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Bryozoans from the Middle Jurassic of Balin, Poland: a revision of material described by A.E. REUSS (1867)

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(With 13 figures and 1 table)

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Abstract

In 1867 A.E. REUSS described 19 species of cyclostome bryozoans from the Middle Jurassic (Upper Bathonian-Lower Callovian) of Balin, between Katowice and Krakow in southern Poland. Eight of these species were considered to be new. This paper revises the Balin bryozoan fauna based on the type material of REUSS and other specimens in the collections of the Natural History Museum, Vienna. A total of 23 species are recognizable in this collection, making it among the most diverse of Jurassic bryozoan faunas known. The four REUSS species (*Hyporosopora tenera*, *Mesenteripora*? *conferta*, *Mesonopora concatenata*, *Theonoa minuta*) regarded as senior synonyms are redescribed in full, while the nomenclature of the remaining species is updated. Lectotypes are chosen for *Berenicea insignis* REUSS, 1867, *Diastopora conferta* REUSS, 1867, und *Pavotubigera minuta* REUSS, 1867. Emphasis is placed on the morphology of the gonozooids, which were surprisingly neglected by REUSS (1867), to distinguish between closely similar species, as well as the potential taxonomic value of pseudopore shape as revealed using SEM. Many of the species present at Balin occur in the Bathonian of Normandy.

Keywords: Bryozoa, Cyclostomata, Jurassic, Poland, taxonomy, lectotypification

Zusammenfassung

1867 beschrieb A.E. REUSS 19 Arten von cyclostomen Bryozoen aus dem Mittleren Jura (Oberes Bathonium - Unteres Callovium) von Balin, zwischen Kattowitz und Krakau in Südpolen. Acht dieser Arten wurden von ihm als neu erachtet. Die vorliegenden Arbeit revidiert die Bryozoenfauna von Balin auf der Grundlage des REUSS'schen Originalmaterials und anderen Proben aus der Sammlung des Naturhistorischen Museums in Wien. Insgesamt konnten 23 Arten dokumentiert werden, womit die Fauna von Balin eine der diversesten Bryozoenfaunen des Ober-Jura darstellt. Der Großteil der Bryozoenarte von Balin tritt auch im Bathonium der Normandie auf. Vier der von REUSS aufgestellten Arten (*Hyporosopora tenera, Mesenteripora? conferta, Mesonopora concatenata, Theonoa minuta*) werden hier als gültig erachtet und neu beschrieben. Die Systematik der übrigen Arten wurde aktualisiert. Für *Berenicea insignis* REUSS, 1867, *Diastopora conferta* REUSS, 1867, und *Pavotubigera minuta* REUSS, 1867 werden hier Lectotypen festgelegt. Zur Unterscheidung nahe verwandter Arten wird hier vor allem die Morphologie der Gonozooide genutzt, welche von REUSS überraschenderweise vernachlässigt wurden. Als weiteres wichtiges Merkmal von hohem taxonomischen Wert dient die Form der Pseudoporen, die mithilfe eines Rasterelektronenmikroskops untersucht wurde.

Schlüsselwörter: Bryozoa, Cyclostomata, Jura, Polen, Taxonomie, Lectotypen

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Introduction

The Jurassic bryozoan fauna from Balin, near Krakow in Poland (Fig. 1) is one of the few to have been described in the 19th century from outside the western European countries of France, England or Germany. A.E. REUSS, who is better known for his work on Tertiary bryozoans (VÁVRA 2002), monographed the cyclostome bryozoans from the Braunen Jura of Balin in a paper that also dealt with corals and sponges (REUSS 1867). According to REUSS, the Balin fauna comprised 19 species of bryozoans, of which 8 were considered by him to be new. REUSS was familiar with the works of the French naturalists LAMOUROUX (1821), MILNE EDWARDS (1838), MICHELIN (1841-48), HAIME (1854) and D'ORBIGNY (1850a, 1850b, 1851-54) on the Middle Jurassic bryozoans of France and England, and was able to identify the remaining 11 bryozoans in the Balin fauna as species previously described by these authors. Note that the supposed bryozoan *Neuropora raristellata* REUSS, 1867 belongs to a genus now placed in the Porifera (KAZMIERCZAK & HILLMER 1974).

The Balin bryozoan fauna has been totally neglected since the time of REUSS. This can be explained in part by the fact that it has not been possible to collect fresh material from this locality for many years (M. KROBICKI pers comm. 2005). However, it also reflects the general paucity of research on Jurassic bryozoans worldwide. The only major monograph published on Jurassic bryozoans during the past one hundred years is that of WALTER (1970). Although WALTER's work mainly focused on the French Jurassic bryozoans, regardless of their geographical provenance, and provided updated identifications. Judging by the verification symbol 'V' in his synonymy lists, it appears that WALTER personally examined at least some of the material from Balin that had been described by REUSS (1867). He accepted only two of REUSS's species as senior synonyms, regarded four as junior synonyms of species previously described from western Europe, and placed question marks against the two remaining new species.



Fig. 1: Map showing the location of Balin in Poland.

In view of the importance of the Balin bryozoan fauna, not only historically but also as an outlier from the main centre of known Middle Jurassic bryozoan diversity that is situated in western Europe (TAYLOR & ERNST 2008), this paper sets out to revise the bryozoans described by REUSS (1867). Collections of other fossils from Balin housed in the Naturhistorischen Museum, Wien were also searched to locate additional bryozoans.

Geological Setting

The bryozoans described by REUSS (1867) come from the 'Balin Oolite', a condensed and reworked ferruginous carbonate deposit less than a metre in thickness (DELANCE et al. 1993; TARKOWSKI et al. 1994; MANGOLD et al. 1996). Ammonite evidence (MAN-GOLD et al. 1996) dates the Balin Oolite as Late Bathonian (*retrocostatum* and *discus* zones) to Early Callovian (*herveyi*, *koenigi* and *calloviense* zones), possibly with the base of the Middle Callovian (*jason* zone) also present. However, the brachiopods are apparently indicative of the Early and Middle Callovian (DELANCE et al. 1993). The Balin Oolite is rich in fossils. Aside from bryozoans, brachiopods and ammonites, the Balin Oolite also contains sponges, corals, bivalves, gastropods, crinoids and echinoids (THIERRY et al. 1992). The skeletons of many of these marine invertebrates acted as substrates for encrustation by bryozoans and various other organisms. These sclerobionts include foraminifera (e.g. Figs 3C, 8C), bivalves, thecidean brachiopods, serpulid worms, and the *Spirorbis*-like microconchid worm *Punctaconchus* recently described from the British and French Aalenian-Bathonian by VINN & TAYLOR (2007).

Systematic palaeontology

Full species descriptions and synonymies are given only for those species described by REUSS (1867) that are not regarded as junior synonyms of species introduced in earlier papers. These species are *Hyporosopora tenera* (REUSS, 1867), *Mesenteripora? con-ferta* (REUSS, 1867), *Mesonopora concatenata* (REUSS, 1867), *Theonoa minuta* (REUSS, 1867) and '*Berenicea' exilis* REUSS, 1867. For all other species, the comprehensive synonymies given by WALTER (1970) should be consulted, although comments on certain key features are included under the respective Remarks sections.

Material was imaged optically using an Axiomatic digital microscope. Selected specimens were studied and imaged with a LEO 1455VP scanning electron microscope at the Natural History Museum, London. This low vacuum instrument is able to take large uncoated specimens, generating images using back-scattered electrons (BSE). Because BSE images are sensitive to compositional variations, the ferruginous oncoidal growths on some of the Balin specimens show up as bright patches.

All described specimens are housed in the Naturhistorischen Museum, Wien (NHMW). Table 1 summarises the re-identifications of the specimens described by REUSS (1867).

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Table 1: Jurassic bryozoan specimens in the REUSS Collection (NHMW) from Balin with the original name given to them by REUSS (1867), revised name, and names of any associated species with the same number (usually encrusting the same substrate).

