# Global diversity of bryozoans (Bryozoa or Ectoprocta) in freshwater: an update

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**Abstract**. The present study updates a previous paper on the global diversity of freshwater bryozoans. Currently there are about 94 bryozoan species known to occur in freshwater habitats: 74 phylactolaemate and 20 gymnolaemate species. Roughly 51% of those species are confined to one zoogeographic region.

**Key words**. Bryozoa, Ectoprocta, Phylactolaemata, Gymnolaemata, taxonomy, species diversity, generic diversity, zoogeography, phylogeny.

## 1. Introduction

Bryozoa or Ectoprocta are small benthic aquatic invertebrates growing as colonies of connected zooids on submerged substrates. They feed on suspended organic particles which they capture with a whorl of ciliated tentacles (lophophore). Of the estimated 5700 (d'Hondt 2005) or even 8000 (Ryland 2005) extant species of bryozoans, only a small number are found in freshwater habitats. Most of these belong to the exclusively freshwater-inhabiting class Phylactolaemata and reproduce asexually by means of statoblasts (buoyant floatoblasts and fixed sessoblasts), which are very important for species identification. A small number of freshwater bryozoan species belong to the essentially marine class Gymnolaemata (order Ctenostomatida).

Continental bryozoans are found in all types of waterbodies: ponds, lakes, rivers, estuaries. Some Phylactolaemates and some typically freshwater gymnolaemates occasionally occur in slightly brackish waters, e.g. *Plumatella repens, P. fungosa, Fredericella sultana, Paludicella articulata* (Loppens 1905, 1908a Carrada 1964, Occhipinti Ambrogi & d'Hondt 1981), and some gymnolaemates traditionally included in the freshwater list have a clear preference for brackish water (Loppens 1908b, Annandale 1911, 1915, Jebram & Pisano 1980, Occhipinti Ambrogi & d'Hondt 1981, Massard & Geimer 2008).

## 2. Taxonomy, species and generic diversity

In a paper written for an ambitious editorial project whose publication initially scheduled for 2006 was delayed until 2008, we estimated in January 2006 that there were about 88 valid freshwater bryozoan species worldwide (Massard & Geimer 2008). After the discovery of new species in Thailand (Wood et al. 2006) the worldwide number of species has now risen to about 94, divided into 24 genera and 10 families (Table 1).

Taxonomic splitting of species and discovery of new species have significantly increased the number of phylactolaemate species during the last years: from about 40 phylactolaemate species (Mukai 1999) to some 69 species in our January 2006 checklist (Massard & Geimer 2008), and to about 74 in October 2006 due to the new species described by Wood et al. (2006).

As a result of their taxonomic splitting some species formerly considered as cosmopolitans had their biogeographical range considerably diminished. According to Wood (2002) only *Plumatella casmiana* now approaches a cosmopolitan status.

Table 1. Numeric data for the different taxa of freshwater Bryozoa.

