

Toarcian bryozoans from Belchite in north-east Spain

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Synopsis

A small fauna of bryozoans is described from the Upper Toarcian of Belchite near Zaragoza, Spain. *Microeciella* gen. nov. is proposed for bereniciform tubuloporinids previously assigned to *Microecia* but differing from the type species of that genus in having small gonozooids with ovate dilated portions. Together with the type species of *Microeciella*, *M. beliensis* sp. nov., the Belchite bryozoans consist of *M. reflexa* sp. nov., '*Proboscina*' cf. *divisi* Vine and an undetermined bereniciform tubuloporinid. *M. reflexa* is unusual in having an erect ancestrular tube from which a daughter zooid descends to re-establish contact with the substrate. The identity of various genera used for tubuloporinids of the '*Berenicea*' type is discussed.

Introduction

Few records exist of Jurassic bryozoans from countries other than England, France and Germany, and the great majority of described species occur in rocks of mid-Jurassic age. These geographical and stratigraphical limitations inhibit a close understanding of bryozoan evolution at a time when the Cyclostomata were entering an important period of diversification. Therefore, the discovery of a small but well-preserved bryozoan fauna from the Toarcian of Spain is significant and warrants description in this short paper. It also provides the opportunity to discuss the identity of several genera which have been proposed to subdivide so-called '*Berenicea*', a bryozoan ubiquitous in the Jurassic.

Material is deposited in the palaeontological collections of the British Museum (Natural History), abbreviated BM(NH), and in the collections of the Departamento de Paleontología, Universidad de Zaragoza, abbreviated UZ. All figured material is in the BM(NH).

Previous records of Toarcian bryozoans

When describing a small bryozoan fauna from the Toarcian of Banne in the Saône-Rhône Basin of France, Walter (1970 : 244) remarked on the rarity of bryozoans in Toarcian deposits. The Banne bryozoans are of early Toarcian age (*falciferum* Zone) and consist of *Radicipora radicipiformis* (Goldfuss) and *Neuropora* sp., the latter now considered to be a sclerosponge genus (Każmierczak & Hillmer 1974). Also from France, Dumortier (1874) described two species from Crussol: *Diastopora crussolensis* is a discoidal bereniciform tubuloporinid but his figures (Dumortier 1874 : pl. 48, figs 11, 12) do not reveal the presence of gonozooids necessary for a more up-to-date generic attribution; *Berenicea garnieri* is indeterminable from the figure (1874 : pl. 48, fig. 13) and may not even be a bryozoan.

From the 'Ob. Lias' Quenstedt (1852 : 637; pl. 56, fig. 10) described *Diastopora liasica*, a straggly probosciniiform tubuloporinid without visible gonozooids.

Spiropora liassica Tate, 1875, is an erect, vinculariiform cyclostome which occurs in the

U. Pliensbachian of England but was also recorded by Tate in the Toarcian '*Leptaena*' Bed at May in Normandy.

Walford (1887) described *Tubulipora inconstans* from the Transition Bed (Toarcian) at Appletree near Banbury, and Badby near Daventry, both in the English Midlands. This erect cyclostome was placed in synonymy with *Mesenteripora wrighti* Haime, 1854, by Walter & Powell (1973).

One of the few Jurassic bryozoans hitherto recorded from North America is *Heteropora tipperi* Henderson & Perry from early Toarcian rocks in British Columbia (Henderson & Perry 1981).

Including the species described in the present paper, the worldwide diversity of Toarcian bryozoans so far described amounts to about 10 species. However, these include a fairly wide variety of forms, suggesting that a much greater number of species lived in Toarcian times than is evident from current knowledge of the fossil record.

The Toarcian of Belchite

Belchite is situated 40 km SSE of Zaragoza in the north-east of Spain. A Jurassic sequence of Sinemurian to Bathonian age has been described by Sequeiros *et al.* (1978). Bryozoan-encrusted shells of the large bivalve *Plagiostoma* occur in the 3 m of rock designated Beds 29–34. These lie within the upper part of the Turmiel Marls Formation (Goy *et al.* 1976) and are Upper Toarcian. The ammonites from Beds 29–34 suggest that they span the *variabilis*, *thouarsense*, *insigne* and *pseudoradiosa* Zones.

Sequeiros & Mayoral (1982) and Mayoral & Sequeiros (1981) have studied the palaeoecology of the encrusting epifauna and boring infauna of shells from various parts of the Belchite succession. A sample of almost 100 *Plagiostoma* shells has been collected from the U. Toarcian. Although Mayoral & Sequeiros (1981) regarded these as *P. gigantea* (Sowerby) they differ from the type specimen of this species and are more appropriately named *P. cf. hersilia* (d'Orbigny). The shells are encrusted by serpulids (*Dorsoserpula*, *Cycloserpula*, *Tetraserpula*), thecidean brachiopods, cemented bivalves and the bryozoans described herein which Mayoral & Sequeiros (1981) identified provisionally as *Berenicea* sp. and *Stomatopora* sp. Scanning electron microscopy undertaken during the present study has revealed two additional encrusters, a planispirally-coiled foraminifer and a straight tubular microfossil that may also be a foraminifer.

Systematic descriptions

Order CYCLOSTOMATA Busk, 1852

Suborder TUBULOPORINA Milne-Edwards, 1838

? Family ONCOUSOECIIDAE Canu, 1918

Genus *MICROECIELLA* nov.

DIAGNOSIS. Tubuloporina with multiserial colonies, fan-shaped or discoidal (bereniciform); gonozooids small with a long proximal frontal wall similar to that of autozooids, and a dilated distal frontal wall which is longitudinally ovate in outline; oeciopores small, circular or transversely elongate, located subterminally.

TYPE SPECIES. *Microeciella beliensis* sp. nov.; L. Jurassic (U. Toarcian) of Belchite, near Zaragoza, Spain.

REMARKS. Jurassic bereniciform and probosciniiform tubuloporinids having small gonozooids with longitudinally ovate dilated frontal walls and small oeciopores have been assigned (e.g. Walter 1970, Taylor 1981) to *Microecia* Canu, 1918. This assignment is now considered to be unsuitable because the type species of *Microecia* by original designation, the

living *Diastopora sarniensis* Norman, 1864, has large gonozooids with broad dilated frontal walls penetrated by autozooids. However, in his original description of *Microecia*, Canu (1918) noted its small gonozooids. The other extant species referred by Canu to *Microecia* is *Diastopora suborbicularis* Hincks, 1880, which does have gonozooids matching those of Canu's description. For this reason Harmelin (1976a) proposed that *D. suborbicularis* should replace *D. sarniensis* as the type species of *Microecia*. Harmelin acknowledged that a decision of the I.C.Z.N. would be needed to validate this substitution. In its absence the genus *Microecia* is defined by its valid type species *D. sarniensis* which Harmelin (1976a: 136) considers to be a species of *Plagioecia* Canu, 1918. The gonozooid of *D. suborbicularis* suggests affinities with *Hyporosopora* Canu & Bassler, 1929 (see p. 127).