Registered	Reuss (1867)	Revised identification/s	Associated
1855/0011/0096	Diastopora fenestrata Reuss, 1867	Multisparsa lamellosa (Michelin, 1845)	bijozodn species
1855/0011/0097	<i>Berenicea concatenata</i> REUSS, 1867	Mesonopora concatenata (Reuss, 1867)	
1855/0011/0100	<i>Diastopora lamourouxi</i> Milne Edwards, 1838	Diastopora? sp.	
1855/0040/0094a	<i>Heteropora conifera</i> (Lamouroux, 1821)	<i>Ceriocava corymbosa</i> (Lamouroux, 1821)	
1855/0040/0094b	<i>Heteropora conifera</i> (Lamouroux, 1821)	<i>Ripisoecia conifera</i> (Lamouroux, 1821)	
1855/0040/0095	Heteropora conifera (Lamouroux, 1821)	<i>Ceriocava corymbosa</i> (Lamou- Roux, 1821)	
1866/0057/0001	Stomatopora dichotoma (Lamouroux, 1821)	Stomatopora corallina (D'Orbigny, 1850)	
1866/0057/0002a	Stomatopora dichotoma (Lamouroux, 1821)	Stomatopora dichotomoides (D'ORBIGNY, 1850)	
1866/0057/0002b	Stomatopora dichotoma (Lamouroux, 1821)	<i>Stomatopora recurva</i> Waagen, 1867	
1866/0057/0003a	<i>Stomatopora bouchardi</i> HAIME, 1854	<i>Stomatopora recurva</i> WAAGEN, 1867	
1866/0057/0003b	<i>Stomatopora bouchardi</i> HAIME, 1854	Stomatopora dichotomoides (D'ORBIGNY, 1850)	
1866/0057/0005a	<i>Stomatopora bouchardi</i> HAIME, 1854	Stomatopora dichotomoides (D'ORBIGNY, 1850)	'Berenicea' spp.
1866/0057/0005b	Stomatopora bouchardi Haime, 1854	Stomatopora dichotomoides (d'Orbigny, 1850); Stomatopora bajocensis (d'Orbigny, 1850)	' <i>Berenicea</i> ' sp.
1866/0057/0006	Stomatopora dichotomoides (d'Orвigny, 1850)	Stomatopora dichotomoides (d'Orbigny, 1850); Stomatopora bajocensis (d'Orbigny, 1850); Stomatopora recurva WAAGEN, 1867	<i>'Berenicea'</i> sp.
1866/0057/0007	<i>Berenicea diluviana</i> Lamouroux, 1821	Hyporosopora sauvagei (Gregory, 1896)	<i>'Berenicea'</i> sp.
1866/0057/0008	<i>Berenicea diluviana</i> Lamouroux, 1821	Hyporosopora sauvagei (Gregory, 1896)	<i>'Berenicea'</i> sp.; <i>Oncousoecia</i> sp.
1866/0057/0009a	<i>Berenicea diluviana</i> Lamouroux, 1821	Hyporosopora sauvagei (Gregory, 1896)	
1866/0057/0009b	<i>Berenicea diluviana</i> Lamouroux, 1821	<i>Reptomultisparsa</i> cf. <i>norberti</i> Hara & Taylor, 1996	
1866/0057/0010	<i>Berenicea diluviana</i> Lamouroux, 1821	<i>Multisparsa eudesiana</i> (Milne Edwards, 1838)	

Registered number	Reuss (1867) identification	Revised identification/s	Associated bryozoan species
1866/0057/0011a	<i>Berenicea insignis</i> Reuss, 1867	Multisparsa eudesiana (Milne Edwards, 1838)	
1866/0057/0011b	Stomatopora dichotoma (Lamouroux, 1821)	<i>Stomatopora recurva</i> WAAGEN, 1867	<i>Microeciella</i> sp.
1866/0057/0012a	Berenicea insignis Reuss 1867	<i>Reptomultisparsa</i> aff. <i>cobra</i> (Рітт & Тномаs, 1969)	
1866/0057/0012b	Berenicea insignis Reuss 1867	' <i>Berenicea'</i> sp.	?Hyporosopora sp.; Stomatopora recurva WAAGEN, 1867
1866/0057/0013	<i>Berenicea striata</i> Haime, 1854	Reptomultisparsa cf. norberti Hara & Taylor, 1996; ?Hy- porosopora sauvagei (Gregory, 1896)	
1866/0057/0014	Berenicea striata Haime, 1854	?Hyporosopora incrustans (BEAN, 1839)	<i>Microeciella</i> sp.; ? <i>Hyporosopora</i> sp.
1866/0057/0015	Berenicea striata HAIME, 1854	'Berenicea' sp.	
1866/0057/0016	Berenicea microstoma Michelin, 1845	Hyporosopora sp.	
1866/0057/0017	<i>Berenicea verrucosa</i> Milne Edwards, 1838	Hyporosopora sauvagei (Gregory, 1896)	
1866/0057/0018	<i>Diastopora lucensis</i> Haime, 1854	<i>Microeciella</i> sp.	Stomatopora dichotomoides (D'ORBIGNY, 1850);
1866/0057/0019	Berenicea tenera Reuss, 1867	?Hyporosopora sauvagei (Gregory, 1896); ?	'Berenicea' sp.; ?Stomatopora recurva WAAGEN, 1867
1866/0057/0020	Berenicea exilis Reuss, 1867	'Berenicea' exilis Reuss, 1867	
1866/0057/0021	Berenicea exilis Reuss, 1867	'Berenicea' exilis Reuss, 1867	Stomatopora sp.
1866/0057/0023	<i>Diastopora lucensis</i> Haime, 1854	Mesenteripora michelini BLAINVILLE, 1830	
1866/0057/0024	<i>Diastopora michelini</i> MILNE EDWARDS, 1838	Mesenteripora? conferta (Reuss, 1867)	
1866/0057/0025	<i>Diastopora michelini</i> MILNE Edwards, 1838	'Berenicea' sp.	
1866/0057/0026	<i>Diastopora conferta</i> Reuss, 1867	Mesenteripora? conferta (Reuss, 1867)	<i>Multisparsa eudesiana</i> (Milne Edwards, 1838)
1866/0057/0027	<i>Diastopora conferta</i> Reuss, 1867	Mesenteripora michelini BLAINVILLE, 1830	Stomatopora spp.
1866/0057/0028	<i>Diastopora fenestrata</i> Reuss, 1867	Multisparsa lamellosa (Michelin, 1845)	

Registered number	Reuss (1867) identification	Revised identification/s	Associated bryozoan species
1866/0057/0029	<i>Pavotubigera minuta</i> Reuss, 1867	<i>Theonoa minuta</i> (Reuss, 1867)	
1867/0008/0219	<i>Berenicea striata</i> HAIME, 1854	<i>Multisparsa eudesiana</i> (Milne Edwards, 1838)	Stomatopora sp.; 'Berenicea' sp.; Oncousoecia sp.; Idmonea sp.
1867/0008/0220a	Berenicea tenera Reuss, 1867	Hyporosopora tenera (Reuss, 1867)	
1867/0008/0220b	Berenicea tenera Reuss, 1867	Hyporosopora undulata (Міснеція, 1845)	

Order Cyclostomata BUSK, 1852

Suborder Tubuliporina MILNE EDWARDS, 1838

Family Stomatoporidae PERGENS & MEUNIER, 1886

Genus Stomatopora BRONN, 1825

Stomatopora bajocensis (D'ORBIGNY, 1850)

- 1850a Alecto bajocensis D'ORBIGNY: 288
- 1867 Stomatopora bouchardi HAIME REUSS: 2 (partim)
- 1963 Stomatopora bajocensis (D'ORBIGNY) ILLIES: 74, pl. 7, figs 1-2
- 1970 Stomatopora bajocensis (D'ORBIGNY) WALTER: 36, pl. 1, fig. 7

Material: NHMW 1866/0057/0005b (encrusting an oyster fragment, the specimen apparently identified by REUSS as *Stomatopora bouchardi* HAIME, 1854), NHMW 1866/0057/0006.

R e m a r k s: This species was not identified by REUSS (1867) in his collections from Balin. However, two fragmentary colonies of *S. bajocensis* are present, one encrusting an ammonite and a better example preserving a dozen zooids on a bivalve shell. Even though the important early astogenetic stages are lacking, the size of the zooids – up to 0.75 mm long and about 0.20 mm wide – is characteristic of *S. bajocensis* among known Jurassic species of this uniserial cyclostome genus.

Occurrence: This species was previously recorded by WALTER (1970) from the Upper Aalenian-Upper Bathonian of France and England, and by ILLIES (1963) from the Bajocian of Germany.

Stomatopora dichotomoides (D'ORBIGNY, 1850)

(Fig. 2A)

- 1850a Alecto dichotomoides D'ORBIGNY: 288
- 1867 *Stomatopora dichotoma* LAMOUROUX REUSS: 2 (partim), non pl. 1, fig. 3 [= *S. recurva* WAAGEN]
- 1867 Stomatopora dichotomoides D'ORBIGNY REUSS: 3 (partim)



Fig. 2: Photographs of cyclostome bryozoans from the Balin Oolite (Bathonian-Callovian) of Balin, Poland, in the Reuss Collection, NHM, Vienna. A: *Stomatopora dichotomoides* (D'ORBIGNY, 1850); corroded colony on cracked substrate; 1866/0057/0002a. B: *Stomatopora corallina* (D'ORBIGNY, 1850); small colony; 1866/0057/0001. C: *Stomatopora recurva* WAAGEN, 1867; branches partly overgrown by ferruginous oncolitic accretion; 1866/0057/0011b. D: *Oncousoecia* sp.; fragment of oligoserially-branched colony; 1867/0008/0219. E: *Multisparsa lamellosa* (MICHELIN, 1845); bifoliate branch; 1866/0057/0028. F: *Reptomultisparsa* cf. *norberti* HARA & TAYLOR, 1996; discoidal colony with gonozooids visible in top right; 1866/0057/0009b. Scale bars: A, C, D, E = 2 mm; B, E = 1 mm.

- 1963 Stomatopora dichotomoides (D'ORBIGNY) ILLIES: 73, pl. 8, figs 1-2, pl. 5, fig. 4, pl. 7, fig. 3, pl. 9, figs 1-3
- 1970 Stomatopora dichotomoides (D'ORBIGNY) WALTER: 39, pl. 1, fig. 9

Material: NHMW 1866/0057/0002a (on interior of pectinid), 1866/0057/0003b, 1866/0057/0005a (encrusting an *Entolium*-like bivalve), 1866/0057/0005b, 1866/0057/0006, 1866/0057/0018.

R e m a r k s: REUSS (1867) did not figure *S. dichotomoides* and the sole specimen (1866/0057/0006) in his collection labelled with this name consists of an ammonite encrusted by numerous bryozoans, among which are three different species of *Stomatopora: S. dichotomoides, S. bajocensis* and *S. recurva. S. dichotomoides* has a very similar colony-form to *S. bajocensis* (see GARDINER & TAYLOR 1982), being strictly uniserial but with somewhat larger zooids, about 0.25 mm in width. Internodes between branch bifurcations typically comprise two zooids but can contain from one to four or even more zooids.