| Taxon | Families | Genera | Species |
|---|---|---|---|
| Gymnolaemata Allman, 1856 | 5 | 8 | 20 |
| Victorellidae Hincks, 1880 | | 4 | 8 |
| *Bulbella* Braem, 1951 | | | 1 |
| *Sineportella* Wood & Marsh, 1996 | | | 1 |
| *Tanganella* Braem, 1951 | | | 2 |
| *Victorella* Saville Kent, 1870 [a] | | | 4 |
| Pottsiellidae Braem, 1940 | | 1 | 1 |
| *Pottsiella* Kraepelin, 1887 | | | 1 |
| Paludicellidae Allman, 1885 | | 1 | 2 |
| *Paludicella* Gervais 1836 | | | 2 |
| Arachnidiidae Hincks, 1877 | | 1 | 1 |
| *Arachnoidea* (Moore, 1903) | | | 1 |
| Hislopiidae Jullien, 1885 | | 1 | 8 |
| *Hislopia* Carter, 1858 [b] | | | 8 |
| Phylactolaemata Allman, 1856 | 5 | 16 | 74 |
| Fredericellidae Hyatt, 1868 | | 2 | 6 |
| *Fredericella* Gervais 1838 | | | 5 |
| *Internectella* Gruncharova, 1971 [c] | | | 1 |
| Plumatellidae Allman, 1856 | | 9 | 59 |
| *Afrindella* Annandale, 1912 [d] | | | 3 |
| *Australella* Annandale, 1910 | | | 1 |
| *Gelatinella* Toriumi, 1955 | | | 1 |
| *Hyalinella* Jullien, 1885 [e] | | | 5 |
| *Plumatella* Lamarck, 1816 [f] | | | 40 |
| *Stephanella* Oka, 1908 [g] | | | 1 |
| *Stolella* Annandale, 1909 | | | 2 |
| *Swarupella* Shrivastava, 1981 | | | 3 |
| *Varunella* Wiebach, 1974 | | | 3 |
| Pectinatellidae Lacourt, 1968 [h] | | 1 | 1 |
| *Pectinatella* Leidy, 1851 | | | 1 |
| Cristatellidae Allman, 1856 | | 1 | 1 |
| *Cristatella* Cuvier, 1798 | | | 1 |
| Lophopodidae Rogick, 1935 | | 3 | 7 |
| *Asajirella* Oda & Mukai, 1989 | | | 1 |
| *Lophopodella* Rousselet, 1904 | | | 5 |
| *Lophopus* Dumortier, 1835 | | | 1 |
| Ectoprocta Nitsche, 1870 | 10 | 24 | 94 |

[a] Wood et al. (2006) consider *Victorella bengalensis* Annandale, 1908 as a synonym of *Victorella pavida*, whereas in our checklist they are listed as distinct species.
[b] Incl. *Norodonia* Jullien, 1880 and *Echinella* Korotnev, 1901.
[c] Combines traits of the Fredericellidae and the Plumatellidae; closer to Plumatellidae according to Gruncharova [Grancarova] (1971); placed among the latter by Vinogradov (2004), and among the Fredericellidae by Wood & Okamura (2005).
[d] Listed as *Afrindella* Wiebach, 1964 by Bock (2005) and in his wake by Massard & Geimer (2008). In fact the taxon *Afrindella* was introduced as a new subgenus by Annandale in 1912 (Annandale & Kemp 1912) with *Plumatella (Afrindella) tanganyikae* (Rousselet, 1907) as type species; it was raised to genus level by Marcus (1942) and Wiebach (1964), the latter moreover defining a new type species, namely *Afrindella philippinensis* Kraepelin, 1887 (= *Plumatella philippinensis* Kraepelin, 1887). Lacourt (1968) does not take into account the genus *Afrindella;* he calls *Plumatella tanganyikae* Rousselet, 1907 a doubtful species, and considers *Plumatella (Afrindella) testudinicola* Annandale, 1912 as *Fredericella*

*australiensis* Goddard, 1909, erroneously, as pointed out by Wiebach (1974).
[e] Placed by Vinogradov (2004) in a new family accepted by Wood et al. (2006): Hyalinellidae Vinogradov, 2004.
[f] Vinogradov (2004) has introduced the new genus *Leptoblastella* with the species: *Leptoblastella casmiana* (= *Plumatella casmiana* Oka, 1908).
[g] One single known species (*Stephanella hina* Oka, 1908) for which Lacourt (1968) created the family of the Stephanellidae, whereas for other bryozoologists *Stephanella* remained a member the Plumatellidae. Mukai (1990, 1999), Vinogradov (2004) and Okuyama et al. (2006) consider Lacourt's family as valid.
[h] In spite of Lacourt (1968) many authors continued to consider *Pectinatella* as belonging to the Lophopodidae (Bushnell 1973, 1974, Geimer & Massard 1986, Wood 1989). Wood & Okamura (2005) now accept Lacourt's Pectinatellidae. Mukai (1999) estimated that the genera *Pectinatella* (with the single species *P. magnifica*) and *Cristatella* (with the single species *C. mucedo*) should be united in the family Cristatellidae; the study of Okuyama et al. (2006) tends to corroborate this idea not adopted in the present table for practical and historical reasons.

