

The role of bryozoans in fossil reefs—an example from the Middle Devonian of the Western Sahara

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Abstract Stenolaemate bryozoans with their stable calcitic skeletons play a significant role in reef building. In the Middle Devonian Sabkhat Lafayrina reef complex (Western Sahara), bryozoans are abundant and diverse. Although they do not form part of the principal framework of reefs, bryozoans are involved significantly in reef growth, especially in the initial stage. In this way, bryozoans are important with respect to initiating reef growth. They contribute greatly to sediment stabilization, making it possible for principal reef builders to grow on hardened and stabilized substrates, and also play sediment-baffling and sediment-filling roles. The aim of this study is to document the diversity of bryozoans in a Middle Devonian reef complex and to estimate their potential for initiation and contribution to reef structures.

Keywords Reefs · Bryozoa · Devonian · Western Sahara · Ecology

Introduction

Bryozoans are aquatic colonial animals, usually with calcitic skeleton, occurring mainly in marine habitats. They are known since the Lower Ordovician and have a fossil

record with more than 20,000 extinct species. In the Palaeozoic, bryozoans inhabited various marine environments, being often rock-forming. In several time intervals, bryozoans played a relatively important role as reef-building organisms. The first bryozoan reefs are recorded from the Middle Ordovician (Cuffey 1977; McKinney et al. 1987; Vermeij 1987), a time interval that is characterized by a significant radiation of marine skeletal biota with a near-threefold increase in the number of known families (Sepkoski 1993). Silurian reefs were abundant and diverse. They occupied different facies settings from nearshore, to mid-outer shelf, and to deeper water settings, marking a period of probably warm climate that was connected with high sea-level stands (e.g., Wood 1999; Copper 2002). The Devonian period, particularly the Mid-Late Devonian (Givetian-Frasnian) is considered to represent possibly the largest global expansion of reefs in the Phanerozoic (Copper 1989, 2002). During this “greenhouse” interval, the sea level was high. Extensive reef tracts occurred around the world, such as in Canada, South China, central Asia, and North Africa, and also throughout Europe. These reefs were diverse and widespread and were dominated by microbialites, calcified cyanobacteria, and large metazoans, especially stromatoporoids and tabulate corals, whereas Carboniferous and Permian reefs were dominated by algae and mud mound communities, with minor participation of poriferans, echinoderms, bryozoans, and brachiopods (Fagerstrom 1987, 1994). The faunal diversity in Devonian reefs is high, with metazoan reef builders showing a tremendous variety of complex morphologies. However, there are only a few Devonian cases in which bryozoans were substantially involved in reefs and bioherms (e.g., Hedinger 1989; McKinney and Kříž 1986; Wyse Jackson 2006). Frequently, they are associated with so-called “algal laminites” (Smith 1981; Hollingworth and Tucker 1987; Paul 1996)

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and thrombolithic microbial crusts (Flajs and Hüssner 1993; Flajs et al. 1996). The stromatolites and thrombolites form a hard substrate, which is necessary for the development of an overgrowing bryozoan framework. Bryozoans often played an important role in the pioneer communities of reefs, even if they were not principal reef constructors. They stabilized and trapped sediment, paving the way for the main reef builders (Cuffey 1970, 1977, 2006; Hollingworth and Tucker 1897). Furthermore, bryozoans occupied cryptic habitats and interspaces in reefs, often showing a high diversity.

In the Devonian, the taxonomic diversity of bryozoans underwent significant changes. The Silurian faunas were dominated by trepostome bryozoans. Bifoliate cryptostomes were also abundant and diverse in Silurian communities. During the Devonian, fenestrate bryozoans became important, whereas trepostomes and bifoliate cryptostomes diminished markedly. These changes also marked a shift from mainly branched, massive, or encrusting colony forms to planar unilaminar ones, like those of meshed fenestrates. This colony form provided a significant success for fenestrates in the Late Palaeozoic (McKinney 1986). Advantages of these colony forms were improved feeding (due to occupying higher tiers and larger colony volumes per unit substrate area), and reduction in competition on the

substrate (McKinney and Jackson 1989). Erect fenestrate colonies also enhanced sediment trapping with their feeding currents, essentially contributing to mud mound building (McKinney et al. 1987). Fenestrates were involved significantly in Carboniferous and Permian reefs and bioherms. Erect rhabdomesine bryozoans also became diverse during the Devonian. However, due to their small size, they were not as important as fenestrates in reefal structures.