O c c u r r e n c e : WALTER (1970) gave the range of *S. dichotomoides* as Upper Aalenian-Upper Bathonian and noted the occurrence of the species in France, England and Germany (see also ILLIES 1963). The Balin occurrence thus extends the geographical range of this species to Poland and the geological range possibly up to the Lower Callovian.

Stomatopora corallina (D'ORBIGNY, 1850) (Figs 2B, 3A-D)

1850b	Alecto	bajocensis	D'	ORBIGNY:	25	

- 1867 *Stomatopora dichotoma* LAMOUROUX REUSS: 2 (partim), non pl. 1, fig. 3 [= *S. recurva* WAAGEN]
- 1970 Stomatopora corallina (D'ORBIGNY) WALTER: 38, pl. 1, figs 10-12

Material: NHMW 1866/0057/0001.

R e m a r k s: Only one colony, comprising about 15 zooids, can be attributed to *S. corallina*, a species less common in the European Jurassic than either *S. bajocensis* or *S. dichotomoides*. Although the ancestrula is not preserved, the high angle (c. 120°) of the most proximal bifurcation (Fig. 3A) suggests that the colony may preserve the early stages of astogeny. Characteristic of *S. corallina* are the very narrow proximal parts of the zooids, as a consequence of which the two daughter zooids at branch bifurcations may not be in direct contact (Fig. 3B). Zooids are relatively large, being up to 1.18 mm long and about 0.38 mm wide. The widely spaced pseudopores are teardrop shaped and up to 12 µm long by about 10 µm wide (Fig. 3D).

Sharing the same bivalve shell substrate as the Balin colony of *S. corallina* are adnate foraminifera that can be identified as *Discoramulina* (see HARMELIN & VENEC-PEYRE 1992). In one case, a foram evidently caused deformation in the growth of a bryozoan zooid (Fig. 3C).

O c c u r r e n c e : WALTER (1970) recorded *S. corallina* from the Callovian and Oxfordian of Germany, and the Saône-Rhône and Aquitaine basins of France but not, significantly, from the Bathonian of Normandy which shares many other species with Balin.

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Fig. 3: Scanning electron micrographs of *Stomatopora* from the Balin Oolite (Bathonian-Callovian) of Balin, Poland, in the Reuss Collection, NHM, Vienna. A-D: *Stomatopora corallina* (D'ORBIGNY, 1850); 1866/0057/0001. A: earliest preserved zooids showing a high-angled bifurcation suggesting proximity to ancestrula. B: later bifurcation in which the two daughter zooids are not touching. C: growth distorted around the foraminifer *Discoramulina*. D: pseudopores. E-F: *Stomatopora recurva* WAAGEN, 1867; 1866/0057/0011b. E: oblique view of bifurcation. F: pseudopores, some infilled with material (?pyrite) appearing bright due to high electron emission. Scale bars: A, B, E = 500 µm; C = 200 µm; D, F = 100 µm.

Stomatopora recurva WAAGEN, 1867 (Figs 2C, 3E-F)

- 1867 Stomatopora recurva WAAGEN: 647, pl. 32, fig. 9a, b
- 1867 Stomatopora dichotoma LAMOUROUX REUSS: 2 (partim), pl. 1 fig. 3
- 1867 Stomatopora bouchardi HAIME REUSS: 2 (partim)
- 1867 Stomatopora dichotomoides D'ORBIGNY REUSS: 3 (partim)
- 1970 Stomatopora recurva WAAGEN WALTER: 42, pl. 1, figs 5-6

Material: NHMW 1866/0057/0002b (on exterior of modiolid), 1866/0057/0003a, 1866/0057/0006, 1866/0057/0011b (REUSS 1867: pl. 1, fig. 3a, b; given by mistake as fig. 4 in the text), 1866/0057/0012b. Questionably assigned: NHMW 1866/0057/0019.

R e m a r k s : This is the most robust of the four species of *Stomatopora* present at Balin. Colonies are pseudouniserial, the proximal parts of younger zooids initially running along the sides of the branches before coming to occupy the branch median axis (note that this feature is not evident in scanning electron micrographs which do not show the 'septa' between zooids, e.g. Fig. 3E). In the Balin specimens branches are often curved, up to 0.83 mm wide, with one to three apertures per internode, and apertures spaced about 1 mm apart. Peristomes are preserved to a maximum length of 0.13 mm, the longest examples terminating in a transversely elongate aperture 0.15 by 0.20 mm in diameter. Early astogenetic stages are present in specimen NHMW 1866/0057/0003, the protoecium being 0.25 mm wide, and the ancestrula 0.50 mm long, with an aperture about 0.08 mm in diameter. A single zooid is budded from the ancestrula, after which the branch divides at the high angle (c. 180°) typical for the first bifurcation in colonies of *Stomatopora* (GARDINER & TAYLOR 1982). In another specimen (NHMW 1866/0057/0002), branches can be traced back to a reparative regrowth from a broken branch. Growth pattern in S. recurva seems less regularly patterned than in either S. bajocensis or S. dichotomoides. Pseudopores in the Balin material are about 15 µm in length, teardrop-shaped and densely spaced (Fig. 3F).

Specimen NHMW 1866/0057/0006, a large ammonite substrate, is interesting in that it is encrusted by three different species of *Stomatopora* (*S. recurva*, *S. bajocensis* and *S. dichotomoides*), as well as '*Berenicea*' sp., serpulids, the microconchid *Punctaconchus*, cemented bivalves and thecidean brachiopods. It is unclear which (or how many) of the three *Stomatopora* species REUSS (1867) regarded as *S. dichotomoides*.

Occurrence: The identification of *S. recurva* at Balin extends the upward range of this species recorded previously from the Upper Aalenian and Lower Bajocian of Germany, France and England (WALTER 1970).

Family Oncousoeciidae CANU, 1918 Genus *Oncousoecia* CANU, 1918

> Oncousoecia sp. (Fig. 2D)

Material: NHMW 1866/0057/0008, 1867/0008/0219.

R e m a r k s : REUSS (1867) did not formally identify this species but it is represented in his collection by two colonies, the best of which encrusts the same substrate as a bryozoan

identified by REUSS as *Berenicea striata* HAIME, 1854 (NHMW 1867/0008/0219). The ribbon-like colonies of the Balin species of *Oncousoecia* usually have triserial or quadriserial branches and large zooids, up to 1.88 mm long by 0.33-0.40 mm wide, with subcircular apertures about 0.20-0.25 mm in diameter. Frontal walls are convex and have somewhat longitudinally elliptical pseudopores, zooidal boundaries being very distinct under an optical microscope. Unfortunately, neither of the Balin specimens is fertile.

Occurrence: *Oncousoecia* is a long-ranging genus, known from the Aalenian (?Sinemurian) to Recent (see TAYLOR & ZATON 2008).

Genus Microeciella TAYLOR & SEQUEIROS, 1982

Microeciella sp. (Fig. 4A-C)

1867 Diastopora lucensis HAIME – REUSS: 9 (partim)

Material: NHMW 1866/0057/0011b, 1866/0057/0014, 1866/0057/0018. In addition, a batch of rhynchonellid brachiopods from Balin includes on individual encrusted by a small colony of this species, registered as 2007z0167/0002.

R e m a r k s: All of the Balin colonies of this lobate encrusting species (Fig. 4A) are fertile, showing the small ovoidal gonozooids (Fig. 4B) that are characteristic of *Microeciella*. In specimen NHMW 2007z0167/0002, these measure about 1.13 mm in total length, 0.80 mm inflated length and 0.53 mm in width, the subterminal ooeciopore being transversely elongate and small (c. 0.05 x 0.08 mm). The small autozooids are about 0.53 mm long by 0.15 mm wide, with longitudinally elongate apertures approximately 0.10 x 0.08 mm in diameter. Pseudopores are elongate slits up to 18 µm long (Fig. 4C). Specimen NHMW 1866/0057/0018, a broken colony of *Microeciella* sp., was apparently identified as *Diastopora lucensis* HAIME, 1854 by REUSS (1867).

Autozooidal dimensions and other characteristics of this species are most similar to those of M. pollostos TAYLOR & WILSON, 1999 from the Middle Jurassic Carmel Formation of Utah but the latter species has somewhat narrower gonozooids. Further work is needed to ascertain whether the Balin material represents a new species.

Family Multisparsidae BASSLER, 1935

Genus Multisparsa D'ORBIGNY, 1853

Multisparsa lamellosa (MICHELIN, 1845) (Figs 2E, 4D-F)

- 1845 Diastopora lamellosa MICHELIN: 241, pl. 56, fig. 11
- 1867 Diastopora fenestrata REUSS: 11, pl. 2, fig. 5
- 1970 Multisparsa lamellosa (MICHELIN, 1845) WALTER: 65, pl. 6, figs 1-8

Material: NHMW 1855/0011/0096, 1866/0057/0028.