Microeciella is here proposed for bereniciform tubuloporinids with small gonozooids having longitudinally ovate dilated frontal walls. Apart from the type species, *M. beliensis* sp. nov., two other Jurassic species are referred to *Microeciella*, *M. reflexa* sp. nov. and *Microecia matisconensis* Walter, 1970. Probosciform tubuloporinids with similar gonozooids (e.g. *Diastopora belemnitarum* d'Orbigny, 1850, *Microecia southwellensis* Taylor, 1981, *Proboscina ornata* Vine, 1893, all from the Jurassic) may require a second new genus but their revision is beyond the scope of this paper.

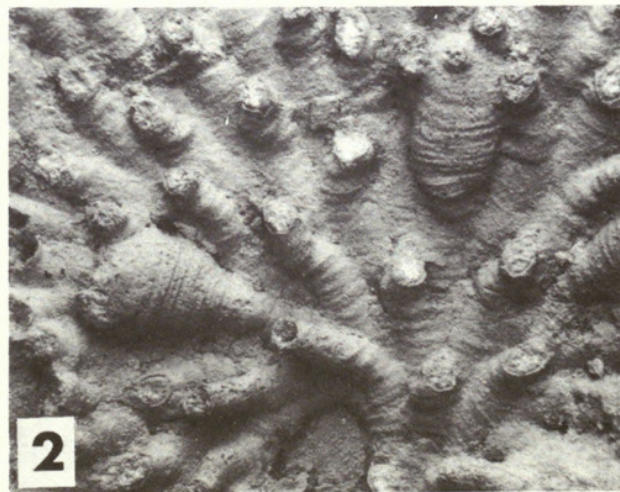
Gonozooids of *Microeciella* differ minimally from autozooids; the distal, densely pseudoporous frontal wall of the gonozooid is dilated to a comparatively small degree and is preceded by a long, proximal frontal wall which is indistinguishable from the frontal wall of an autozooid. Gonozooids occupy the same budding position as autozooids. Therefore, on the assumption that bryozoan gonozooids evolved from autozooids by progressive partitioning of reproductive function within colonies and concomitant morphological differentiation, the gonozooids of *Microeciella* may be regarded as primitive for the Tubuloporina. This inference is supported by the stratigraphically early occurrence of the genus. The gonozooids of *Microeciella* would appear to be more primitive than the tiny gonozooids budded on the peristomes of some living stomatoporids (Harmelin 1974) which were considered by Harmelin (1976b: 612) to represent the most primitive form of tubuloporinid gonozooid.

Microeciella beliensis sp. nov.

Figs 1, 2, 8, 10

DIAGNOSIS. *Microeciella* having small autozooids and gonozooids with circular ooeciopores.

HOLOTYPE. BM(NH) D.53321, colony a (Figs 1, 13); U. Toarcian, Belchite, Zaragoza, Spain. L. Sequeiros Coll.



Figs 1, 2 *Microeciella beliensis* gen. et sp. nov. U. Toarcian, Belchite, Spain. Fig. 1, holotype, D.53321, colony a; $\times 10$. Fig. 2, paratype, D.53321, colony b, showing two gonozooids; $\times 27$. Together with Figs 3–5, these are scanning electron micrographs of uncoated specimens taken using back-scattered electrons in a CFACS environmental chamber.

PARATYPES. BM(NH) D.53321, colonies b (Fig. 2), c; UZ SBE-4(a-c), SBE-10, SBE-17(a, b). All U. Toarcian, Belchite.

DESCRIPTION. Colony small (generally <5 mm in diameter), encrusting, multiserial, bereniciform – initially fan-shaped but becoming discoidal (Fig. 1) with 'windows' of substrate visible between early zooids and lateral lobes of the fan. Ancestrula overgrown by later zooids. Fan-shaped peripheral subcolonies may develop between areas of inactive growth margin.

Autozooids slender, frontal walls about 0.80 mm long and 0.20 mm wide. Apertures are longitudinally elongate, small, their diameter varying between 0.14×0.12 mm and 0.08×0.06 mm depending on preservation of the peristome which tapers distally and has a maximum observed length of 0.23 mm. Peristome inclined at an acute angle to the colony surface. Terminal diaphragms and ontogenetic zonation not apparent.

Table 1 Gonozooid dimensions (mm) in *Microeciella beliensis* gen. et sp. nov. Abbreviations: \bar{x} = mean; SD = standard deviation; CV = coefficient of variation; Nz = number of gonozooids measured; Nc = number of colonies sampled; R = observed range; tgl = total length of gonozooid frontal wall; igl = length of inflated distal frontal wall; gw = width of frontal wall (maximum).

	\bar{x}	SD	CV	Nz	Nc	R
tgl	1.10	0.137	12.5	14	5	0.75–1.28
igl	0.65	0.083	12.8	16	6	0.51–0.78
gw	0.37	0.022	6.0	15	6	0.33–0.41

Gonozooids (see Table 1 for dimensions) present in all colonies examined. A long proximal frontal wall, indistinguishable from that of an autozooid, gives rise to a dilated, distal frontal wall, which is small and ovate to subpyriform (Fig. 2), and densely pseudoporous. Ooeciopore located subterminally, smaller than autozooid apertures, approximately circular and 0.05–0.06 mm in diameter. Ooeciostome curved slightly proximally, maximum observed length 0.08 mm.

REMARKS. The trivial name *beliensis* derives from the Roman city of Belia, which was situated close to the type locality of Belchite.

Microeciella matisconensis (Walter) resembles *M. beliensis* but the gonozooid of this French Callovian species differs from that of *M. beliensis* in being wider (0.50–0.60 mm) and in having a marked constriction between the proximal and distal dilated portions of the frontal wall.

Microeciella reflexa sp. nov.

Figs 3–5, 7–8

DIAGNOSIS. *Microeciella* having autozooids of moderate size; gonozooids constricted and arched at the transition between proximal and distal inflated frontal wall; ooeciopores transversely elliptical; erect ancestrular tube budding a second generation zooid which descends to the substrate and grows at 90° to the principal growth direction of the ancestrula.

HOLOTYPE. BM(NH) D.53320, colony a (Figs 3, 4, 11); U. Toarcian, Belchite, Zaragoza, Spain. L. Sequeiros Coll.

PARATYPES. BM(NH) D.53320, colonies b–m (Figs 6, 7, 11); D.53321, colony d (Figs 5, 13), D.53323, S.E.M. stub (Figs 9, 10) and colonies a–b; D.53324a–b, D.53325, D.53326 (Fig. 12), UZ SBE-4(d), SBE-6, SBE-23, SBE-24. All U. Toarcian of Belchite.

