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Freshwater bryozoans: a zoogeographical reassessment

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ABSTRACT: Significant changes have occurred since the publication of Bushnell's 1973 paper on the zoogeography of freshwater bryozoans. There have been important new field surveys, the number of recognized species has nearly doubled and the taxonomic foundation is much more solid. Taxonomic revisions and the re-examination of misidentified material have diminished the reported ranges of many species. Such no-longer-widespread species include *Plumatella emarginata, P. repens, P. longigemmis, Stolella indica, Fredericella sultana*, and *Gelatinella toanensis*. An assumption of dispersal by migrating waterfowl explains the narrow, intercontinental ranges of several species. In other instances the dispersal patterns suggest human activities as a major contributing factor. Some species are clearly more vagile than others for reasons currently unknown. Asia, Africa, and South America are still largely unexplored for freshwater bryozoans. Nearly half of all known species are reported from only one or two collections. At a time when extinctions among freshwater animals have reached an unprecedented high rate, endemic bryozoan species may warrant special vigilance and protection. New initiatives are needed to inventory species in large, unexplored regions.

1 INTRODUCTION

1.1 *Biogeography*

With many groups of organisms, biogeography is an inexact science. It seeks to understand spatial patterns in species distribution and biological diversity. It examines, among other things, the roles of biotic, climatic, historical, and other factors in shaping a species' current and past occurrence. In pursuit of this knowledge, those of us asking biogeographic questions assume first that we have accurate distribution data, and second that all the species involved have been correctly identified. However, species inventories are often very uneven, and experienced taxonomists are scarce, making the biogeographic foundation rather unsteady. With full knowledge of these shortcomings, we forge ahead with a third assumption: that the unavoidable uncertainty will not make a significant difference in the long run.

1.2 *Bushnell (1973) paper*

At the Second Conference of the International Bryozoology Association a thoughtful paper was introduced by John Bushnell (1973) on the zoogeography of freshwater bryozoans. In this contribution Bushnell acknowledged the restricted distribution of many phylactolaemate species: holarctic for *Cristatella, Paludicella, Plumatella fungosa*, and *P. fruticosa*; neaarctic for *Pectinatella*, mostly Ethiopian for the gelatinous lophopodids, and so on. Several species were seen as cosmopolitan, including *Plumatella repens, P. emarginata, Hyalinella punctata*, and *Fredericella sultana*. Other species were regarded as highly restricted in their distribution: *Stephanella hina, Gelatinella toanensis, Internectella bulgarica*, and *Hyalinella orbisperma*. Bushnell attributed the differences in species distribution mainly to the nature of their primary disseminules, the dormant statoblasts. Some statoblasts have adherent qualities for dispersal by waterfowl, others were thought to achieve an ideal balance of size and weight for dispersal by wind. Additional factors might include statoblast resistance to desiccation and freezing as well as statoblast productivity and the timing of statoblast release.

In the thirty years since these ideas were published there have been significant additions to the knowledge of phylactolaemate distribution and taxonomy. This paper provides a brief summary of those advances and their biogeographic implications.

2 DEVELOPMENTS SINCE 1973

2.1 *Biological surveys*

Table 1 summarize the major regional surveys for freshwater bryozoans conducted over the past thirty

years. All but one of these have been conducted in temperate regions of the world, leaving the freshwater tropics still largely unexplored.

2.2 *Endemic species*

Bushnell noted that among his 39 described phylactolaemate species, 33% were known from only one or two specimens or sites. This proportion of so-called endemic species has now increased to 45%. As expected, most of these occur in Africa, Asia, and South America where the least work has been conducted. Only *Stephanella hina* has come off the "endemic" list, its originally described range in eastern Asia now extended to both coasts of North America (Smith 1989a, Marsh & Wood, this volume). Yet to be confirmed is the likelihood that the "endemic" North American *Plumatella orbisperma* also occurs in both the United Kingdom and in northern Europe.