R e m a r k s: This erect bifoliate cyclostome has distinctively-shaped autozooids with frontal walls sunken beneath the raised and rounded interzooidal walls (Fig. 4E), and

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Fig. 4: Scanning electron micrographs of cyclostome bryozoans from the Balin Oolite (Bathonian-Callovian) of Balin, Poland, in the Reuss Collection, NHM, Vienna. A-C: *Microeciella* sp.; 1866/0057/0011b. A: colony lobe with deroofed gonozooid. B: gonozooid. C: pseudopores. D-F: *Multisparsa lamellosa* (MICHELIN, 1845); 1866/0057/0028. D: corroded frond. E: well preserved autozooids with thick boundary walls. F: pseudopores and a granular boundary wall. Scale bars: A, B, E = 500 μ m; C, F = 200 μ m; D 1 mm.

subcircular apertures often set someway back from the distal edge of the zooid which, in certain zooids, is drawn forwards almost to a point. The Balin material was placed in a new species, *Diastopora fenestrata*, by REUSS (1867) but is clearly synonymous with *Diastopora lamellosa* MICHELIN, as was recognized by WALTER (1970). Both specimens from Balin are predominantly embedded in rock matrix but a few autozooids are visible around the weathered edges, more in REUSS's unfigured (NHMW 1866/0057/0028) than his figured specimen (NHMW 1855/0011/0096). The longitudinally elongate gonozooids that characteristise *M. lamellosa* are not visible in the Balin material. SEM reveals the granular fabric of the salient interzooidal boundary walls on the colony surface and also the morphology of the pseudopores which are slit-like in pristine frontal walls (Fig. 4F) but become subcircular at deeper levels in abraded walls.

Occurrence: According to WALTER (1970), this is a long-ranging species (Upper Aalenian-Lower Callovian) that occurs in the Anglo-Normandy and Saône-Rhône basins as well as at Balin.

Multisparsa eudesiana (MILNE EDWARDS, 1838) (Fig. 5A-B)

- 1838 Diastopora eudesiana MILNE EDWARDS: 225, pl. 14, figs 1, 1a
- 1867 Berenicea diluviana LAMOUROUX REUSS: 6 (partim), non pl, 1, fig. 5 [= Hyporosopora sauvagei (GREGORY, 1896)]
- 1867 Berenicea insignis REUSS: 6 (partim), pl. 1 fig. 4
- 1867 Berenicea striata HAIME REUSS: 7 (partim), non pl. 1, fig. 5 [= ?Hyporosopora sauvagei (GREGORY, 1896)]
- 1970 Multisparsa eudesiana (MILNE EDWARDS) WALTER, 69, pl. 5, figs 4-6, 8-10

Material: NHMW 1866/0057/0010, 1866/0057/0011a (lectotype of *B. insignis* REUSS, 1867), 1866/0057/0026, 1867/0008/0219.

R e m a r k s: The two specimens included by REUSS (1867) in his new species *Berenicea insignis* represent different species. Only the figured specimen (NHMW 1866/0057/0011a) is here regarded as *B. insignis* and is designated as the lectotype of the species; the second specimen (NHMW 1866/0057/0012a) is described below as *Reptomultisparsa* aff. *cobra* (PITT & THOMAS, 1969). However, the REUSS collection contains three additional bryozoan colonies that are here regarded as *B. insignis*. Among these is one of the bryozoans (NHMW 1867/0008/0219) that REUSS identified as *Berenicea striata* HAIME, 1854.

The synonymy of *Berenicea insignis* REUSS, 1867 with *Multisparsa eudesiana* (MILNE EDWARDS, 1838) was verified by WALTER (1970) and the current study tentatively accepts this opinion, although it should be noted that all of the material from Balin comprises unilamellar, mostly encrusting colonies whereas *M. eudesiana* is typically found as bifoliate erect colonies in the French Bathonian.

No gonozooids are evident in the Balin specimens. However, the lectotype of *Berenicea insignis* shows the large autozooids (Fig. 5A) that are characteristic of *M. eudesiana*: frontal length averages 1.50 mm (SD 0.166 mm, range 1.18-1.73 mm, n = 10), frontal width 0.33 mm (SD 0.018 mm, range 0.30-0.35 mm, n = 10), apertural length 0.15 mm

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Fig. 5: Scanning electron micrographs of multisparsid cyclostome bryozoans from the Balin Oolite (Bathonian-Callovian) of Balin, Poland, in the Reuss Collection, NHM, Vienna. A-B: *Multisparsa eudesiana* (MILNE EDWARDS, 1838); 1867/0057/0011a. A: autozooids. B: pseudopores. C-F: *Reptomultisparsa* aff. *cobra* (PITT & THOMAS, 1969); 1866/0057/0012a. C: autozooids. D: apertures and frontal walls. E: gonozooid with ooeciopore arrowed. F: pseudopores. Scale bars: A = 500 μ m; B, F = 100 μ m; C, E = 1 mm; D = 200 μ m.

(SD 0.030 mm, range 0.10-0.20 mm, n = 10) and apertural width 0.15 mm (SD 0.023 mm, range 0.10-0.18 mm, n = 10). These dimensions match well with the values given by WALTER (1970) for autozooidal length (1.6-2 mm) and width (0.30-0.35 mm) in *M. eudesiana*. The colony is thin, usually exposing only one generation of zooids at the growing edge. Zooidal boundary walls are well defined in the Balin specimens, peristomes are preserved up to a length of 0.20 mm, terminal diaphragms are rare and pseudopores are elongates slits, about 15 µm long by a few microns wide (Fig. 5B).

Occurrence: According to WALTER (1970), *M. eudesiana* is known only from the Upper Bathonian of Normandy and from Balin.

Genus Reptomultisparsa D'ORBIGNY, 1853

Reptomultisparsa aff. cobra (PITT & THOMAS, 1969) (Fig. 5C-F)

1867 Berenicea insignis REUSS: 6 (partim), non pl. 1, fig. 4 [=Multisparsa eudesiana (MILNE EDWARDS, 1838)]
aff. 1969 Berenicea cobra PITT & THOMAS: 34, pl. 3, figs 1, 3

Material: NHMW 1866/0057/0012a (encrusting larger of the two bivalve substrates).

R e m a r k s: One of the specimens apparently placed by REUSS (1867) in his new species *Berenicea insignis* belongs to a group of species that includes *Reptomultisparsa walfordiana* (CANU & BASSLER, 1922), *R. cobra* (PITT & THOMAS, 1969), *R. incrustans* (D'ORBIGNY, 1850) and *R. microstoma* (MICHELIN, 1845). These bereniciform cyclostomes construct typically large multilamellar colonies with planar surfaces, the autozooidal frontal walls being very flat and lacking significant peristomes (Fig. 5C). Gonozooids are longitudinally elongate, inconspicuous because of their low profile, and have ooeciopores larger than the surrounding autozooidal apertures.

The Balin colony contains at least three gonozooids, all partly obscured by adherent sediment, which are about 2-3 mm long, with subcircular ooeciopores 0.25 mm in diameter (Fig. 5E). Autozooids measure 1.25-2.38 mm long by 0.30-0.47 mm wide and have subcircular apertures, many occluded by terminal diaphragms (Fig. 5D). Pseudopores are pinprick-like, about 10 μ m in diameter and moderately dense (Fig. 5F).

Autozooids are significantly larger than other species in this group. For example, type specimens of *R. walfordiana*, *R. microstoma* and *R. cobra* have respectively the following autozooidal frontal wall length and width dimensions: $0.59-0.92 \ge 0.17-0.21$ mm; $0.46-0.79 \ge 0.15-0.19$ mm; $0.71-1.28 \ge 0.18-0.22$ mm. In terms of autozooidal size, therefore, the Balin species is closest to *R. cobra*, although the autozooids are considerably larger and the gonozooids proportionally shorter in the Balin specimen suggesting that it could be an undescribed species. However, the medoicre preservation of the single known specimen does not favour the description of a new species.

Occurrence: All of the species in this group were originally described from the Bathonian, although WALTER (1970) considered the range of *R. microstoma* to be Upper Aalenian-Lower Callovian and *R. incrustans* Upper Aalenian-Upper Bathonian. *R. cobra* was originally described from the Lower Bathonian.

Reptomultisparsa cf. norberti HARA & TAYLOR, 1996 (Figs 2F, 6A-C)

- 1867 *Berenicea diluviana* LAMOUROUX REUSS: 6 (partim), non pl, 1, fig. 1 [= *Hyporosopora sauvagei* (GREGORY, 1896)], non pl. 1, fig. 2 [= *Multisparsa eudesiana* (Milne Edwards, 1838)]
- 1867 Berenicea striata HAIME REUSS: 7 (partim), non pl, 1, fig. 5 [= ?Hyporosopora sauvagei (GREGORY, 1896)]
- cf. 1996 Reptomultisparsa norberti HARA & TAYLOR: 93, figs 4-8

M a t e r i a 1: NHMW 1866/0057/0009b (encrusting modiolid bivalve), 1866/0057/0013 (encrusting broken bivalve).

R e m a r k s : Two discoidal bereniciform colonies, both fertile, resemble *Reptomultisparsa norberti* HARA & TAYLOR, 1996, a species previously known from the Oxfordian of Baltów in the Holy Cross Mountains of Poland. Autozooidal apertures seem to be slightly larger and more longitudinally elongate in the Balin material where they measure about 0.18 by 0.13 mm compared with 0.12 mm in the Baltów material, but this difference could conceivably reflect the poorer preservation of the Balin specimens, given that abrasion may cause apertures in tubuliporine cyclostomes to become enlarged and more elongate. The gonozooids have a similar morphology in colonies from the two localities, measuring about 1.5 mm long by 0.5-0.65 mm wide, with transversely elongate ooeciopores which are slightly smaller and less compressed in the Balin specimens (0.13 x 0.18 mm) than those from Baltów (0.10 x 0.25 mm). Pseudopores are elongate but not well defined in the Balin material (Fig. 6C).