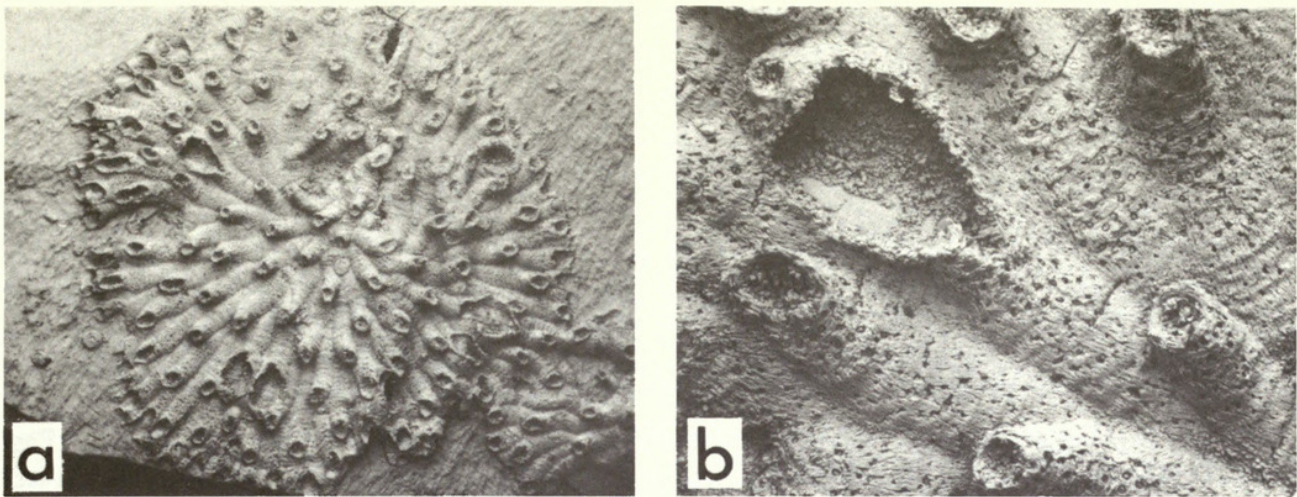


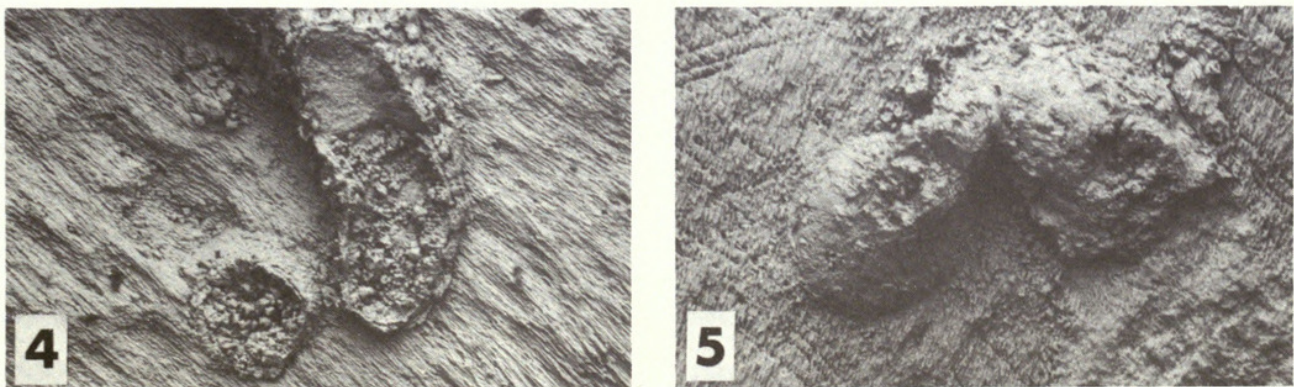
Fig. 3 *Microeciella reflexa* gen. et sp. nov. U. Toarcian, Belchite, Spain. **Holotype**, D.53320, colony a. a, general view of colony; $\times 6$. b, gonozooid with dilated part of frontal wall abraded; $\times 40$.

DESCRIPTION. Colony encrusting, multiserial, fan-shaped or discoidal bereniciform (Fig. 3a). Peripheral fan-shaped subcolonies may develop, some overgrowing earlier zooids. There is a substantial increase in zooid size during early astogeny.

Protoecium 0.17–0.20 mm in diameter, giving rise to an obliquely inclined erect ancestrular tube which is free of the substrate (Fig. 6). The ancestrula, overgrown in large colonies, buds a second generation zooid which descends to re-establish contact with the substrate. In abraded colonies (Fig. 5a) the resultant break in continuity of the basal lamina between protoecium and the remainder of the adnate colony is clearly seen. Zooid budded from the ancestrula is orientated at about 90° to the growth direction of the ancestrula (Fig. 5b). This bend in growth direction is left-handed in some colonies, right-handed in others.

Autozooids moderately large, elongate, with frontal walls averaging in length 0.92 mm (observed range 0.71–1.16 mm) and in width 0.23 mm (observed range 0.20–0.27 mm). Apertures longitudinally elongate, up to 0.20×0.12 mm in autozooids lacking peristomes but smaller when the distally tapering peristome is preserved. Peristomes bend to become almost perpendicular to the colony surface. Some autozooids possess terminal diaphragms though ontogenetic zonation is not clearly developed.

Gonozooids developed in a minority of colonies (see Table 2 for dimensions). A long proximal frontal wall, indistinguishable from that of an autozooid, gives rise to a dilated distal frontal wall, small and ovate to subpyriform in outline shape. Frontal wall is arched



Figs 4, 5 *Microeciella reflexa* gen. et sp. nov. U. Toarcian, Belchite, Spain. Early growth stages (cf. Fig. 6). Fig. 4, paratype, D.53320, colony a, abraded specimen showing break in continuity between protoecium and second zooid on the substrate; $\times 70$. Fig. 5, paratype, D.53320, colony m, small colony consisting of protoecium, erect ancestrular tube, and a second zooid which is orientated at 90° to the ancestrula; $\times 67$.

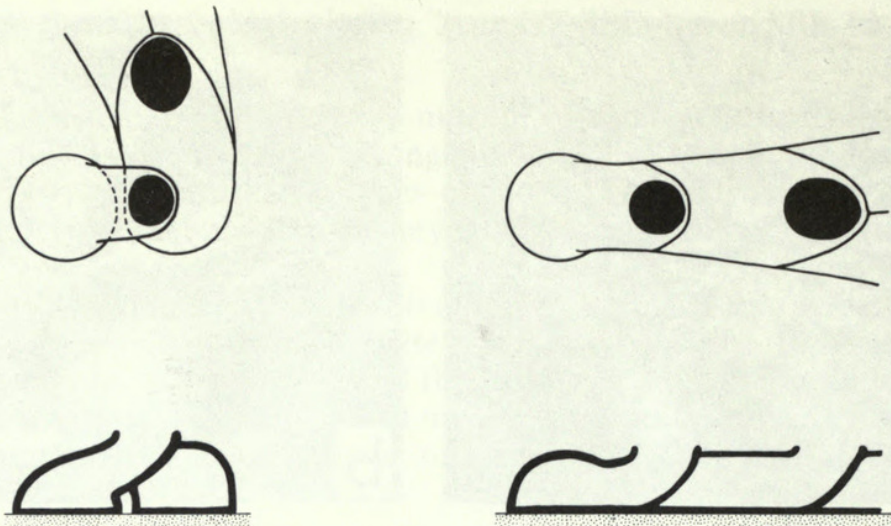
***Microeciella reflexa*****conventional tubuloporinid**

Fig. 6 Diagram contrasting the early growth stages of *Microeciella reflexa* gen. et sp. nov. and a conventional tubuloporinidean cyclostome. Colonies are shown in surface view (above) and in vertical section (below). In *M. reflexa* an erect ancestrular tube, free of the substrate (stippled), arises from the protoecium. Budded from the ancestrula is a second generation zoid which descends to the substrate and is orientated at 90° to the ancestrula.