## 3. Zoogeography and distribution

The zoogeographical distribution of freshwater bryozoans has been analysed by Lacourt (1968), Bushnell (1973), Rao (1992) and Wood (2002). The checklist compiled for the present paper includes a total of 94 species (Tables 2-4, Fig. 1). Forty-nine species (52,1 %) are limited to one zoogeographic region: 13 gymnolaemates (13.8%) and 36 phylactolaemates (38.3%). Twenty-four of these 49 species are known only from a very restricted area (one or two sites).

The alleged European occurrence of *Plumatella javanica* Kraepelin, 1906 mentioned by Bushnell (1973) and Wiebach & d'Hondt (1978) is in fact due to a mistake made by Bushnell when drawing his distribution maps (Massard & Geimer 2005). Lacourt's record of *Fredericella australiensis* in Belgium (Lacourt 1968) is probably erroneous (Wood & Okamura 2004, Massard & Geimer 2005); its alleged Russian occurrences (Lacourt 1968, Vinogradov 2006) have to be confirmed, and so has the identification of *Stolella indica* reported from the Rhine by Franz (1992).

The numerous reports of *Plumatella fruticosa* from South America and the Indian area are

Table 2. Number of genera recorded in the various zoogeographic regions.

| Taxon | PA | NA | NT | AT | OL | AU | PAC | World |
|---|---|---|---|---|---|---|---|---|
| Gymnolaemata | 6 | 4 | 4 | 2 | 3 | 2 | - | 8 |
| Victorellidae | 3 | 2 | 1 | 1 | 1 | 1 | - | 4 |
| Pottsiellidae | - | 1 | 1 | - | - | - | - | 1 |
| Paludicellidae | 1 | 1 | 1 | - | 1 | 1 | - | 1 |
| Arachnidiidae | 1 | - | - | 1 | - | - | - | 1 |
| Hislopiidae | 1 | - | 1 | - | 1 | - | - | 1 |
| Phylactolaemata | 13[a] | 9[a] | 6 | 8[a] | 14 | 4 | 1 | 16 |
| Fredericellidae | 2 | 1 | 1 | 1 | 2 | 1 | - | 2 |
| Plumatellidae[b] | 6 | 4 | 3 | 6 | 9 | 2 | 1 | 9 |
| Pectinatellidae | 1 | 1 | 1 | - | 1 | - | - | 1 |
| Cristatellidae | 1 | 1 | - | - | - | - | - | 1 |
| Lophopodidae | 3 | 2 | 1 | 1 | 2 | 1 | - | 3 |
| Total | 19 | 13 | 10 | 10 | 17 | 6 | 1 | 24 |

PA: Palaearctic; NA: Nearctic; NT: Neotropical; AT: Africotropical; OL: Oriental; AU: Australasian; PAC: Pacific Oceanic Islands.
[a] Including *Stolella* (occurrence/identification to be confirmed).
[b] Including *Stephanella* and *Hyalinella*.

Table 3. Zoogeographical distribution (number of species per family in the different zoogeographic regions).