2.3 *Advances in taxonomy*

The taxonomy of phylactolaemate bryozoans has advanced considerably, mainly through the examination of statoblasts by scanning electron microscopy. The sclerotized outer surface of statoblasts carries a richly detailed surface relief that remains constant through successive generations, even under varying environmental conditions (e.g., Wood 1996, 2001a). These features have become very useful in taxonomic work. As a result, Bushnell's original list of 39 described species has now nearly doubled to 77, including 24 new species and the confirmation of 14 others. Species once considered to be *Fredericella sultana* now include *F. indica*, which itself probably comprises several distinct species (Økland & Økland 2001); *F. australiensis* and *F. browni* also are independently valid species (Wood & Wood 2000). Species once identifiable as *Plumatella repens* are now known also to include *P. nitens, P. nodulosa, P. orbisperma, P. recluse, P. rugosa*, and *P. similirepens* (Wood 2001c). Similarly, *Plumatella reticulata* and *P. mukaii* are now distinguished from P. *emarginata* (Wood 1988, 2001b). There appear to be at least two species currently identified as *P. fungosa* (Wood and Okamura, in prep.).

This clearer diagnosis of phylactolaemate species has also revealed a significant number of misidentifications in the literature. Returning to original specimens we find, for example, that Rogick's (1943) *Stolella indica* in Pennsylvania is actually *Plumatella rugosa*; that Lacourt's (1968) *Plumatella toanensis* does not really occur in either South America or Australia (Wood 1998), and that Annandale's (1911) *Plumatella fruticosa* and *Plumatella punctata* were not found in India after all (Wood, in prep.). In most cases the taxonomic errors are understandable. Species diagnoses were until recently based largely on colony morphology, which is often unreliable.

Table 1. Specific references to collections and surveys summarized in Figure 1.

Asia	
India	Rao 1985, Wiebach 1974a, Annandale 1911
Indonesia	Vorstman 1928a, b, 1930
Japan	Toriumi 1941a
Korea	Toriumi 1941b
Taiwan	Toriumi, 1942
Central America	
Costa Rica	Roush 1998
Europe	
Belarus	Mikaevich, in prep.
Germany (Rhine)	Franz 1992
Ireland	Smyth 1994
Israel	Massard & Geimer 1991a, 1994, Massard et al. 1992
Italy	Viganò 1965
Luxembourg	Geimer & Massard 1986
Sweden	Borg, 1936
Tenerife	Massard & Geimer 1990, 1991b
United Kingdom	Mundy 1980, Wood & Okamura, in prep.
North America	
Illinois	Marsh & Wood, in prep.
Kansas	Ellis, in prep.
Massachusetts	Smith 1989b.
Mexico	Rioja 1940a, b, Bushnell 1968
Michigan	Bushnell 1965a, b, c
Louisiana	Everitt 1973.
Ohio	Rogick 1935, Wood 1989
Ontario/ Quebec	Ricciardi & Reiswig 1994.
Pacific NW	Marsh & Wood (this volume)
Pacific	
Australia	Riek 1946, Wood 1998
New Zealand	Wood et al. 1998
South America	
Argentina	Cazzaniga 1989.
Brazil	Wiebach 1967, 1970a, b, 1974b Marcus 1941, 1942 Bonetto & Cordiviola 1965

2.4 *Revision of distribution data*

With the recognition of new species and the reexamination of old ones has come a revision of distribution data. From a scan of the existing literature, Bushnell (1973) concluded that *Fredericella sultana, Plumatella repens*, and *P. emarginata* were "cosmopolitan" species with a worldwide distribution. Now that these species have been split into several others

their ranges have diminished considerably. In addition to the species list above, ranges have also been trimmed for *Plumatella javanica* and *Stolella evelinae* (Wood & Wood 2000). Only *Plumatella casmiana* now approaches cosmopolitan status, although it is not yet reported from South America. From these changes comes the growing realization that freshwater bryozoans are not dispersed as rapidly or as easily as we once thought.