Table 2 Gonozooid dimensions (mm) in *Microeciella reflexa* gen. et sp. nov. For abbreviations see Table 1.

	\bar{x}	SD	CV	Nz	Nc	R
tgl	1.22	0.092	7.6	8	3	1.05–1.35
igl	0.56	0.120	21.3	9	3	0.39–0.80
gw	0.38	0.044	11.7	10	3	0.32–0.45

upwards (Fig. 7b) and somewhat constricted in width (Fig. 7a) between proximal and distal parts of the gonozooid. Ooeciopore subterminal, transversely elliptical (Fig. 3b), and at about 0.07×0.09 mm in diameter, smaller than autozoid apertures. Ooeciostomes not preserved.

REMARKS. This species is characterized by its distinctive early growth stages with an erect ancestrular tube and a second generation zoid bent or 'reflexed' by about 90° to the growth direction of the ancestrula.

M. reflexa is distinguished from *M. beliensis* by the larger size of its autozooids, apparent in Fig. 13, and the arched and constricted transition between proximal and distal parts of the gonozooid frontal wall which is very similar in size in both species (compare Tables 1 and 2). Colonies of *M. reflexa* are often larger than those of *M. beliensis* but some gonozooids are less frequently developed. Like *M. beliensis*, *M. reflexa* differs from *M. matisconensis* (Walter) in having narrower gonozooids. Details of early astogeny, another potential distinguishing feature, are unknown in both *M. beliensis* and *M. matisconensis*.

Family **STOMATOPORIDAE** Pergens & Meunier, 1886

'Genus **PROBOSCINA** Audouin, 1826'

'*Proboscina*' cf. *divisi* Vine, 1893

MATERIAL. BM(NH) D.53327, colony a; UZ SBE-6, SBE-8, SBE-13. U. Toarcian, Belchite, Zaragoza, Spain. L. Sequieros Coll.

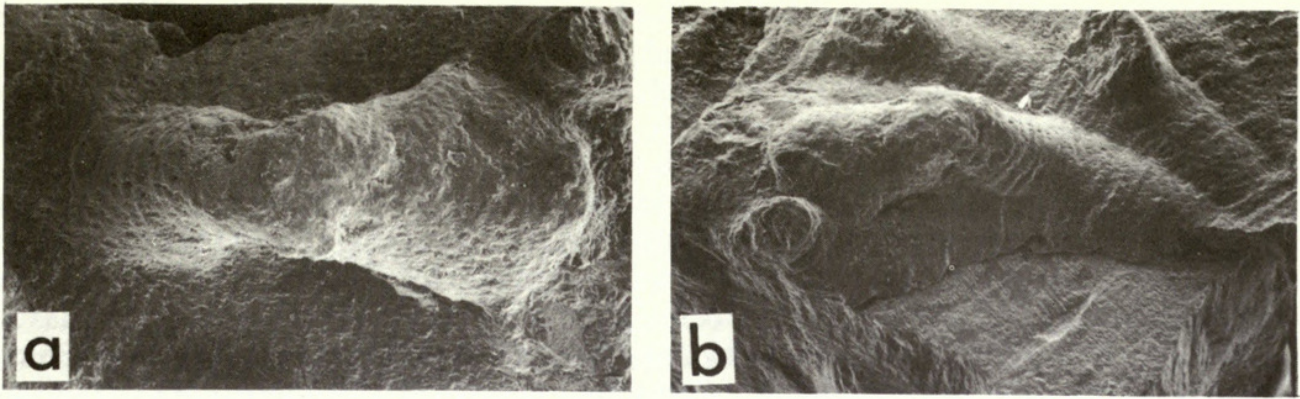
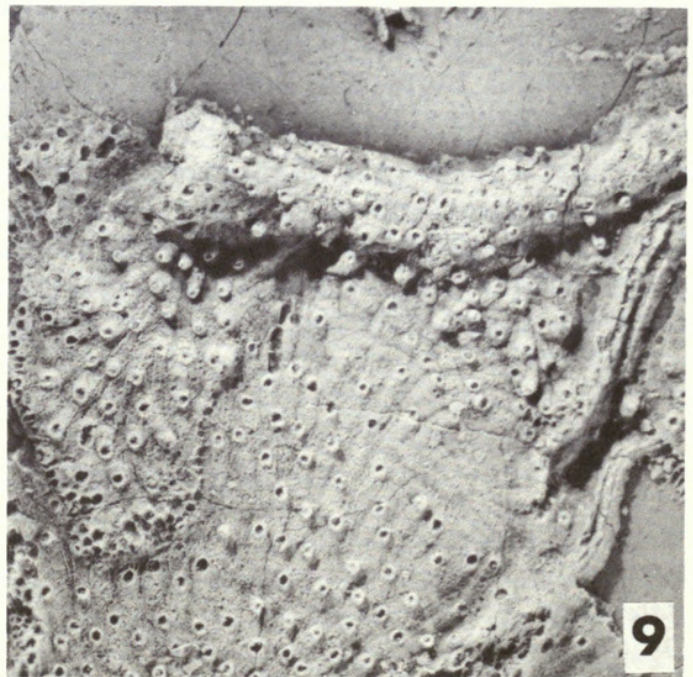
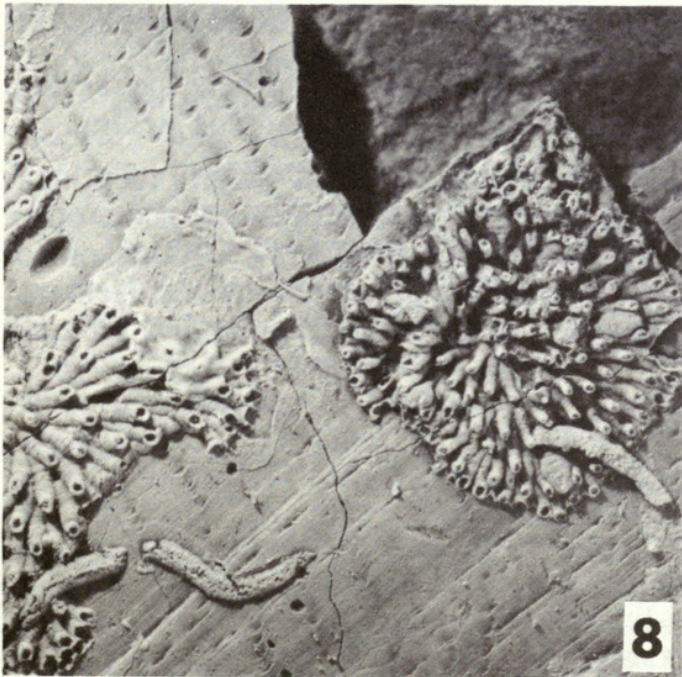


Fig. 7 *Microeciella reflexa* gen. et sp. nov. U. Toarcian, Belchite, Spain. Gonozooid morphology. Scanning electron micrographs of coated paratype, D.53323. a, gonozooid viewed from above showing constriction between proximal and distal dilated parts of the frontal wall; oeciopore obscured by sediment; $\times 70$. b, the same gonozooid viewed in oblique profile illustrating the arched transition between proximal and distal dilated parts of the frontal wall; $\times 40$.