In the Middle Devonian Sabkhat Lafayrina reef complex, Western Sahara (Scholz et al. 2005; Jansen et al. 2006; Königshof and Kershaw 2006; Fig. 1), abundant and diverse bryozoans were found in different parts of the described reef complex. The bryozoans play a significant role in the development of initial parts of reef as well as in certain facies inside and around the reef complex.

Materials and methods

The morphology of the Sabkhat Lafayrina reef was recently mapped and described (Königshof and Kershaw 2006). The bryozoan palaeontology and sedimentology were investigated using thin sections studied with a transmitted light binocular microscope. More than 200 thin sections of different sizes (28×48 mm, 50×50 mm, and 50×75 mm)

Fig. 1 Location of the Sabkhat Lafayrina reef complex in the Tindouf Basin (star) near Samara, Western Sahara



were used for bryozoan taxonomy and microfacies study. The material is housed at the Senckenberg Museum (Frankfurt am Main, Germany).

Geological setting

The Sabkhat Lafayrina reef complex is located on the southern flank of the Tindouf Basin (Western Sahara, Fig. 1), which is bounded on the south by the Precambrian Reguibat Massif and on the north and west by the African fold belt. Devonian reef structures which were developed at the northern fringes of Gondwana in a high palaeolatitude of about 45°S (Copper 2002; Golonka 2002; Scotese 2003) are mainly composed of stromatoporoids and corals accompanied by other organisms such as crinoids, brachiopods, and bryozoans. The Sabkhat Lafayrina reef complex is well preserved. Due to a lack of current vegetation cover, the reef structure in outcrop is revealed in three dimensions, and it is not tectonically deformed. Based on the first investigations in the late 1960s by Dumestre and Illing (1967) and recent studies by Wendt and Kaufmann (2006), six reef cycles can be distinguished in the Givetian of the Uein Terguet area. The reef basement is characterized by dark grey, thick-bedded oolites overlaying siltstones and sandstones. The reef cycles are separated by marly sedimentation. The Sabkhat Lafayrina reef complex, which was described recently (Jansen et al. 2006; Königshof and Kershaw 2006), represents the fourth reef cycle in the Uein Terguet area. The reef structure mainly consists of bulbous and tabular stromatoporoids up to 2.5 m across with a variety of tabulate and rugose corals. Corals of the genus *Mesophyllum*, which occur in three characteristic horizons, are very abundant. The occurrence of *Heliolites porosus* indicates a Late Givetian age.

Bryozoans are mostly associated with crinoidal limestones and stromatoporoid bindstones in the basal parts of the reef structure (Fig. 2). These limestones overlay sandstones and contain brachiopods as well as bryozoans. Sediments with abundant bryozoans are mostly represented by grainstones. The uppermost part of the reef structure is built up by large stromatoporoids which represent the last stage in reef development preserved.

Bryozoan growth forms and faunal diversity in the Sabkhat Lafayrina reef complex

Skeletal bryozoans develop various growth forms as an adaptation to different environmental parameters. The growth form of a colony is constructed by the skeletons of individuals (autozoecia), by different polymorphs and by extrazoecial skeleton. Some groups, such as cystoporid