| Taxon | PA | NA | NT | AT | OL | AU | PAC | World |
|---|---|---|---|---|---|---|---|---|
| Gymnolaemata | 10 (6) | 4 (1) | 6 (1) | 2 (1) | 8 (4) | 2 | 0 (0) | 20 (13) |
| Victorellidae | 5 (4) | 2 (1) | 1 | 1 (1) | 2 (1) | 1 | - | 8 (7) |
| Pottsiellidae | - | 1 | 1 | - | - | - | - | 1 (0) |
| Paludicellidae | 1 | 1 | 2 | - | 1 | 1 | - | 2 (0) |
| Arachnidiidae | 1 | - | - | 1 | - | - | - | 1 (0) |
| Hislopiidae | 3 (2) | - | 2 (1) | - | 5 (3) | - | - | 8 (6) |
| Phylactolaemata | 34 (5) | 28 (4) | 24 (7) | 20 (4) | 39 (14) | 14 (2) | 2 (0) | 74 (36) |
| Fredericellidae | 4 | 4 | 3 (1) | 2 | 4 | 2 | - | 6 (1) |
| Plumatellidae | 24[b] (5) | 20[b] (4) | 19[c] (6) | 14[b] (3) | 30 (13) | 11 (2) | 2 | 59 (33) |
| Pectinatellidae | 1 | 1 | 1 | - | 1 | - | - | 1 (0) |
| Cristatellidae | 1 | 1 | - | - | - | - | - | 1 (0) |
| Lophopodidae | 4 | 2 | 1 | 4[d] (1) | 4[d] (1) | 1 | - | 7 (2) |
| Total | 44[a] (11) | 32[b] (5) | 30[c] (8) | 22[bd] (5) | 47[cd] (18) | 16 (2) | 2 (0) | 94 (49) |

PA: Palaearctic; NA: Nearctic; NT: Neotropical; AT: Africotropical; OL: Oriental; AU: Australasian; PAC: Pacific Oceanic Islands. World = total of species per taxon (one given species often occurring in more than one zoogeographic region, the sum of the species numbers of the different regions normally exceeds the total number of species of the family). Number in brackets = number of species confined to one zoogeographic region only.

[a] Including *Fredericella australiensis, Plumatella javanica, Stolella indica* (occurrence/identification to be confirmed).

[b] Including *Stolella indica* Annandale, 1909 (occurrence/identification to be confirmed).

[c] Not including *Plumatella fruticosa* (occurrence/identification to be confirmed).

[d] Including *Lophopodella stuhlmanni* Kraepelin, 1914 (doubtful species, considered as *L. carteri* by Toriumi 1974) and *Victorella bengalensis* Annandale, 1908 (considered as synonym of *V. pavida* by Wood et al. 2006).

Table 4. Checklist and zoogeographical distribution of the considered freshwater bryozoan species.

| Zoogeographic region | PAe | PAa | PA | NA | NT | AT | OL | AU | PAC |
|---|---|---|---|---|---|---|---|---|---|
| Gymnolaemata | | | | | | | | | |
| *Arachnoidea raylankesteri* (Moore, 1903) | | x | x | | | x | | | |
| *Bulbella abscondita* Braem, 1951 | x | | x | | | | | | |
| *Hislopia cambodgiensis* (Jullien, 1885) | | x | x | | | | x | | |
| *Hislopia corderoi* Mañé-Garzón, 1959 | | | | | x | | | | |
| *Hislopia lacustris* Carter, 1858 | | | | | x | | x | | |
| *Hislopia malayensis* Annandale, 1916 | | | | | | | x | | |
| *Hislopia moniliformis* (Annandale, 1911) | | | | | | | x | | |
| *Hislopia natans* Wood et al., 2006 | | | | | | | x | | |
| *Hislopia placoides* (Korotnev, 1901) | | x | x | | | | | | |
| *Hislopia sinensis* (Jullien, 1880) | | x | x | | | | | | |
| *Paludicella articulata* (Ehrenberg, 1831) | x | x | x | x | x | | | x | |
| *Paludicella pentagonalis* Annandale, 1916 | | | | | x | | x | | |
| *Pottsiella erecta* (Potts, 1884) | | | | x | x | | | | |
| *Sineportella forbesi* Wood & Marsh, 1996 | | | | x | | | | | |
| *Tanganella muelleri* (Kraepelin, 1887) | x | | x | | | | | | |
| *Tanganella symbiotica* (Rousselet, 1907) | | | | | | x | | | |
| *Victorella bengalensis* Annandale, 1908 | | | | | | | x | | |

