincing evidence is presented, the existence of sessoblasts in this species should be considered doubtful.

*Hyalinella africana* is known from only two small specimens from Zimbabwe (Wiebach 1964). On the basis of statoblast morphology, Lacourt (1968) considered this species to be a *Plumatella*, and Wiebach (1973) later admitted the possibility that *H. africana* is a synonym of *Plumatella longigemmis* (Annandale).

For the most common (and possibly the only undisputed) member of the genus, *H. punctata*, Lacourt (1968) provided a description of "rarely found" sessoblasts without reference to any particular specimen or locality. Grančarova (1968) reported the presence of sessoblasts in Bulgarian colonies, but Wiebach (1973) was unable to confirm her finding from an examination of the same material. Toriumi (1972) noted that a number of European specimens of *P. repens* have been erroneously identified as *H. punctata*, and Massard and Geimer (1991) suggested that reports of sessoblasts in *H. punctata* were the result of previous workers confusing this species with the hyaline forms of *P. repens* and *P. fungosa*.

Rao *et al.* (1985) mention the occurrence of sessoblasts in certain specimens of *H. punctata* collected from central India, but previous collections of this species in India (Annandale 1910; Rao 1976) contained no sessoblasts. Sessoblasts were not found in *H. punctata* collected in Luxembourg (Geimer and Massard 1986), nor were they found in those from Japan, Korea, and Taiwan (Toriumi 1941a, 1941b, 1942), nor during any of the detailed regional North American studies from Lake Erie (Rogick 1935), Michigan (Bushnell 1965), Massachusetts (Smith 1989), Ohio (Wood 1989), and Quebec (A. Ricciardi, unpublished data). Sessoblasts were similarly absent from laboratory-reared colonies reported by Rogick (1945) and Mukai *et al.* (1987), and from 13 generations reported by Toriumi (1972). The possibility that sessoblast formation in *H. punctata* occurs within a narrow range of environmental conditions must be considered unlikely given the absence of sessoblasts from the wide range of natural and experimental populations described above.

The environmental factors controlling sessoblast formation, and the functional differences between floatoblasts and sessoblasts, have not been fully established. In many phylactolaemate species (e.g., Plumatellidae), it is likely that floatoblasts are primarily disseminules and that larger sessoblasts serve mainly in seasonal recruitment of new colonies (Pourcher and d'Hondt 1987; Karlson 1991). With ample yolk reserves, a large statoblast capsule may more easily survive prolonged periods of seasonal drought or cold weather. In those species (e.g., Lophopodidae) known to form only floatoblasts, the capsule is always relatively large, similar in size to a normal sessoblast. Such floatoblasts must serve dual roles of dissemination and seasonal recruitment. In *H. punctata*, the large size of the floatoblast (maximum 765  $\mu\text{m}$  length  $\times$  489  $\mu\text{m}$  width; Wood 1989) suggests that it, too, serves these dual functions. Therefore, it would be surprising to discover sessoblasts in this species.

*Hyalinella vaihiriaie* Hastings is the only North American *Hyalinella* species previously reported to produce sessoblasts

(Rogick and Brown 1942). The statoblasts of *H. vaihiriaie* are remarkably different from those of any other known species of *Hyalinella*. The floatoblasts are oval, acutely pointed at the poles, and laterally asymmetric. Sessoblasts reported by Rogick and Brown (1942) from a specimen collected at Bear River, Utah, have a distinct reticulation (Fig. 6), similar to that which covers the floatoblast capsule (Cassaniga 1988). The reticulation consists of a uniform network of ridges enclosing hexagonal pits without any visible interstitial tubercles, unlike that which occurs on *H. orbisperma* statoblasts.

Much of the confusion regarding the existence of sessoblasts in *Hyalinella* is clearly the result of a broad morphological overlap among described species of *Plumatella* and *Hyalinella* (Toriumi 1956, 1972; Wiebach 1973). With the exception of the Bear Creek *H. vaihiriaie*, every one of the *Hyalinella* species mentioned above has been placed in the genus *Plumatella* at some time, and there has not been a single undisputed specimen of *Hyalinella* in which the production of sessoblasts could be confirmed. The discovery of sessoblasts in *H. orbisperma*, far from settling the issue, raises the question of whether this species properly belongs in the genus *Plumatella*.

#### *Comparison with Stephanella hina* Oka

Because of apparent similarities in floatoblast shape and certain colonial features, Bushnell (1965) advocated a comparative study of *H. orbisperma* and *Stephanella hina* in the event that sessoblasts be found in *H. orbisperma* colonies. Floatoblasts of both species are round, but those of *S. hina* have a sharply reticulated surface without tubercles (Mukai 1990; Smith 1988), while those of *H. orbisperma* have tubercles combined interstitially with small reticulations (Fig. 2). Furthermore, one of the valves of the *S. hina* floatoblast consistently bears a distinctive central projection (Mukai 1990; Smith 1988; Wood 1979) which is lacking in *H. orbisperma*. Smith (1988) noted that the small lophophore, small number of tentacles, and fine structure of the statoblasts of *S. hina* were sufficient to distinguish it from the genera *Hyalinella* and *Plumatella*. Recently, Mukai (1990) has shown from Japanese specimens of *S. hina* that the developing floatoblast acquires a unique orientation with respect to the funiculus, making a close affinity with any other known species unlikely. Because of the wide morphological differences between *Stephanella* and the other genera of phylactolaemate bryozoans, it has been proposed that the genus be placed in its own family (Mukai 1990). These considerations argue against linking *H. orbisperma* with *S. hina*.

#### *Comparison with Plumatella species*

Some specimens of *P. repens* and *P. fungosa* have round floatoblasts with a pointedly convex ventral capsule, quite similar to that of *H. orbisperma*, although the annulus is typically much wider (A. Ricciardi and T. S. Wood, personal observation). A characteristic feature of *Plumatella* floatoblasts is a lightly raised fenestral reticulation with a small tubercle in the center of each defined cell; this feature is found in every *Plumatella* species (except *P. fruticososa* Allman) recorded in Europe and North America, but is absent in virtually all other species (Bushnell and Rao 1979; Geimer and Massard 1986; Mundy 1980; Wood 1979). Sessoblasts of European and North American *Plumatella* species bear prominent tubercles on the frontal valve. Tubercles on the sessoblasts of *P. repens*, *P. fungosa*, and *P. coralloides* Allman, illustrated in SEM photographs by Geimer and Massard (1986), are enclosed in a faint reticulation of the same type that occurs in the floatoblast. The capsular surface of the *H. orbis-*

*sperma* floatoblast (Fig. 2) and sessoblast (Fig. 5) clearly shows the reticulation and tubercles of a typical *Plumatella*. This finding is persuasive evidence of a strong affinity with *Plumatella*, and implies that *H. orbisperma* is a species closely related to the *repens*–*fungosa*–*coralloides* group. On the basis of the morphological evidence presented above, we suggest that the species' original name, *Plumatella orbisperma* Kellicott, be restored.

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