DESCRIPTION. Colony encrusting, consisting of narrow, multiserial, bifurcating branches (probosciform); about 0.3–0.7 mm and 3–4 zooids wide. Early (? first) angle of bifurcation is 180° , later bifurcations are generally less than 90° and sometimes asymmetrical. Branches apparently flanked by kenozooids which taper in height towards the edge of the branch.

Autozooids with slightly convex frontal walls averaging about 0.71 mm in length (observed range 0.62–0.82 mm) and 0.20 mm in width (observed range 0.18–0.23 mm). Apertures longitudinally elongate, about 0.14×0.11 mm in zooids lacking peristomes. Peristomes up to 0.15 mm long, distally tapering, and curved until approximately perpendicular to the colony surface. Gonozooids absent.



Figs 8, 9 Photomicrographs of bryozoans from the U. Toarcian of Belchite, Spain. Fig. 8 (left), D.53321, colony d, paratype of *Microeciella reflexa* gen. et sp. nov., and (right) D.53321, colony a, holotype of *Microeciella beliensis* gen. et sp. nov. Illustrating the difference in zooid size between the two species; $\times 8$. Fig. 9, D.53327, colony b, the undetermined bereniciform tubuloporinid; after overgrowing a serpulid, a lobe of the colony has spiralled back to overgrow earlier-formed zooids (centre left); slightly beneath centre right is an area of the colony composed of kenozooids and devoid of apertures; $\times 6$.

REMARKS. This species is represented by four poorly-preserved colonies. They resemble *Proboscina divisi* Vine, 1893, described from the Bathonian of Thrapston in Northamptonshire, but zooid size in the Belchite bryozoans is slightly smaller than in Vine's type specimen of *P. divisi* (BM(NH) D.31142).

Jurassic palaeontologists (e.g. Vine 1893, Gregory 1896*b*) have traditionally used the name *Proboscina* for tubuloporinids with adnate colonies in which the zooids are arranged in narrow, multiserial, bifurcating branches—i.e. the probosciniiform growth-form (see Taylor, 1976: text-fig. 2B). *Proboscina* was founded by Audouin (1826) for living cyclostomes having this colony growth-form. The type species, *P. boryi* Audouin, has well-developed gonozooids. However, in many Jurassic species, including the one from Belchite, gonozooids are unknown. These species seem either to have lacked gonozooids or perhaps to have had gonozooids which were budded high on the delicate peristomes of autozooids (Harmelin 1974) and not fossilized. Their assignment to *Proboscina* is inappropriate but the creation of a new generic name must await description of a more complete and better preserved suite of specimens than that from Belchite. In the meantime, '*Proboscina*' is written in quotations.

Family uncertain

Undetermined bereniciform tubuloporinid

Fig. 9

MATERIAL. BM(NH) D.53327, colony b; U. Toarcian, Belchite, Zaragoza, Spain. L. Sequeiros Coll.

DESCRIPTION. A single large colony, encrusting, multiserial (bereniciform), with a lobate expansion which spirals proximally to overgrow earlier-forward zooids. Early astogenetic zones not preserved.

Autozooids large with frontal walls averaging 1.11 mm in length (observed range 0.90–1.43 mm) and 0.31 mm in width (observed range 0.27–0.33 mm). Apertures longitudinally elongate in zooids lacking peristomes, smaller and approximately circular in zooids preserving distally tapering peristomes.

Kenozooids numerous, some occurring singly between autozooids, others aggregated. They are smaller and narrower than autozooids, and lack apertures. Gonozooids lacking.

REMARKS. The absence of gonozooids in this single specimen precludes generic identification. The colony and its constituent zooids are significantly larger than those of the other Belchite species. This colony could represent a later growth stage of *M. reflexa* if the zone of astogenetic increase in zooid size is very extensive in *M. reflexa*. However, the occurrence of numerous kenozooids, unknown in *M. reflexa*, may suggest that the specimen is a separate species.

Generic attribution of '*Berenicea*' species

With the proposal of the new genus *Microeciella* it is opportune to evaluate the generic attribution of the numerous tubuloporinid species which are conventionally referred to *Berenicea*. The genus *Berenicea* has been used for sheet-like encrusting tubuloporinids of Ordovician to Recent age, though Palaeozoic examples are now regarded as *Sagenella* Hall (see Brood, 1975). However, the precise identity of *Berenicea* is a matter of contention, and it is clear that the name has been applied to a wide diversity of species varying in their affinities to one another and to other tubuloporinids.

Berenicea was proposed by Lamouroux (1821: 80) when describing three new species, *B. prominens* and *B. annulata* from the Recent, and *B. diluviana* from the Jurassic. Lamouroux did not designate a type species. *B. prominens* is usually quoted as the type species of *Berenicea* (e.g. Bassler 1953, Brood 1972). However, the earliest designation of *B.*

prominens as type species appears to have been by Gregory (1896a), postdating a designation of *B. diluviana* made by Reuss (1867). Therefore, *B. diluviana* has priority and is the valid type species of *Berenicea*. As with *B. prominens* (see Brood, 1972 : 176), the identity of *B. diluviana* is obscure; Lamouroux's figures of the species are extremely stylized and his original material is said by Walter (1970) to have been lost during a fire at Caen in 1944. *B. diluviana* could be any of a number of species, now assigned to several genera, which occur in the type region of Caen. Therefore, the genus *Berenicea* is best regarded as a *nomen dubium*.

Diastopora, also proposed by Lamouroux (1821), has been used as an alternative to *Berenicea* by many bryozoologists. The type species by monotypy of this genus is *Diastopora foliacea* Lamouroux from the Jurassic. Walter's (1970) redescription, based on a neotype and other specimens, shows *D. foliacea* to have large erect colonies of unilamellar branches forming wide tubes or foliaceous fronds. Therefore, *Diastopora* is unsuitable as a substitute for so-called *Berenicea* whose colonies are encrusting and typically small.

Species of '*Berenicea*' are most easily discriminated using characters of the gonozooid. These show much greater variability between putative species than do the relatively uniform and simple autozooids. Gonozooidal characters were used by Canu (1918) and Canu & Bassler (1922, 1926, 1929) as the basis for several new genera and families. The systematic work of Canu & Bassler has been severely criticized (e.g. Harmer 1931) and the validity of their cyclostome genera questioned (e.g. Brood 1972). Many of Canu & Bassler's taxa seem to have been founded on trivial differences but this should not lessen the value of gonozooidal characters for recognizing groupings of species regarded as genera. The identity and validity of these 'gonozooid genera', and of a few earlier genera of '*Berenicea*' type, rests on their defining type species. The following genera may be considered.

1. *Rosacilla* Roemer, 1840. The type species of this genus, given by Bassler (1935 : 192), is *Aulopora flabelliformis* Roemer, 1839 from the German Cretaceous. (This is not to be confused with *Cellepora flabelliformis* von Hagenow, 1839, the species listed first by Roemer (1840) in his description of *Rosacilla*, which may be the same as *Diplosolen pavonius* Voigt, 1929 (Voigt 1959).) Hillmer (1971 : 72) redescribed *A. flabelliformis* Roemer, noting the absence of gonozooids in the type material he studied. Gonozooids tend to be developed in only a small minority of colonies belonging to any particular cyclostome species known to have gonozooids and this may account for their absence in available specimens of *A. flabelliformis*. However, if it were to be established by examining a large, preferably topotype, population of *A. flabelliformis* that the species did not possess gonozooids, then *Rosacilla* may be an appropriate genus for species of '*Berenicea*' lacking gonozooids.