| Zoogeographic region | PAe | PAa | PA | NA | NT | AT | OL | AU | PAC |
|---|---|---|---|---|---|---|---|---|---|
| *Victorella bergi* Abrikosov, 1959 | | x | x | | | | | | |
| *Victorella continentalis* Braem, 1911 | | x | x | | | | | | |
| *Victorella pavida* Saville Kent, 1870 | x | | x | x | x | | x | x? | |
| Phylactolaemata | | | | | | | | | |
| *Afrindella philippinensis* (Kraepelin, 1887) | | | | | x | x | x | | |
| *Afrindella tanganyikae* (Rousselet, 1907) | | | | | | x | | | |
| *Afrindella testitudinicola* (Annandale, 1912) | | | | | | | x | | |
| *Asajirella gelatinosa* (Oka, 1891) | | x | x | | x | | x | | |
| *Australella indica* Annandale, 1915 | | x | x | | | x | x | | |
| *Cristatella mucedo* Cuvier, 1798 | x | x | x | x | | | ? | | |
| *Fredericella australiensis* Goddard, 1909 | x? | x? | x? | x | x | | x | x | |
| *Fredericella browni* (Rogick, 1945) | | | | x | x | | | | |
| *Fredericella crenulata* (Reymond-Marcus, 1946) | | | | | x | | | | |
| *Fredericella indica* Annandale, 1909 | x | | x | x | | x | x | | |
| *Fredericella sultana* (Blumenbach, 1779) | x | x | x | x | | x | x | x | |
| *Gelatinella toanensis* (Hozawa & Toriumi, 1940) | | x | x | | a | a | x | a | |
| *Hyalinella diwanensis* Rao et al., 1985 | | | | | | | x | | |
| *Hyalinella iheringi* Meissner, 1893 | | | | | x | | | | |
| *Hyalinella lendenfeldi* (Ridley, 1886) | | | | | | | x | x | |
| *Hyalinella minuta* (Toriumi, 1941) | | x | x | | | | x | | |
| *Hyalinella punctata* (Hancock, 1850) | x | x | x | x | x | x? | x? | | |
| *Internectella bulgarica* Gruncharova, 1971 | x | | x | | | | x | | |
| *Lophopodella capensis* (Sollas, 1980) | | x | x | | | x | | | |
| *Lophopodella carteri* (Hyatt, 1866) | x | x | x | x | | x | x | x | |
| *Lophopodella pectinatelliformis* Lacourt, 1959 | | | | | | | x | | |
| *Lophopodella stuhlmanni* Kraepelin, 1914 | | | | | | x | x | | |
| *Lophopodella thomasi* Rousselet, 1904 | | | | | | x | | | |
| *Lophopus crystallinus* Pallas, 1768 | x | x | x | x | | | | | |
| *Pectinatella magnifica* (Leidy, 1851) | x | x | x | x | x | | x | | |
| *Plumatella agilis* (Marcus, 1942) | | | | | x | x | x | x | |
| *Plumatella angarensis* Vinogradov, 1985 | | x | x | | | | | | |
| *Plumatella bigemmis* Annandale, 1919 | | | | | | | x | | |
| *Plumatella bombayensis* Annandale, 1908 | x | | x | | | | x | | |
| *Plumatella bushnelli* Wood, 2001 | | | | x | | | | x | |
| *Plumatella carvalhoi* (Marcus, 1942) | | | | | x | | | | |
| *Plumatella casmiana* Oka, 1907 | x | x | x | x | x | x | x | | |
| *Plumatella chulabhornae* Wood et al., 2006 | | | | | | | x | | |
| *Plumatella crassipes* Wiebach, 1974 | | | | | x | | | | |
| *Plumatella emarginata* Allman, 1844 | x | x | x | x | x | x | x | x | |
| *Plumatella evelinae* (Marcus, 1941) | | | | x | x | x? | | | |
| *Plumatella fruticosa* Allman, 1844 | x | x | x | x | ? | | ? | | |
| *Plumatella fungosa* (Pallas, 1768) | x | x | x | x | | | ? | x | |
| *Plumatella ganapati* Rao et al., 1985 | | | | | | | x | | |
| *Plumatella geimermassardi* Wood & Okamura, 2004 | x | | x | | | | | | |
| *Plumatella javanica* Kraepelin, 1906 | | x? | x? | x? | x? | x? | x | | x? |
| *Plumatella longigemmis* (Annandale, 1915) | | | | | x | x? | x | x | |
| *Plumatella marcusi* Wiebach, 1970 | | | | | x | | | | |
| *Plumatella marlieri* Wiebach, 1970 | | | | | | x | | | |
| *Plumatella mongoliensis* Vinogradov, 1985 | | x | x | | | | | | |
| *Plumatella mukaii* Wood, 2001 | | x | x | x | x | | x | | |