For example, nearly a century after *Paludicella articulata* was reported from the Dunedin city waterworks in New Zealand (Hamilton 1902), Wood et al. (1998) found that it was still there and not to be found elsewhere in the country. *Plumatella nitens* still occurs in a narrow band across northern United States, not venturing far into Canada nor migrating below the 41st north parallel (Wood 1996).

3 EXPLAINING DISJUNCT POPULATIONS

Spotty field work across the globe has also revealed in apparently disjunct populations and other odd distribution patterns. *Plumatella reticulata* is abundant in North America from Ohio to Oregon, extending at least as far south as Panama (Wood, unpublished). However, it has also been documented from a single site in Israel (Massard et al. 1992). *Plumatella bushnelli*, is much less common, known only from similar habitats in North Carolina and New Zealand (Wood 2001a). *Asajirella gelatinosa* is reported in Asia from Korea and Japan to the Indian subcontinent, but it also occurs in Panama (Wood & Okamura 1999).

3.1 *Importance of migratory waterfowl*

Bushnell pointed out the likely importance of migrating waterfowl in distributing bryozoans. The possibility of waterfowl to transport viable statoblasts on their feathers or in their gut was first demonstrated by Brown (1933). Microsatellite analysis, revealing gene flow among populations of *Cristatella mucedo* along a major migratory waterfowl route, has strengthened this view (Freeland et al. 2000a). Among the effective agents of such passive dispersal would be those birds breeding in the circumpolar arctic, and subarctic regions which then migrate along flyways that roughly follow continental coastlines. Such birds tend to be waterfowl that congregate in fresh water habitats: Pacific loon, Yellow-billed loon, Black-bellied plover, Sanderling, and others (Elphick 1995, Scott & Rose 1996).

Passive dispersal of statoblasts along these migratory routes offers the best explanation for the distribution of such bryozoan species as *Plumatella mukaii* and *Stephanella hina*. *Plumatella mukaii*, long mistaken for *P. emarginata*, is known from India, Indonesia, and Japan (Wood 2001b); it has also been recently documented in the Western Hemisphere: in Oregon and Chile (Fig. 1). What appears to be a highly disjunct distribution may, in fact, be a continuous range along the major north-south flyways. This would be confirmed if the species were found in a band along the western regions of both North and South America. Unfortunately, most of these areas are completely unexplored in terms of their phylactolaemate species. *Stephanella hina*, was originally known only from Japan and Korea (Oka 1908, Toriumi 1955), but is now known to occur in North America: in Oregon (Marsh & Wood, this volume), New England (Smith 1989a) and Virginia (Wood, unpubl.). Here again, the widely scattered sites occur along flyways of circumpolar breeding birds, suggesting that this bryozoan may actually have a narrow, continuous range through the coastal states. Other bryozoan species benefitting from this avian dispersal may include *Pectinatella magnifica*, a North American species now appearing in Japan and Korea; and *Fredericella indica*, the major fredericellid in North America which is also represented both in Asia and northern Europe. Yet if birds were the primary dispersing agent, one would expect these species to occur also in western Alaska and eastern Siberia where Asian and American flyways converge. To my knowledge, these regions also remain unexplored.

If *Plumatella mukaii* and *Stephanella hina* can be dispersed in this way, should we not expect to find other Asian species as well along coastal North America? Where are *Plumatella bombayensis, P. vorstmani, P. longigemmis*, and *Hyalinella minuta*? It is possible that the arctic climate functions as a filter for many species. Successful dispersal along this route requires thriving populations to be maintained throughout the nesting range of the migratory birds. Only a few species may be adapted to such varied conditions. For some time I have noted that statoblasts of many tropical species tolerate desiccation well, but do not survive cold storage. Statoblasts that remain viable after long refrigeration include those of *Cristatella mucedo, Plumatella fungosa, P. fruticosa,*