Occurrence: *Reptomultisparsa norberti* was originally described from the Upper Oxfordian of Poland. If the Balin material belongs to the species then its range is extended down into the Lower Callovian, possibly even Upper Bathonian.

Genus Idmonea LAMOUROUX, 1821

Idmonea sp.

Material: NHMW 1867/0008/0219.

R e m a r k s : This fragmentary, partly sediment-covered colony of *Idmonea* encrusts a calcitic bivalve along with several other cyclostomes. The poorly preserved colony has branches about 1 mm wide comprising 4-5 zooids, possibly with marginal kenozooids. Autozooids are small and short, about 0.55 mm long by 0.25 mm wide, with apertures measuring 0.13 mm. Although the colony is fertile, the gonozooid is obscured by sediment apart from a portion of densely pseudoporous frontal wall. The Balin species of *Idmonea* appears more gracile than the two species previously described from the Jurassic [*I. triquetra* LAMOUROUX, 1821 and *I. alfredi* (HAIME, 1854); see WALTER 1970], but the available material is insufficient to justify its recognition as a new species.

Occurrence: The genus *Idmonea* has a recorded range of Aalenian to ?Maastrichtian.

Family Plagioeciidae CANU, 1918 Genus Diastopora LAMOUROUX, 1821

Diastopora? sp. (Figs 6D, 7A)

1867 Diastopora lamourouxi MILNE EDWARDS - REUSS: 9, pl. 2, fig. 4

Material: NHMW 1855/0011/0100.

R e m a r k s: The figured specimen (NHMW 1866/0057/0022) identified by REUSS (1867) as *Diastopora lamourouxi* could not be located at the time of the current study. However, two other REUSS specimens, registered under the number NHMW 1855/0011/0100, undoubtedly belong to this species. As with the figured specimen, these infertile colonies are unilamellar and at least one of them has the form of a broad tube ('cavariiform') (Fig.



Fig. 6: Scanning electron micrographs of cyclostome bryozoans from the Balin Oolite (Bathonian-Callovian) of Balin, Poland, in the Reuss Collection, NHM, Vienna. A-C: *Reptomultisparsa* cf. *norberti* HARA & TAYLOR, 1996; 1866/0057/0009b. A: edge of colony with gonozooids. B: gonozooid with ooeciopore arrowed. C: pseudopores. D: *Diastopora*? sp.; autozooids; 1855/0011/0100. Scale bars: A, B, D = 1 mm; C = 100 μ m.

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Fig. 7: Photographs of cyclostome bryozoans from the Balin Oolite (Bathonian-Callovian) of Balin, Poland, in the Reuss Collection, NHM, Vienna. A: *Diastopora*? sp.; bifurcating tubular colony; 1855/0011/0100. B: *Hyporosopora sauvagei* (GREGORY, 1896); part of discoidal encrusting colony with multiple gonozooids; 1866/0057/0017. C: *Hyporosopora tenera* (REUSS, 1867); holotype colony; 1867/0008/0220a. D: *Mesenteripora michelini* BLAINVILLE, 1830; autozooids with typically elongate apertures; 1866/0057/0023. E: *Mesenteripora? conferta* (REUSS, 1867); part of paralectotype colony; 1866/0057/0024. F: *'Berenicea' exilis* REUSS, 1867; worn colony; 1866/0057/0020. Scale bars: A, B, C, E = 2 mm; D, F = 1 mm.

7A). The elongate autozooids have relatively flat frontal walls (Fig. 6D) but zooidal boundaries are clearly visible under an optical microscope. Autozooids tend to broaden slightly around the subcircular or longitudinally elongate apertures, which are sometimes closed by terminal diaphragms. In *Diastopora lamourouxi* MILNE EDWARDS pseudopores are gull-shaped. Unfortunately, pseudopores could not be clearly resolved in the Balin material. Autozooids in the Balin material are smaller in some dimensions than *D. lamourouxi*: autozooidal length ranges from 0.88 to 1.25 mm in the Balin material (cf. 1.2-1.4 mm in *D. lamourouxi*, fide WALTER 1970), width is 0.23-0.28 mm (cf. 0.3-0.35 mm), and autozooidal aperture diameter measures 0.13-0.15 mm by 0.10-0.13 mm (cf. about 0.20 mm). Therefore, the Balin material is considered not to be *D. lamourouxi*. Even assignment to the genus *Diastopora* is equivocal in view of the occurrence of similar unilamellar colonies among other Jurassic genera such as *Patulopora* TAYLOR & WILSON, 1999.

O c c u r r e n c e : *Diastopora* has previously been recorded from the Upper Aalenian to Lower Callovian (WALTER 1970) stages of the Jurassic but the genus also occurs in the Valanginian and Hauterivian stages of the Cretaceous (WALTER 1986).

Genus Hyporosopora CANU & BASSLER, 1929

Hyporosopora sauvagei (GREGORY, 1896) (Figs 7B, 8A-F)

- 1839 *Tubipora incrustans* BEAN: 58
- 1867 Berenicea diluviana LAMOUROUX REUSS: 6 (partim), pl. 1, fig. 1 only
- ? 1867 Berenicea striata HAIME REUSS: 7 (partim), pl. 1, fig. 5
- 1867 Berenicea verrucosa MILNE EDWARDS REUSS: 7, pl. 1, fig. 7
- ? 1867 *Berenicea tenera* REUSS: 8 (partim), non pl. 1, fig. 9 [= *Hyporosopora tenera* (REUSS, 1867)]
 - 1896a Berenicea sauvagei GREGORY: 43
 - 1896b Berenicea sauvagei GREGORY GREGORY: 82, pl. 3, fig. 4
 - 1970 Plagioecia sauvagei (GREGORY) WALTER: 126, pl. 13, figs 1-4

Material: NHMW 1866/0057/0007, 1866/0057/0008, 1866/0057/0009a (on fragmentary bivalve), 1866/0057/0017. Questionably assigned: NHMW 1866/0057/0013, 1866/0057/0014, 1866/0057/0019.

R e m a r k s: BEAN's (1839) 'zoophyte' species *Tubipora incrustans* from the Middle Jurassic of Yorkshire in northern England has generally been overlooked. The original description is extremely brief and non-diagnostic, and there is no accompanying figure. However, the type specimen in the collections of the Natural History Museum, London, registered number B4854, permits the species to be distinguished as a senior synonym of *Berenicea sauvagei* GREGORY, 1896a. However, since *Tubipora incrustans* seems not to have been used in a taxonomic work since before 1899 it can be considered a *nomen oblitum* and set aside in favour of the junior synonym *Berenicea sauvagei* GREGORY, 1896.

This species is one of the commonest encrusting bryozoans from Balin, being referred to by REUSS (1867) using two, three or even possibly four separate names (the uncertainty is because it is unclear to which of several different species encrusting the same substrate REUSS was actually referring). The best specimen of *H. sauvagei* in the REUSS Collection is NHMW 1866/0057/0017 (Fig. 7B), which REUSS described and figured as

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Fig. 8: Scanning electron micrographs of *Hyporosopora sauvagei* (GREGORY, 1896) from the Balin Oolite (Bathonian-Callovian) of Balin, Poland, in the Reuss Collection, NHM, Vienna; 1866/0057/0017. A: growing edge. B: autozooids. C: pseudopores on autozooid frontal wall fouled by a tiny formaninifer (lower left). D: transition from proximal to distal dilated part of gonozooid frontal wall showing change in pseudopore density. E: gonozooid. F: two juxtaposed gonozooids (ooeciopores arrowed). Scale bars: A, B, E, F = 500 μ m; C, D = 100 μ m.

Berenicea verrucosa MILNE EDWARDS. This 20 mm-wide colony has 16-17 gonozooids, some contiguous and distorted in shape (Fig. 8F) and some without roofs but nonetheless displaying the shape characteristic of *H. sauvagei*, i.e. subtriangular to boomeranglike with lateral lobes prolonged distally of the ooeciopore. Gonozooid width ranges up to about 2.6 mm, while the slightly transverse ooeciopore measures 0.10 by 0.11 mm. In one example, the ooeciostome is bent proximally (Fig. 8E). Generally only one or two generations of zooidal buds are visible at the growing edge (Fig. 8A). Autozooidal frontal walls average about 0.30 mm in width. Peristomes of moderate length are often preserved. Most autozooidal apertures are closed by terminal diaphragms (Fig. 8B). Pseudopores are teardrop-shaped (Fig. 8C), about 12 μ m long, but slightly smaller and noticeably denser in the dilated distal parts of the gonozooids (Fig. 8D).

Occurrence: WALTER (1970) gave the range of this species as Upper Bajocian-Upper Bathonian, but the specimen of *Tubipora incrustans* described by Bean (1839) is from the Cornbrash Formation of Yorkshire which is here Lower Callovian.

Hyporosopora tenera (REUSS, 1867)

(Figs 7C, 9A-F)

1867 Berenicea tenera REUSS: 8 (partim), pl. 1, fig. 9

M a t e r i a 1: NHMW 1867/0008/0220a (holotype); in addition to the figured specimen, the reverse side of the encrusted mollusc bears a small infertile colony that is likely to be conspecific. The two other specimens identified as this species by REUSS (1867) are different species, NHMW 1866/0057/0019 possibly being *H. sauvagei*, and NHMW 1867/0008/0220b here identified as *H. undulata*.

Description: Colony encrusting, multiserial, unilamellar, sheet-like, discoidal (Fig. 7C), the holotype colony elliptical in outline with a maximum diameter of 8.5 mm; growing edge thin, generally exposing only one generation of zooids (Fig. 9B). Ancestrula overgrown by coalescent lateral lobes of colony during early astogeny (Fig. 9A).