| Zoogeographic region | PAe | PAa | PA | NA | NT | AT | OL | AU | PAC |
|---|---|---|---|---|---|---|---|---|---|
| *Plumatella nitens* Wood, 1996 | | | | x | | | | | |
| *Plumatella nodulosa* Wood, 2001 | | | | x | | | | | |
| *Plumatella orbisperma* Kellicott, 1882 | | | | x | | | | | |
| *Plumatella osburni* (Rogick & Brown, 1942) | | x | x | | x | | | | |
| *Plumatella patagonica* Wiebach, 1974 | | | | | x | | | | |
| *Plumatella recluse* Smith, 1992 | | | | x | | | | | |
| *Plumatella repens* (Linné, 1758) | x | x | x | x | x | x | x | x | |
| *Plumatella reticulata* Wood, 1988 | x | x | x | x | x | | | | |
| *Plumatella rieki* Wood, 1998 | | | | | | | | x | |
| *Plumatella rugosa* (Wood et al., 1998) | x | | x | x | | | | x | |
| *Plumatella sedimentata* Vinogradov, 1985 | | x | x | | | | | | |
| *Plumatella siamensis* Wood et al., 2006 | | | | | | | x | | |
| *Plumatella sibiriensis* Vinogradov, 1985 | | x | x | | | | | | |
| *Plumatella similirepens* Wood, 2001 | x | | x | x | | | | | |
| *Plumatella siolii* Wiebach, 1970 | | | | | x | | | | |
| *Plumatella suwana* Wood et al., 2006 | | | | | | | x | | |
| *Plumatella vaihiriae* (Hastings, 1929) | | | | x | x | | | x? | x |
| *Plumatella velata* Wood, 1998 | | | | | | | | x | |
| *Plumatella vorstmani* Toriumi, 1952 | | x | x | | | | x | | |
| *Stephanella hina* Oka, 1908 | | x | x | x | | | x | | |
| *Stolella himalayana* Annandale, 1911 | | | | | | | x | | |
| *Stolella indica* Annandale, 1909 | x? | | x? | x? | | x? | x | | |
| *Swarupella andamanensis* (Rao, 1961) | | | | | | | x | | |
| *Swarupella divina* Wood et al., 2006 | | | | | | | x | | |
| *Swarupella kasetsartensis* Wood et al., 2006 | | | | | | | x | | |
| *Varunella coronifera* Wiebach, 1974 | | | | | | | x | | |
| *Varunella gemmata* Wiebach, 1976 | | | | | | x | | | |
| *Varunella indorana* Wiebach, 1974 | | | | | | | x | | |

PA: Palaearctic (PAe: European part; PAa: Asian part); NA: Nearctic; NT: Neotropical; AT: Africotropical; OL: Oriental; AU: Australasian; PAC: Pacific Oceanic Islands.
x : present.
x? : mentioned in the literature, but occurrence/identification needs confirmation.
? : doubtful (here considered as absent).
a : absent (mentioned in the literature as the result of a misidentification).

due to misidentifications and actually must be assigned to *P. philippinensis* (Lacourt 1968). Wood confirms that *P. fruticosa* has not been found in India (Wood 2002, in litt. 2006), so the records mentioned by Annandale (1911), Rao et al. (1985), Rao (1992) must be reconsidered. It should be noted that Rao et al. (1985) consider *P. fruticosa* as a synonym of *P. philippinensis* (listed as *Afrindella philippinensis* in our Table 4).