2. *Reptomultisparsa* d'Orbigny, 1853. This was created for multilamellar tubuloporinids resembling *Berenicea*. Without naming a type species d'Orbigny (1853) referred five species to the genus: *Diastopora diluviana* Milne-Edwards, 1838 (*non Berenicea diluviana* Lamouroux), an opinion shared by later revisers (Buge & Fischer 1970; Walter 1970). As three new species *Reptomultisparsa dutempleana*, *R. glomerata* and *R. congesta* from the Cretaceous. D'Orbigny (1853) placed his own earlier species *Diastopora incrustans* d'Orbigny, 1850 in synonymy with '*Diastopora diluviana* Milne-Edwards (*non* Lamouroux)', an opinion shared by later revisers (Buge & Fischer, 1970; Walter, 1970). As Milne-Edwards (1838) did not intend his *Diastopora diluviana* to be a new species but merely a new generic attribution of *Berenicea diluviana* Lamouroux (the type species of *Berenicea* Lamouroux), *Diastopora incrustans* d'Orbigny is considered to be the valid name for this species. It was left to Gregory (1896b : 151) to designate the type species of *Reptomultisparsa*, giving it as '*R. microstoma* (Mich.), syn. *R. diluviana*, Edw. & Mich. (*non* Lamx.); i.e. Gregory placed *Diastopora microstoma* Michelin in synonymy with the species correctly called *Diastopora incrustans* d'Orbigny. This synonymy has not been accepted by later revisers (see Walter, 1970) and furthermore it is evident from a subsequent publication (Gregory 1896c) that the species called *Reptomultisparsa microstoma* (Michelin) by Gregory is *Diastopora incrustans* d'Orbigny. Therefore, Gregory misidentified *Diastopora microstoma* Michelin when designating it as the type species of *Reptomultisparsa*. In

accordance with Article 70(a) of the International Code of Zoological Nomenclature (see Buge & Fischer 1970), a case has been submitted to the Commission requesting that *Diastopora incrustans* d'Orbigny be designated as the type species of *Reptomultisparsa*. This distinctive species occurs as large multilamellar colonies on gastropod shells which are thought to have been occupied by hermit crabs (Buge & Fischer 1970). The gonozooids (Fig. 10) are very large, longitudinally elongate (fusiform) and have large oeciopores.

3. *Dacryopora* Terquem, 1855. In a list of fossils from the Calcaire Ferrugineux (Jurassic) of Moselle, Terquem (1855 : 26) included *Dacryopora archiaci* Haime. This is the first use of the genus *Dacryopora* and the type species, by monotypy, is *Berenicea archiaci* Haime, 1854, a species which Haime described from material in the Terquem Collection of the Moselle region. Walter (1970 : 214) was unable to recover the type specimen of *B. archiaci* Haime from the Terquem Collection in the Paris School of Mines. Haime's original figures (1854 : pl. 9, figs 11a, b) are of a discoidal bereniciform colony with moderately large, longitudinally elongate gonozooids, apparently having a narrow distal 'neck' leading from the dilated frontal wall to an oeciopore which is about the same size as the autozooidal apertures. With the exception of this unusual neck, the gonozooid in *Dacryopora* is similar in shape to that of *Reptomultisparsa*, but smaller. *Dacryopora* may perhaps be regarded as a junior synonym of *Reptomultisparsa*.

4. *Microecia* Canu, 1918. As discussed above (p. 119), the type species of this genus is the Recent *Diastopora sarniensis* Norman, 1864. This is regarded as a species of *Plagioecia* Canu, 1918 by Harmelin (1976a).

5. *Plagioecia* Canu, 1918. The type species of *Plagioecia* by original designation is the Recent *Tubulipora patina* Lamarck, 1816. The gonozooid, fully described by Harmelin

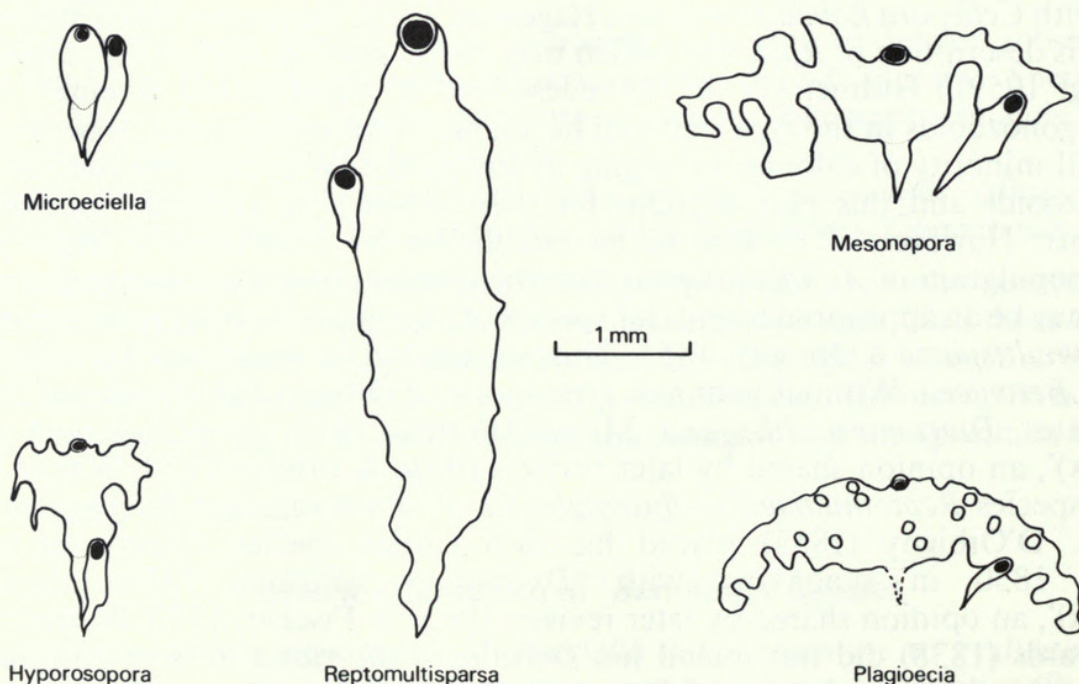


Fig. 10 Gonozooid morphology in various genera of bereniciform tubuloporinids drawn from specimens of type species. A single accompanying autozooid is shown in each case to give the relative scale of the gonozooid. The absolute scale is indicated by the 1 mm scale bar which applies to all gonozooids. Drawings were made from the following specimens: *Microeciella beliensis* gen. et sp. nov., paratype, D.53321, colony b; U. Toarcian, Belchite, Spain. *Hyporosopora typica* Canu & Bassler, D.13337; U. Bathonian (Bradford Clay), Bradford-on-Avon, England. *Reptomultisparsa incrustans* (d'Orbigny), D.53328; U. Bathonian, St Aubin-sur-mer, France. *Mesonopora concatenata* (Reuss) (= *Mesonopora typica* Canu & Bassler), 51342; U. Bathonian (Bradford Clay), Bradford-on-Avon, England. *Plagioecia patina* (Lamarck), Zoology Department 1976.8.14.14; Recent, Marseille, France.