Autozooids small, elongate, about 0.38-0.53 mm long by 0.13 mm wide; frontal walls convex, crossed by faint growth lines (Fig. 9C), zooidal boundaries clearly defined; pseudopores longitudinally elongate, often dagger-shaped, tapering distally, small, about 3 μ m wide (Fig. 9D). Apertures longitudinally elliptical, small, about 0.05-0.08 mm in diameter; terminal diaphragms common, sparsely pseudoporous or non-pseudoporous; preserved peristomes low.

Gonozooids broad, with transversely elongate (Fig. 9E), inflated frontal walls, bulbous, subtriangular, distal edge straight or slightly convex, margins indented slightly by autozooidal apertures; eight examples evident in the holotype, the two with intact roofs having total lengths of 1.13 and 1.20 mm, brood chamber lengths of 1.13 and 1.33 mm, and widths of 0.73 and 0.78 mm; floor pustulose. Ooeciopore terminal, smaller than an autozooecial aperture, transversely elliptical, about 0.08 mm wide (Fig. 9F).

R e m a r k s: WALTER (1970: 220) placed a question mark against this species in his tabulation of Jurassic bryozoans. The holotype is well preserved and has no fewer than eight gonozooids, none of which can be seen in the figure of REUSS (1867). The shape

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Fig. 9: Scanning electron micrographs of *Hyporosopora tenera* (REUSS, 1867) from the Balin Oolite (Bathonian-Callovian) of Balin, Poland, in the Reuss Collection, NHM, Vienna; 1867/0008/0220a, holotype. A: proximal zooids. B: growing edge. C: autozooids. D: pseudopores. E: gonozooid. F: broken ooeciopore (arrowed). Scale bars: A, B, C, E = 500 μ m; D, F = 100 μ m.

of the gonozooids allows unequivocal assignment of the REUSS species to *Hyporosopora*. Species of this genus differ mostly in zooidal dimensions and it can be exceedingly difficult to tell them apart, especially in material from different localities in which ecophenotypic variations may introduce 'noise'. Nevertheless, *H. tenera* does appear to differ from its most closely similar congener, *H. typica* CANU & BASSLER, 1929, which has larger autozooids, 0.20-0.30 mm wide compared with those of *H. tenera* which are less than 0.20 mm.

Occurrence: Balin Oolite (Upper Bathonian or Lower Callovian), Balin, Poland.

Hyporosopora undulata (MICHELIN, 1845)

(Figs 10A-B)

- 1845 Diastopora undulata MICHELIN: 242, pl. 56, fig. 15
- ? 1867 Berenicea tenera REUSS: 8 (partim), non pl. 1, fig. 9 [= Hyporosopora tenera (REUSS, 1867)]
 - 1970 Mesenteripora undulata (MICHELIN) WALTER: 107, pl. 11, figs 1-8

Material: NHMW 1867/0008/0220b.

R e m a r k s: The REUSS (1867) specimen here assigned to *H. undulata* is infertile but possesses the transversely ridged colony surface that is characteristic of this and a few other Jurassic bereniciform bryozoans (see HARA & TAYLOR 1996). In the Balin specimen the autozooids are about 0.30 mm in width with subcircular apertures 0.15 mm in diameter, larger than those in other transversely-ridged Jurassic cyclostomes. The transverse ridges are spaced a little less than 0.1 mm apart (Fig. 10B) and the growing edge exposes one or two generations of zooidal buds (Fig. 10A).

Occurrence: WALTER (1970) gave the range of this species as Upper Bathonian-Lower Callovian.

Hyporosopora sp.

1867 Berenicea microstoma MICHELIN – REUSS: 8, pl. 1, fig. 6
1867 Berenicea insignis REUSS: 7 (partim), non pl. 1, fig. 4 [=Multisparsa eudesiana (MILNE EDWARDS, 1838)]

Material: NHMW 1866/0057/0016. Questionably assigned: NHMW 1866/0057/0012b (encrusting small bivalve), 1866/0057/0014.

R e m a r k s: The bryozoan incorrectly identified by REUSS (1867) as *Berenicea micros-toma* MICHELIN was depicted in his figure with a strong transverse ornament. However, this is not evident in the colony itself, even though the specimen clearly matches the figure of REUSS (1867: pl. 1, fig. 6). A broken, partly sediment-covered gonozooid is present near the edge of the colony and another, de-roofed gonozooid closer to the centre. These have the subtriangular shapes typical of *Hyporosopora*. The autozooids are smaller (c. 0.25 mm wide) than those of *H. sauvagei* but larger than *H. tenera*, and have less crowded apertures than *Mesonopora concatenata* (REUSS). Two other infertile specimens among the REUSS material probably belong to this un-named species of *Hyporosopora* but they lack gonozooids.

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Fig. 10: Scanning electron micrographs of cyclostome bryozoans from the Balin Oolite (Bathonian-Callovian) of Balin, Poland, in the Reuss Collection, NHM, Vienna. A-B: *Hyporosopora undulata* (MICHELIN, 1845); 1867/0008/0220b. A: autozooids and growing edge. B: detail of autozooids showing transverse ridges. C-F: *Mesenteripora? conferta* (REUSS, 1867); 1866/0057/0026, holotype. C: folded bifoliate branch. D: autozooids. E: terminal diaphragms closing autozooidal apertures. F: pseudopores. Scale bars: A, C, D = 1 mm; B, E = 500 μ m; F = 100 μ m.

Mesenteripora michelini BLAINVILLE, 1830 (Fig. 7D)

- 1830 Mesenteripora michelini BLAINVILLE, 1830: 397
- 1867 Diastopora lucensis HAIME REUSS: 9
- 1867 *Diastopora conferta* REUSS: 10 (partim), non pl. 2, fig. 6 [=*Mesenteripora*? *conferta* (REUSS, 1867)]
- 1970 Mesenteripora michelini BLAINVILLE WALTER: 102, pl. 9, figs 2-6

Material: NHMW 1866/0057/0023, 1866/0057/0027.

R e m a r k s: Specimens of this, the type species of *Mesenteripora*, are unmistakable. The bifoliate fronds are folded into corrugations and the autozooids are very elongate, in some parts of colonies having apertures with almost straight proximal edges and nearly pointed distal edges (Fig. 7D). The frontal wall width of 0.20 mm measured in the Balin material corresponds exactly with the size given by WALTER (1970: 102) for *M. michelini*. One of the Balin colonies (NHMW 1866/0057/0027) exposes the base. This has a rugose basal lamina, suggesting that the colony may have lived attached to a soft-bodied, organic substrate.

A specimen (NHMW 1866/0057/0024) identified as *Diastopora* [=*Mesenteripora*] *michelini* by REUSS (1867) is *Mesenteripora*? *conferta* (REUSS, 1867), while another (NHMW 1866/0057/0025) is an indeterminate encrusting tubuliporine referable only to the form-genus '*Berenicea*'. In contrast, specimens placed by REUSS in *Diastopora lucensis* HAIME and his new species *Diastopora conferta* do belong to *Mesenteripora michelini*.

O c c u r r e n c e : According to WALTER (1970), *M. michelini* ranges from Upper Aalanian to Upper Bathonian and has been found in France and England. The Balin occurrence may therefore extend the upward range into the Callovian.

Mesenteripora? conferta (REUSS, 1867)

(Figs 7E, 10C-F)

- 1867 Diastopora conferta REUSS: 10 (partim), pl. 2, fig. 6
- 1867 *Diastopora michelini* MILNE EDWARDS REUSS: 10 (partim)
- 1970 Mesonopora conferta (REUSS) WALTER: 135, pl. 10, figs 3-4

M a t e r i a 1: NHMW 1866/0057/0026 (lectotype designated herein), 1866/0057/0024 (paralectotype). Note that specimen NHMW 1866/0057/0026 does not exactly match REUSS's low magnification figure (Pl. 2, fig. 6a), leaving reason to doubt that it is the specimen on which the figure was based. A second specimen in the same tray is a unilamellar bryozoan with large zooids and is not conspecific with the main piece.

Description: Colony erect, bifoliate with folded, bifurcating fronds (Fig. 10C); fronds thick, about 0.75 mm; several generations of zooids visible at growing edges. Ancestrula and early astogeny unknown.

Autozooids moderately large, frontal wall length variable (Fig. 10D), about 0.50-1.12 mm, width 0.25-0.35 mm. Apertures large, longitudinally elongate, averaging 0.20

by 0.18 mm, usually occluded by terminal diaphragms (Fig. 10E) apart from those close to growing edge; terminal diaphragms evenly pseudoporous; pseudopores of frontal wall subcircular to teardrop-shaped, small, about 7-9 μ m long (Fig. 10F).

Gonozooids not observed.

R e m a r k s: Neither of the available specimens are well preserved, both being partly embedded in hard matrix and weathered where the colony surface is exposed. Because the gonozooid is unknown in this species WALTER (1970) assigned it questionably to *Mesonopora* (see below). However, the corrugated bifoliate colony suggests that *Mesenteripora* is a more likely genus for the reception of REUSS's species, pending the discovery of gonozooids which are needed to make a more certain assignment.

Compared with other Jurassic species of *Mesenteripora*, the autozooids of *M*? *conferta* have wide frontal walls and the fronds are very thick.

Occurrence: Balin Oolite (Upper Bathonian or Lower Callovian), Balin, Poland.