A new phylactolaemate species, *Plumatella geimermassardi*, was recently described from Europe by Tim Wood and Beth Okamura (Wood & Okamura 2004). *Internectella bulgarica* hitherto only reported from Bulgaria, has recently been identified in Thailand, where it is rather common (Wood & Okamura 2005, Wood et al. 2006). On the other hand, species formerly unknown in Europe have been recorded there during the last years: *Fredericella indica, Plumatella bombayensis*, *P. reticulata*, *P. rugosa*, *P. similirepens* (Massard & Geimer 1995a, 1996, 2005, Wood & Okamura 2005, Taticchi & Pieroni 2005, Taticchi et al. 2005, Taticchi et al. 2006).

Some species may extend their distribution area thanks to long distance dispersal of sta-

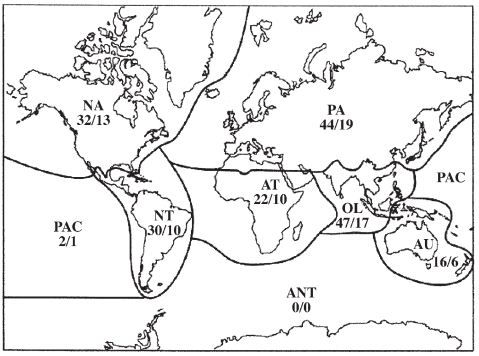



Figure 1. Zoogeographical distribution map (species/genera per region; total: 94/24).
PA: Palaearctic; NA: Nearctic; NT: Neotropical; AT: Africotropical; OL: Oriental; AU: Australasian; PAC: Pacific Oceanic Islands; ANT: Antarctic.

toblasts by migratory waterfowl or by human activity (transport of statoblasts with aquatic plants, fish, navigation, etc.). In Europe this is the case, e.g., for *Plumatella casmiana* (Geimer & Massard 1986, Massard & Geimer 1995b, Massard et al. 2002) and *Pectinatella magnifica* (d'Hondt & Condé 1996, Notteghem 1999, Rodriguez & Vergon 2002, Massard & Geimer 2002, 2005).

Some other species, like *Lophopus crystallinus,* may seem rare because they are often overlooked (Hill et al. 2007). Possibly this is also true for *Fredericella indica* in Europe: first reported from Bavaria in 1994 (Massard & Geimer 1995a, 1996), this pretended 'American' species, appeared to be rather common in Norway (Økland & Økland 2001); and recent data from the Sokli lacustrine sediments in northern Finland reveal the presence of *F. indica* in Europe some 50000 years ago during the Tulppio Interstadial of the last glaciation (Helmens et al. 2007).

## 4. Palaeontology and phylogeny

The most ancient bryozoans are marine stenolaemates from the Lower Ordovician (about 500 million years old) (Ryland 2005, Xia et al. 2007). Traces of fossil marine gymnolaemates are present in the Upper Ordovician (McKinney & Jackson 1991). There are no fossil records of freshwater gymnolaemates. Fossil phylactolaemates are known only by their statoblasts; among the oldest are plumatellid statoblasts from the Upper Permian in the Asian part of the former U.S.S.R. (Vinogradov 1991, 1996) and possibly pectinatellid statoblasts from the Upper Triassic Molteno Formation in South Africa (Kohring & Hörnig 2002, Kohring & Pint 2005).

The phylogeny of the gymnolaemates is illustrated by Todd (2000). First drafts of phylogenetic trees of the Phylactolaematea, which are phylogenetically older than the Gymnolaemata, have been provided by Toriumi (1956), Lacourt (1968) and Mukai (1999). Wood & Lore (2005) have shown that the gelatinous species (Lophopodidae, Pectinatellidae, Cristatellidae) are more primitive than the branching tubular species (Plumatellidae, Fredericellidae). Okuyama et al. (2006) suggest that the gelatinous, but branching *Stephanella hina* is the most basal phylactolaemate, and they support the idea that it does not belong to the Plumatellidae, as still stated by Smith (1988), but to the separate family Stephanellidae created by Lacourt (1968) and accepted by Mukai (1990).

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