(1976a), is broad and crescent-shaped (Fig. 10). Its margins are indented by autozooid apertures, some of which also pierce the frontal wall of the gonozooids away from the margins, and the terminal ooeciopore is transversely elongate with a proximally-directed ooeciostome.

6. *Diaperoecia* Canu, 1918. This genus has been used for Cretaceous–Recent tubuloporinids of varying colony-form, including species of ‘*Berenicea*’ type and vinculariiform species of ‘*Entalophora*’ type. By original designation the type species is *Pustulopora intricaria* Busk, 1875, a Recent tubuloporinid with a vinculariiform colony. It seems inappropriate to assign exclusively bereniciform species to this genus.

7. *Atractosoecia* Canu & Bassler, 1922. The original description of *Atractosoecia* includes two Jurassic species of which *Berenicea edwardsi* Canu, 1913, is cited as the type species. *B. edwardsi* is generally regarded as a junior synonym of *Diastopora incrustans* d’Orbigny (see Buge & Fischer 1970, Walter 1970). If *D. incrustans* is designated the type species of *Reptomultisparsa* by the I.C.Z.N. (see p. 126) then *Reptomultisparsa* and *Atractosoecia* share the same type species and *Atractosoecia* is a junior synonym.

8. *Mesonopora* Canu & Bassler, 1929. Two Jurassic species were included in the original description of this genus, *Mesonopora typica* Canu & Bassler, 1929, being given as the type species. Walter (1970 : 133) placed *M. typica* in synonymy with *Berenicea concatenata* Reuss, 1867. The gonozooid is broad, diffuse, and indented at its margins by apertures of autozooids (Fig. 10). The terminal ooeciopore is transversely elongate. Although similar to the gonozooid of *Plagioecia*, it lacks the distinct crescent-shape of the latter, and autozooids do not pierce the frontal wall away from the margins of the gonozooid.

9. *Hyporosopora* Canu & Bassler, 1929. By original designation the type species of *Hyporosopora* is *H. typica* Canu & Bassler, 1929, of Jurassic age. The gonozooid (Fig. 10) is moderately broad, subtriangular in outline, and has a small, transversely elongate ooeciopore located in a terminal position. In related Jurassic species subtriangular gonozooids were budded during early astogeny but later gonozooids developed forward-projecting lateral lobes giving the gonozooid a boomerang-shape (e.g. Taylor 1981 : text-fig. 3). *Hyporosopora* would appear to be a more appropriate name for certain Jurassic species previously assigned to *Plagioecia* (Walter 1970 : 117–128).

Of the ‘gonozooid genera’ discussed above the following are considered to be recognizable and potentially usable for species of the ‘*Berenicea*’ type: *Reptomultisparsa* (large, longitudinally elongate gonozooids), *Plagioecia* (broad, crescentic gonozooids extensively pierced by autozooids), *Mesonopora* (broad, diffuse gonozooids), *Hyporosopora* (subtriangular or boomerang-shaped gonozooids), and *Microeciella* (small, ovate gonozooids). Further research is needed to establish the possible validity of *Rosacilla* for species lacking gonozooids. It should also be noted that many genera forming erect colonies may have early ‘*Berenicea*’-like growth stages. In addition some genera are diagnosed using characters unrelated to gonozooids, e.g. *Diplosolen* Canu for species with regular nanozooids and *Serpentipora* Brood for species with zigzag-shaped zooids.

Detailed morphological studies of cyclostome bryozoans (e.g. Boardman 1976) reveal the presence of new taxonomic characters which may eventually complement or supersede gonozooidal characters in classification. However, until the range and distribution of these characters is better understood, gonozooidal characters will remain the only convenient means of subdividing the plexus of species informally assigned to ‘*Berenicea*’.

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References

- Audouin, J. V.** 1826. Explication sommaire des planches de Polypes de l'Égypte et de la Syrie. In Savigny, J.-C., *Description de l'Égypte* (Histoire Naturelle) 1 (4) : 225–244. Paris (Commission d'Égypte).
- Bassler, R. S.** 1935. Bryozoa. *Fossilium Cat.*, Berlin, (Pars Animalia) 67 : 1–229.
- 1953. Bryozoa. In Moore, R. C. (ed.), *Treatise on Invertebrate Paleontology*, G. xiii + 253 pp. Lawrence, Kansas.
- Boardman, R. S.** 1976. Taxonomic characters for phylogenetic classifications of cyclostome Bryozoa. *Docums Lab. Géol. Fac. Sci. Lyon* (H.S.) 3 (2) : 595–606.
- Brood, K.** 1972. Cyclostomatous Bryozoa from the Upper Cretaceous and Danian in Scandinavia. *Stockh. Contr. Geol.* 26 : 1–464.
- 1975. Cyclostomatous Bryozoa from the Silurian of Gotland. *Stockh. Contr. Geol.* 28 : 45–119.
- Buge & Fischer, J.-C.** 1970. *Attractosoecia incrustans* (d'Orbigny) (Bryozoa Cyclostomata) espèce bathonienne symbiotique d'un Pagure. *Bull. Soc. géol. Fr.*, Paris, (7) 12 : 126–133.
- Busk, G.** 1875. Cyclostomata. *Catalogue of marine Polyzoa in the collection of the British Museum*, 3. viii + 41 pp., 38 pls. London.
- Canu, F.** 1913. Contributions a l'étude des Bryozoaires fossiles. XIII. Bryozoaires jurassiques. *Bull. Soc. géol. Fr.*, Paris, (4) 13 : 267–276.
- 1918. Les ovicelles des Bryozoaires cyclostomes. Études sur quelques familles nouvelles et anciennes. *Bull. Soc. géol. Fr.*, Paris, (4) 16 : 324–335.
- & **Bassler, R. S.** 1922. Studies on the cyclostomatous Bryozoa. *Proc. U.S. natn. Mus.*, Washington, 61 (22) : 1–160.
- — 1926. Studies on the cyclostomatous Bryozoa. *Proc. U.S. natn. Mus.*, Washington, 67 (21) : 1–124.
- — 1929. Étude sur les Ovicelles des Bryozoaires jurassiques. *Bull. Soc. linn. Normandie*, Caen, (8) 2 : 113–131.
- Dumortier, E.** 1874. *Études paléontologiques sur les dépôts jurassiques du bassin du Rhône*. 337 pp., 62 pls. Paris.
- Goy, A., Gómez, J. J. & Yébenes, A.** 1976. El Jurásico de la Rama Castellana de la Cordillera Ibérica (Mitad Norte). I. Unidades litoestratigráficas. *Estudios geol. Inst. Invest. geol. Lucas Mallada*, Madrid, 32 : 391–423.
- Gregory, J. W.** 1896a. A Revision of the British Jurassic Bryozoa. Part III. The Genus *Berenicea*. *Ann. Mag. nat. Hist.*, London, (6) 17 : 41–49.
- 1896b. A Revision of the British Jurassic Bryozoa. Part IV. The Genera *Reptomultisparsa* and *Diastopora*. *Ann. Mag. nat. Hist.*, London, (6) 17 : 151–155.
- 1896c. The Jurassic Bryozoa. *Catalogue of the fossil Bryozoa in the Department of Geology, British Museum (Natural History)*. 231 pp., 11 pls. London.
- Hagenow, F. von** 1839. Monographie der Rügen'schen Kreideversteinerungen. Abt. I. Phytolithen u. Polyparien. *Neues Jb. Miner. Geogn. Geol. Petrefakt.*, Stuttgart, 1839 : 253–295.
- Haime, J.** 1854. Description des bryozoaires fossiles de la formation jurassique. *Mém. Soc. géol. Fr.*, Paris, (2) 5 : 165–218.
- Harmelin, J.-G.** 1974. A propos d'une forme stomatoporienne typique, *Stomatopora gingrina* Jullien, 1882 (Bryozoaires Cyclostomes), et de son gonozoïde. *J. nat. Hist.*, London, 8 : 1–9.
- 1976a. Les sous-ordre des Tubuloporina (Bryozoaires Cyclostomes) en Méditerranée. *Mém. Inst. océanogr. Monaco* 10 : 1–326.
- 1976b. Evolutionary trends within three Tubuloporina families (Bryozoa, Cyclostomata). *Docums Lab. Géol. Fac. Sci. Lyon* (H.S.) 3 (2) : 607–616.
- Harmer, S. F.** 1931. Recent work on Polyzoa (Presidential address 1931). *Proc. Linn. Soc. Lond.* 143 : 113–168.
- Henderson, C. M. & Perry, D. G.** 1981. A Lower Jurassic heteroporid bryozoan and associated biota, Turnagain Lake, British Columbia. *Can. J. Earth Sci.*, Ottawa, 18 : 457–468.
- Hillmer, G.** 1971. Bryozoen (Cyclostomata) aus dem Unter-Hauterive von Nordwestdeutschland. *Mitt. geol.-paläont. Inst. Univ. Hamburg* 40 : 5–106.
- Hincks, T.** 1880. *A History of British Marine Polyzoa*. 601 pp. London.
- Kaźmierczak, J. & Hillmer, G.** 1974. Sclerosponge nature of the Lower Hauterivian 'Bryozoan' *Neuropora pustulosa* (Roemer, 1839) from Western Germany. *Acta palaeont. pol.*, Warsaw, 29 : 443–453.
- Lamarck, J. B. de** 1816. *Histoire naturelle des animaux sans vertèbres*, 2. 568 pp. Paris.