Genus Mesonopora CANU & BASSLER, 1929

Mesonopora concatenata (REUSS, 1867) $(Ei \approx 11 \text{ A}, E)$

(Fig. 11A-F)

- 1867 Berenicea concatenata REUSS: 9, pl. 1, fig. 8
- 1929 Mesonopora typica CANU & BASSLER: 125, pl. 2, figs 3-4
- 1970 Mesonopora concatenata (REUSS) WALTER: 133, pl. 13, fig. 11, pl. 14, fig. 1

M at e r i a1: NHMW 1855/0011/0097 (holotype). This specimen perfectly matches Pl. 1, fig. 8a of REUSS (1867). In addition, a Balin brachiopod (NHMW 2007z0167/0001) not among the REUSS material is encrusted by three well preserved colonies of *M. concatenata*.

D e s c r i p t i o n : Colony encrusting, multiserial, unilamellar or becoming multilamellar through overgrowth from a C-shaped growing edge, subcircular in outline, reaching at least 8 mm in diameter in non-type material from Balin. Early astogenetic stages not visible in holotype, ancestrula overgrown in other colonies.

Autozooids moderate in size, relatively stout, frontal length 0.65-0.88 mm, width 0.28-0.30 mm in distal zooids from zone of astogenetic repetition; frontal walls distally convex, prominent, pseudopores teardrop-shaped, pointed distally, up to about 10 μ m in diameter, moderately densely-spaced (Fig. 11D). Apertures crowded, tending to be aligned in radial rows (Fig. 11A-B), some apertures contiguous with their distal neighbours but generally offset somewhat, longitudinally elliptical, large, about 0.23-0.30 mm long by 0.15-0.18 mm wide, occasionally slightly pointed distally, older apertures usually occluded by terminal diaphragms (Fig. 11C) with scattered pseudopores smaller than those on frontal walls; peristomes not preserved.

Gonozooids transversely elongate (Fig. 11E), margins often diffuse and indented by autozooidal apertures, brood chamber about 0.5-0.9 mm long, width difficult to determine because of multiple gonozooids situated side-by-side in holotype, 2.20-2.50 mm



Fig. 11: Scanning electron micrographs of *Mesonopora concatenata* (REUSS, 1867) from the Balin Oolite (Bathonian-Callovian) of Balin, Poland. A, B: NHMW 1855/0011/0097 (holotype). A: autozooids, deroofed gonozooid (lower left) and fouling serpulid worm (lower right). B: autozooids showing tendency for apertures to be arranged in longitudinal rows. C-F: NHMW 2007z0167/0001. C: autozooids with apertures closed by terminal diaphragms. D: pseudopores. E: gonozooid. F: ooeciopore (centre). Scale bars: A, B = 1 mm; C, F = 200 μ m; D = 100 μ m; E = 500 μ m.

wide in non-type material from Balin. Ooeciopore not identified in holotype, located terminally and slightly beyond distal margin of inflated frontal wall in non-type material (Fig. 11F), tiny, transversely elliptical, about 0.05 by 0.09 mm in diameter.

R e m a r k s: WALTER (1970) recognized that *Berenicea concatenata* was a senior synonym of *Mesonopora typica* CANU & BASSLER, 1929, the type species of *Mesonopora* CANU & BASSLER, 1929. The broad gonozooids with edges indented by autozooidal apertures are a characteristic feature of *Mesonopora* (TAYLOR & SEQUIEROS 1982). *Mesonopora concatenata* can be distinguished among Jurassic bereniciform cyclostomes by its closely spaced apertures roughly aligned in radial rows. The holotype of *M. concatenata* has an internal C-shaped growing edge, reminiscent of those described from two other Jurassic cyclostomes (TAYLOR 1976), producing an overgrowth possibly as a response to fouling of the colony surface by serpulids.

O c c u r r e n c e : In addition to the Balin Oolite (Upper Bathonian or Lower Callovian), *M. concatenata* has also been recorded from the Upper Bathonian of Normandy and England (WALTER 1970).

Genus Theonoa LAMOUROUX, 1821

Theonoa minuta (REUSS, 1867) (Fig. 12A-F)

- 1867 Pavotubigera minuta REUSS: 3, pl. 2, fig. 8
- 1970 *Theonoa chlatrata* LAMOUROUX WALTER: 190 (partim), non pl. 19, figs 8, 9, 11, non pl. 20, fig. 1 [= *Theonoa chlatrata* LAMOUROUX, 1821]

M a t e r i a 1: NHMW 1866/0057/0029, comprising at least six small colonies encrusting the steinkern of a bivalve, the fertile colony shown here in Fig. 12A-D is designated as the lectotype, the remainder as paralectotypes, including the seemingly infertile colony figured by REUSS (1867: Pl. 2, fig. 8b).

Description: Colony encrusting, multiserial, unilamellar, fan-shaped (Fig. 12A, E), small (< 5 mm diameter), fasciculate, the fascicles initially uniserial but becoming multiserial (Fig. 12C), new fascicles originating both by bifurcation and intercalation, spacing between adjacent fascicles measured centre-to-centre about 0.5 mm. Basal lamina with distal fringe extending about 0.1 mm beyond zooidal budding zone (Fig. 12C). Ancestrula in lectotype corroded (Fig. 12B), protoecium 0.14 mm wide.

Autozooids small, apertures rounded-quadrate in shape, about 0.10 mm in transverse diameter. Pseudopores subcircular, about 10 μ m in diameter (Fig. 12F).

Gonozooid (Fig. 12D) in lectotype obscured proximally, width 0.63 mm, ooeciopore tiny, about 0.05 mm in diameter, subterminal, located atop a slight ooeciostome.

R e m a r k s: Although WALTER (1970) placed *Theonoa minuta* in synonymy with *T. chlatrata* LAMOUROUX, 1821, a species originally described from the Bathonian of Normandy, the small size of the colonies, autozooids and gonozooids in the Balin material suggests that REUSS's species may be distinct. It is currently known only with certainty from Balin, whereas *T. chlatrata* is more widely distributed in time and space,



Fig. 12: Scanning electron micrographs of *Theonoa minuta* (REUSS, 1867) from the Balin Oolite (Bathonian-Callovian) of Balin, Poland, in the Reuss Collection, NHM, Vienna; 1866/0057/0029. A-D: lectotype. A: fan-shaped colony. B: ancestrula with protoecium at lower right. C: growing edge. D: gonozooid with ooeciopore arrowed. E-F: paralectotype. E: colony; F: pseudopores. Scale bars: A, E = 1 mm; B, $D = 200 \mu \text{m}$; $C = 500 \mu \text{m}$; $F = 100 \mu \text{m}$.

being recorded by WALTER (1970) from the Upper Aalenian – Upper Oxfordian of France, England and Germany).

Occurrence: Balin Oolite (Upper Bathonian or Lower Callovian), Balin, Poland.

Family Incertae sedis

'Berenicea' exilis REUSS, 1867 (Fig. 7F)

1867 Berenicea exilis REUSS: 8, pl. 2, fig. 3

M a t e r i a 1: NHMW 1866/0057/0020, 1866/0057/0021. Neither of these specimens can be matched with REUSS'S figure: the putative figured specimen (NHMW 1866/0057/0020) encrusts a different-shaped oyster, whereas the second specimen lacks the distinctive serpulid shown at the top of the figure of REUSS.

R e m a r k s: The status of this species is unclear. Both studied specimens comprise several iron-stained and abraded bereniciform cyclostomes in which gonozooids are not visible. Autozooids are about 0.15 mm wide and have closely spaced, longitudinally elongate apertures measuring about 0.13 by 0.09 mm. WALTER (1970: 219) placed a question mark against the species and provided no redescription. Until better-preserved, fertile material is forthcoming, the affinity of '*Berenicea' exilis* REUSS, 1867 must remain questionable.

Occurrence: Balin Oolite (Upper Bathonian or Lower Callovian), Balin, Poland.

Suborder Cerioporina HAGENOW, 1851 Family Cavidae D'ORBIGNY, 1854 Genus *Ceriocava* D'ORBIGNY, 1854

Ceriocava corymbosa (LAMOUROUX, 1821) (Figs 13A, 14A-C)

- 1821 Millepora corymbosa LAMOUROUX: 87, pl. 83, figs 8-9
- 1867 Heteropora conifera LAMOUROUX REUSS: 12 (partim), pl. 1, fig. 10, pl. 2, fig. 2 only
- 1970 *Ceriocava corymbosa* (LAMOUROUX) WALTER: 148, pl. 15, figs 6-11, pl. 16, figs 1-5
- 1976 *Ceriocava corymbosa* (LAMOUROUX) NYE: 43, pl. 1, fig. 1, pl. 2, fig. 1, pl. 3, figs 1-3, pl. 4, fig. 1, pl. 5, figs 1-3, pl. 6, figs 1-3

Material: NHMW 1855/0040/0094a (larger specimen), 1855/0040/0095. Non-REUSS material: NHMW 2007z0167/0006-0009.

R e m a r k s: The free-walled cerioporine cyclostomes from Balin were all placed by REUSS (1867) in *Heteropora conifera* LAMOUROUX. WALTER (1970) considered these specimens to be *Ceriocava corymbosa* (LAMOUROUX) but study of the REUSS material, plus other specimens from Balin, reveals the presence of two species. These are provisionally identified here as *Ripisoecia conifera* (LAMOUROUX) and *Ceriocava corymbosa*



Fig. 13: Photographs of cerioporine cyclostome bryozoans from the Balin Oolite (Bathonian-Callovian) of Balin, Poland, in the Reuss Collection, NHM, Vienna. A: *Ceriocava corymbosa* (LAMOUROUX, 1821); incipient bifurcating branch formed by overgrowths; 1855/0040/0095. B: *Ripisoecia conifera* (LAMOUROUX, 1821); fungiform colony; 1855/0040/0094b.