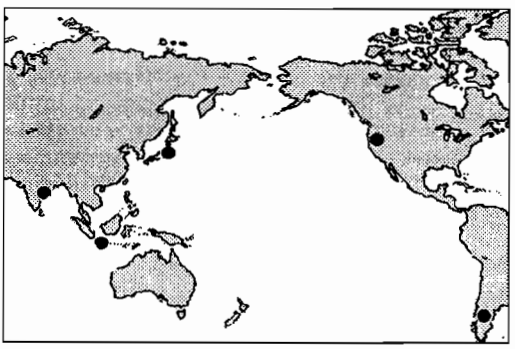

Figure 1. Known world distribution of *Plumatella mukaii*. Some dots represent more than one site.

and *Fredericella sultana*. It therefore comes as no surprise that all of these species have been reported in northern regions of Europe, Asia, and North America. By the same cold storage criterion, we might expect *Fredericella indica* and *Plumatella nitens* to have moved from North America to Asia along avian migration routes as well, but so far no such Asian presence has been reported.

3.2 *Evidence of human influence*

In cases where recent range expansions have been documented, human activity has probably played a major role. *Lophopodella carteri*, described as widespread and abundant in India (Annandale 1911), first appeared in North America around 1930 (Dahlgren 1934) in a shipping canal near Princeton, New Jersey. From there it spread westward across several mountain ranges and major river basins until it now reaches into Oregon (Marsh and Wood, this volume). Masters (1940) cited evidence that the species was being transported with the commercial trade in aquatic plants.

Neck and Fullington (1983) describe how *Pectinatella magnifica*, once known in Texas only from eastern sites, spread across the state as the construction of new reservoirs provided suitable new habitat. The mechanisms for such incremental dispersal cannot be known with certainty, but probably included human activities along with local waterfowl. Dormant statoblasts of any species may be carried from lake to lake on recreational boats and equipment.

Pectinatella magnifica is a common North American species, but within the past three decades it has moved into Japan (Oda 1974) and Korea (Dongsoo Kong, pers. com.). While this is not normally a cold tolerant species, it is conceivable that migratory waterfowl were again responsible. However, it is also very likely that statoblasts were transported with aquatic plants, fish, or other commercial items.

Asajirella gelatinosa is a species whose distribution appears to be very disjunct. It is a difficult species to miss, forming loose, gelatinous colonies more than 20 cm long, and producing the largest statoblasts of any bryozoan species (Lacourt 1968). Its range includes Japan, Korea, Indonesia, and India, but the species also occurs in the Panama Canal as well as in nearby Lago Alajuela, separated from the Canal by a high dam and several miles of river (Wood & Okamura 1999). With no other sites known worldwide, the most likely explanation for this odd distribution is human intervention, possibly related to the activities surrounding the Panama Canal into which the lake drains. Although most labor to build the canal came from the West Indies, over one thousand Chinese laborers were brought in to help build the Panama Railroad from Aspinwall (now Colón) to Gatun (Avery 1915). These immigrants could easily have carried statoblasts with them in their clothing or other articles washed in lake water. If this were the case, one could also expect to find *Asajirella* in California, where over 270,000 Chinese immigrants were registered during 1850-1880 (Chiu, 1960). Unfortunately, there are no published records of phylactolaemate bryozoans anywhere in California. There is also the possibility that shipping traffic through the Canal has introduced statoblasts, just as ships have carried other freshwater species in bilge water to North America from the Ponto-Caspian basin (Ricciardi & Rasmussen, 1999). The salt tolerance of dormant bryozoan statoblasts is likely to be high, and several major Asian ports are situated at the mouth of large rivers. On the other hand, no other Asian bryozoan species are known in Panama. In any case, it is unlikely that *A. gelatinosa* arrived from arctic nesting grounds of migratory waterfowl. Although its cold tolerance has never been tested, evidence so far suggests this is strictly a warm water species.