- Lamouroux, J.** 1821. *Exposition méthodique des genres de l'ordre des polypiers*. viii + 115 pp. Paris.
- Mayoral, E. & Sequeiros, L.** 1981. Significado paleoecológico de algunos epizosos y 'borers' del Jurásico inferior y medio de Belchite (Zaragoza, Cordillera Ibérica). *Cuad. Geol.*, Granada, **10** (for 1979): 121–135.
- Michelin, H.** 1841–48. *Iconographie Zoophytologique*. xii + 348 pp. Paris.
- Milne-Edwards, H.** 1838. Mémoire sur les Crisies, les Hornères, et plusieurs autres polypes vivants ou fossiles, dont l'organisation est analogue à celle des Tubulipores. *Annls sci. nat.*, Paris, (Zool., 2) **9**: 193–238.
- Norman, A. M.** 1864. On undescribed British Hydrozoa, Actinozoa, and Polyzoa. *Ann. Mag. nat. Hist.*, London, (3) **13**: 82–90.
- Orbigny, A. D. de** 1850. *Prodrome de Paléontologie . . .*, **1**. 394 pp. Paris.
- 1851–54. *Paléontologie française. Terrains crétacés. V. Bryozoaires*. 1191 pp. Paris.
- Pergens, E. & Meunier, A.** 1886. La faune des Bryozoaires garumniens de Faxe. *Annls Soc. r. malacol. Belg.*, Brussels, **12**: 181–242.
- Quenstedt, F. A.** 1851–52. *Handbuch der Petrefaktenkunde*. iv + 792 pp. Tübingen.
- Reuss, A. E.** 1867. Die Bryozoen, Anthozoen und Spongiarien des Braunen Jura von Balin bei Krakau. *Denkschr. Akad. Wiss. Wien*, **27**: 1–26.
- Roemer, F. A.** 1839. *Die Versteinerungen des Norddeutschen Oolithen-Gebirges. Ein Nachtrag*. 59 pp. Hannover.
- 1840–41. *Die Versteinerungen des Norddeutschen Kreidegebirges*. iv + 145 pp. Hannover.
- Sequeiros, L., Cólera, I., Valenzuela, R. & Sánchez, I.** 1978. Biostratigrafía del Jurásico (Lias y Dogger) en el sector Belchite–Almonacid de la Cuba (provincia de Zaragoza, cordillera Ibérica). *Estudios geol. Inst. Invest. geol. Lucas Mallada*, Madrid, **34**: 293–298.
- & **Mayoral, E.** 1982. Epizosos y perforantes sobre *Plagiostoma gigantea* (SOW.), *Bivalvia* (Jurásico inferior); un modelo de relaciones entre paleoecología y diagénesis. *Revta Inst. Invest. geol., Diputación prov.*, Barcelona, **34** (for 1980): 149–159.
- Tate, R.** 1875. On Some New Liassic Fossils. *Geol. Mag.*, London, (n.s., dec. 2) **2**: 203–206.
- Taylor, P. D.** 1976. Multilamellar growth in two Jurassic cyclostomatous Bryozoa. *Palaeontology*, London, **19**: 293–306.
- 1981. Bryozoa from the Jurassic Portland Beds of England. *Palaeontology*, London, **24**: 863–875.
- Terquem, O.** 1855. Paléontologie du département de la Moselle. In: *Statistique de la Moselle*. Metz. 40 pp.
- Vine, G. R.** 1893. Notes on the Polyzoa, *Stomatopora* and *Proboscina* groups, from the Cornbrash of Thrapston, Northamptonshire. *Proc. Yorks. geol. polytech. Soc.*, Leeds, (n.s.) **12** (3): 247–258.
- Voigt, E.** 1929. Die Bryozoengattung *Diplosolen* in der Schreibkreide von Rügen. *Mitt. naturw. Ver. Neu-Vorpomm.*, Berlin, **52/56**: 1–8.
- 1959. Revision der von F. v. Hagenow 1839–1850 aus der Schreibkreide von Rügen voröfentlichten Bryozoen. *Beih. Z. Geol.*, Berlin, **8** (25): 1–80.
- Walford, E. A.** 1887. Notes on some Polyzoa from the Lias. *Q. Jl geol. Soc. Lond.* **43**: 632–636.
- Walter, B.** 1970. Les Bryozoaires Jurassiques en France. *Docums Lab. Géol. Fac. Sci. Lyon* **35** (for 1969): 1–328.
- & **Powell, H. P.** 1973. Exceptional preservation in cyclostome Bryozoa from the Middle Lias of Northamptonshire. *Palaeontology*, London, **16**: 219–221.