(LAMOUROUX). The difference between *R. conifera* and *C. corymbosa* is evident by comparing Figures 1 and 2 in Plate 2 of REUSS (1867). These high magnification figures show respectively the mix of autozooidal and smaller kenozooidal apertures found in *R. conifera*, contrasting with the monomorphic autozooidal apertures with thicker interzooidal walls which are characteristic of *C. corymbosa* (compare also Figs 14D and 14A herein). In addition, Balin colonies of *R. conifera* are globular to fungiform (Fig. 13B), whereas those of *C. corymbosa* are ramose and bifurcate (Fig. 13A). Unfortunately, gonozooids are not visible in any of the Balin cerioporines.

Unlike the fixed-walled tubuliporine cyclostomes described above, cerioporines have dynamic growing colony surfaces that can change in appearance during colony growth as the zooids age. A thorough study of such variation within Jurassic cerioporines, utilizing thin sections as well as surface morphology, is needed to refine species-level taxonomy. Conservatively, only four or five cerioporine species are present in the Jurassic but this may be a significant underestimate of their true diversity.

The Balin specimens of *C. corymbosa* have ramose colonies with thick branches each comprising a stack of cap-like overgrowths (Figs 13A, 14A). In this respect they differ from similar colonies of *C. corymbosa* from the Normandy type region with simple branches, NYE (1976: 44) commenting that 'Intrazooidal overgrowths occur, but are generally local in extent.' Nevertheless, *C. corymbosa* as currently understood encompasses a wide range of colony morphotypes (WALTER 1970). Apertural diameter in the Balin material is less than 0.25 mm, compared with the value of 0.30-0.40 mm quoted by WALTER (1979: 151) for French specimens of *C. corymbosa*. Pseudoporous terminal diaphragms occlude many of the autozooidal apertures slightly beneath their distal rims (Fig. 14B). The pseudopores are circular, about 12 μ m wide, and regularly and closely spaced (Fig. 14C). Interzooidal walls are 0.05-0.13 mm thick.

Occurrence: Upper Aalenian to Upper Oxfordian according to WALTER (1970).

Family Heteroporidae WATERS, 1880

Genus Ripisoecia CANU & BASSLER, 1922

Ripisoecia conifera (LAMOUROUX, 1821) (Figs 13B, 14D-F)

- 1821 Millepora conifera LAMOUROUX: 87, pl. 83, figs 6-7
- 1867 *Heteropora conifera* LAMOUROUX REUSS: 12 (partim), pl. 1, fig. 12, pl. 2, fig. 1 only
- 1970 Ripisoecia conifera (LAMOUROUX) WALTER: 160, pl. 16, figs 6-12, pl. 17, figs 1-2
- ? 1976 Reptonodicava globosa MICHELIN NYE: 140, pl. 41, fig. 1, pl. 42, fig. 1, pl. 43, figs 1-3, pl. 44, figs 1-2

Material: NHMW 1855/0040/0094b (smaller specimen). Non-REUSS material: NHMW 2007z0167/0005.

R e m a r k s: The REUSS specimen here attributed to this species is fungiform (Fig. 13B), with growing edges lapping from the head onto the short stalk. Autozooecial apertures are up to 0.30 mm in diameter (cf. 0.25-0.30 mm given by WALTER (1970) for this species), rounded polygonal in shape, and separated by walls 0.05-0.08 mm in thickness with a narrow median ridge. The second specimen is also fungiform and has some apertures closed by terminal diaphragms. These have sparser pseudopores than *Ceriocava corymbosa*.

Occurrence: Upper Bajocian to Lower Callovian according to WALTER (1970).

Discussion

As in most Jurassic bryozoan faunas (TAYLOR & ERNST 2008), encrusting species outnumber erect species among the specimens from Balin. Two encrusting colony-forms predominate: uniserial branching runners (Fig. 2A-C), and multiserial spots or sheets (Figs 2F, 7B, C, F). These represent different strategies for utilizing substrate space in the face of competition from other organisms, the runners being fugitives adept at seeking spatial refuges, and the spots/sheets confrontational strategists better capable of defending the space they occupy (TAYLOR 1979). Almost all Jurassic runner-like cyclostomes are currently placed in the genus *Stomatopora*, notwithstanding issues over the morphology of the type species (*S. dichotoma*) which differs in certain respects from other Jurassic species placed in the genus (e.g. PITT & TAYLOR 1990).

The taxonomy of the multiserial encrusting species is more complex. REUSS (1867), in common with other 19th century taxonomists, assigned the majority to *Berenicea* LAMOUROUX, 1821. More recently a plethora of genera distinguished by the morphology of their gonozooids has been introduced, while '*Berenicea*' itself has been relegated to the status of a form-genus (TAYLOR & SEQUEIROS 1982). Gonozooids are swollen polymorphic zooids used for brooding larvae in cyclostome bryozoans. They are recognized as key features in cyclostome taxonomy at various hierarchical levels, from species through to suborder, and enable the distinction between taxa that may be almost identical in other aspects of their morphology. Not all cyclostome colonies possess gonozooids; in the Jurassic it is not uncommon to find populations in which only 10% of colonies



Fig. 14: Scanning electron micrographs of cerioporine cyclostome bryozoans from the Balin Oolite (Bathonian-Callovian) of Balin, Poland. A-C: *Ceriocava corymbosa* (LAMOUROUX, 1821); NHMW 1855/0040/0095. A: edge of overgrowth. B: autozooids closed by terminal diaphragms and thick interzooidal walls. C: detail showing pseudopores in diaphragm. D-F: *Ripisoecia conifera* (LAMOUROUX, 1821); NHMW 2007z0167/0005. D: colony surface. E: autozooids and kenozooids, some closed by terminal diaphragms, others by sediment. F: detail of terminal diaphragms with pseudopores.

develop gonozooids, making identification problematical if only small numbers of colonies are available for study. Although a rather high proportion of the cyclostomes in the Balin material described by REUSS (1867) possess gonozooids, these features were totally neglected by REUSS. In some instances, his figures seem deliberately to omit gonozooids from specimens that can be observed clearly to possess them in abundance. It can only be presumed that REUSS did not regard gonozooids to be of any taxonomic value.

The availability of SEM makes available another taxonomic character, pseudopore morphology, inaccessible to REUSS and seldom included in subsequent descriptions of Jurassic bryozoan species. Pseudopores are tiny perforations in the skeletal layers of exterior walls closed on the outer surface by a cuticular layer in living cyclostomes. In Jurassic cyclostomes they vary from slit-shaped (e.g. Fig. 5B) to subcircular (e.g. Fig. 5F), teardrop-shaped (e.g. Fig. 8C) or gull-shaped. Differences in pseudopore diameter and spacing are also evident between species. In some instances, closely similar Jurassic tubuliporines can be readily distinguished using pseudopore morphology. However, well-preserved material is needed if pseudopores are to be used taxonomically: regardless of their external shape, pseudopores in abraded specimens tend to be subcircular.

Jurassic bryozoan biogeography is poorly understood, in part reflecting the patchy records of Jurassic bryozoans around the globe. The highest diversities are found in the carbonate facies of the Normandy Bathonian. Bryozoans are noticeably less diverse in the Callovian and succeeding stages of the Upper Jurassic (TAYLOR & ERNST 2008) where bryozoan- and brachiopod-rich carbonates are typically replaced around the Anglo-Paris Basin by clays or coral- and sponge-rich carbonates. HARA (2007) remarked how an easterly migration of facies belts during the Jurassic may have led to a corresponding movement of bryozoan diversity maxima. The fact that species regarded as characteristic of the Normandy Bathonian are present in the probable Callovian of Balin lends support to this notion.

Similarities between the Balin bryozoan fauna and that described from the Bathonian of Normandy are striking. At least 10 (43%) of the 23 species recorded from Balin also occur in the Normandy Bathonian. Conspicuous by their absence at Balin are the narrow branched dendroid tubuliporines characteristic of the Normandy successions, such as *Entalophora annulosa* (MICHELIN, 1845) *E. cellarioides* LAMOUROUX, 1821 and *Bisidmonea tetragona* (LAMOUROUX, 1821). Also missing is the highly distinctive genus *Terebellaria* which is known to range through the Bathonian and Callovian (TAYLOR 1978).

Another comparison can be made with the Callovian of Zalas, which is very close to Balin. HARA (2007) recently figured some of the Zalas bryozoan fauna. This appears to be dominated by encrusting tubuliporines belonging to *Stomatopora* and '*Berenicea*' but their specific identities are as yet unknown. Much further east, in the region of Moscow, a bryozoan fauna comprising 20 species was described by GERASIMOV (1955). This fauna is in the process of being re-evaluated by L.A. VISKOVA (e.g. VISKOVA 2007). Its biogeographical affinity to the bryozoan fauna from the Balin Oolite awaits analysis.

Local conditions at Balin were evidently favourable to the establishment of a bryozoan biota numbering 23 species. By Jurassic standards this is diverse: few Jurassic bryozoan faunas contain more than 20 species (TAYLOR & WILSON 1999). Sedimentary condensation could have contributed to the high diversity at Balin, the extreme time-averaging mixing species that lived at different times through a lengthy geological interval, but the availability of hard substrates over a long period was probably also a significant factor.

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