3.3 *Unexplained distributions*

It is less clear how to explain the widely scattered distribution of the distinctive *Plumatella vaihiriae*. Originally described from a mountain pond in Tahiti (Hastings 1929), the species has since been reported from Argentina (Cazzaniga 1988), Hawaii (Baily-Brock & Hayward 1984), Utah (Rogick, & Brown 1942), Arizona, Wisconsin, South Carolina (Wood & Marsh 1999), and North Carolina (Wood, unpubl.). That all these sites are linked by avian flyways is unquestioned: the east Asian flyway extends across the Pacific through Tahiti and Hawaii to western North America (Miyabayashi & Mundkur, 1999). Rather, it is the apparent scarcity of this species that is so striking. Most of these sites were quite small and isolated: three were wastewater treatment plants, one was a small stream, another was a pond for the culture of freshwater prawns. Such minor sites are often frequented by ducks and other waterfowl, although generally not as stopovers in a long migration route. The only known large population of *Plumatella vaihiriae* is in the highly productive coastal waters of Pamlico Sound, North Carolina. How can we account for this odd distribution in a few very small, isolated sites? Two points are relevant: First, wherever *P. vaihiriae* occurs it dominates, with very rapid growth and an unusually high production of statoblasts. In at least one wastewater plant the bryozoan biomass is regularly harvested and carried away by the truckload (Wood & Marsh 1999). Secondly, what all known sites have in common is a highly eutrophic habitat in which the species thrives. It seems possible that enormous growth and reproductive potential of *P. vaihiriae* in a narrowly defined habitat compensates for the relative scarcity of natural populations. Nevertheless, this apparent scarcity is surely also due to limited recog-

nition in the field. Not a single thorough search has been conducted in the vicinity of any of the known sites.

4 SUMMARY

Advances in phylactolaemate systematics and steady progress in regional surveys have provided valuable new information about the zoogeography of freshwater bryozoans. Since Bushnell=s (1973) paper the number of species worldwide has nearly doubled. Many of those species are known only from highly restricted sites, while a few exhibit wide ranges that parallel seasonal migration routes of circumpolar breeding birds. We need stronger field survey efforts in these areas to more fully understand these patterns. The nesting regions of the migratory waterfowl would be the obvious places to begin. An inventory of freshwater bryozoans along the western coasts of North and South America would also be very useful.

In addition to traditional morphological taxonomy, we are beginning to apply molecular tools to taxonomic and systematic problems among phylactolaemates. A phylogenetic tree at the family level has already been constructed using data from 18S ribosomal DNA (Lore, in prep.). We are next planning to examine genetic differences among species using ITS-1 and perhaps other regions of rDNA. Among other things, this is expected to help unravel certain taxonomic dilemmas among plumatellid and fredericellid bryozoans. At the same time, microsatellite data will continue to be useful for tracking the historical movements of subpopulations (Freeland et al. 2000a).

While some progress is being made in inventorying bryozoans in temperate regions, the phylactolaemate fauna of Asia, Africa, and South America is still practically unknown. The seasonally flooded Amazon forests, for example, have not been touched. Existing data suggest that tropical species tend to have relatively small geographic distribution, yet these are the very areas about which we know the least.

Finally, we are living in a time when documented freshwater extinctions in North America rival those of the forested tropics (Ricciardi and Rasmussen 1999). Similar but unseen species losses may be occurring in freshwater habitats elsewhere. Phylactolaemates comprise the single major group of suspension feeders in fresh water, yet the number of people studying any aspect of these animals could easily meet around a small table. Among other things, we need to be asking why some phylactolaemate species are more easily dispersed than others. Do they have more specialized habitat requirements? Are their statoblasts less tolerant of desiccation, freezing, or long dormancy? Do endemic species warrant special vigilance or protection as freshwater habitats are altered? How are bryozoans being affected by competition with invading zebra mussels and other foreign species? Answers to these questions begin with good field work followed by simple and inexpensive experimental studies. It is not too late to begin.

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