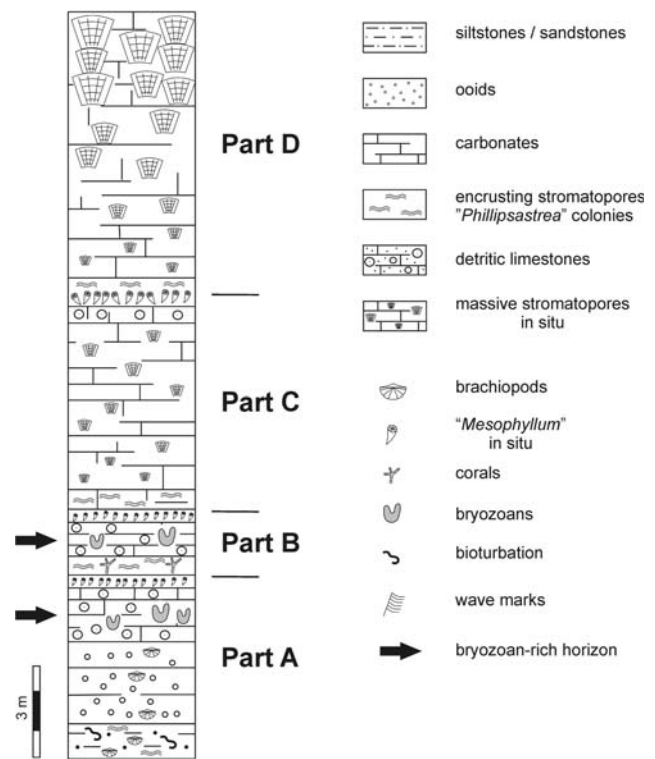


Fig. 2 Generalized lithological profile of the Sabkhat Lafayrina reef complex

bryozoans, can produce large amounts of extrazoecial skeleton. Growth forms of bryozoans serve different aims, but generally two of them are crucial: habitat space occupation (McKinney and Jackson 1989), and regulation of feeding currents (Cowen and Rider 1972; Taylor 1979; McKinney 1981). A very comprehensive classification of growth forms has been suggested by Hageman et al. (1998). The analytical bryozoan growth habit classification is based on 11 characters, which describe the orientation of the colony and its occupation of, and placement in, space, which is very important in understanding the ecological claims of bryozoans.

Taxonomic analysis reveals 21 bryozoan genera in the Sabkhat Lafayrina reef complex so far (Table 1). The most abundant and important genera are fenestrates (eight genera), followed by bifoliate and rhabdomesine cryptostomes (six genera), trepostomes (three genera), and fistuliporids (two genera). Phylloporines, which are regarded as closely related to fenestrates are represented by two genera.

Bryozoans in the Sabkhat Lafayrina reef complex developed different growth forms (Table 1): ramose (ten), reticulate (six), encrusting (three), and pinnate ramose (two). Ramose *Atactotoechus* and tubulose ramose *Fistuliphragma* develop robust stems, with diameters of about 1 cm and 5–15 cm in length. Others are rather delicate branched colonies, with diameters about 1–3 mm. Reticulate bryozoans, *Reteporida*, *?Speotrypa* and *Semicoscinium*

Table 1 Preliminary taxonomic composition, relative abundance (*a* abundant, *c* common, *r* rare) and growth forms of bryozoan fauna from the Sabkhat Lafayrina reef complex

Taxa	Relative abundance	Growth forms
<i>Fistulipora</i> sp.	a	Encrusting
<i>Fistuliphragma</i> sp.	c	Ramose (tubulose)
<i>Leioclema</i> sp.	a	Encrusting
<i>Atactotoechus</i> sp.	c	Ramose
? <i>Cyphotrypa</i> sp.	r	Encrusting
<i>Acanthoclema</i> sp.	a	Ramose
Rhabdomesid sp. indet	r	Ramose
<i>Intrapora</i> sp.	r	Ramose
<i>Euspilopora</i> sp.	c	Ramose
Ptilodictyonid sp. indet 1	r	Ramose
Ptilodictyonid sp. indet 2	r	Ramose
<i>Penniretepora</i> sp.	c	Pinnate ramose
<i>Filites</i> sp.	c	Pinnate ramose
<i>Fenestella</i> sp.	a	Reticulate
<i>Alternifenestella</i> sp.	a	Reticulate
? <i>Speotrypa</i> sp.	r	Reticulate
<i>Reteporidra</i> sp.	a	Reticulate
<i>Rectifenestella</i> sp.	a	Reticulate
<i>Semicoscinium</i> sp.	r	Reticulate
<i>Prolixicella</i> sp. (Ernst and Schroeder 2007)	c	Branched ramose
Phylloporinine sp. indet.	r	Branched ramose

have large and robust colonies, with colonies about 10 cm high and branches more than 1 mm wide. Other fenestellids have smaller colonies (5–7 cm high), with branches about 0.3–0.4 mm wide.

Bryozoans and their sedimentological role in the Sabkhat Lafayrina reef complex

Bryozoans appeared in pioneer communities preceding the reefs, and acted as sediment stabilizers (encrusting cystoporates and trepostomes), sediment baffler (fenestrates) and sediment fillers (all taxonomic groups).

Sediment stabilizing

Encrusting bryozoans e.g., *Fistulipora*, *Leioclema* covered large areas and stabilized the substrate by binding the fine-grained sediment. Large-branched trepostomes (*Atactotoechus*) and cystoporates (*Fistuliphragma*) stabilized the sediment additionally by their colonies, sharing also a sediment filling role (Figs. 3b–f, 4c, d), and providing a suitable substrate for other encrusting organisms, including also bryozoans.

Fig. 3 Microfacies of the reef basal parts in Sabkhat Lafayrina reef complex. **a** Carbonate sediment, stabilized by encrusting trepostome bryozoan *Leioclema* sp. (*Lei*) (SMF-HF-23). **b–f** Grainstones containing different bryozoans: trepostome *Atactotoechus* sp. (*At*), diverse fenestellids (*Fen*), cystoporate *Fistuliphragma* sp. (*Fis*) and rhabdomesine cryptostome *Acanthoclema* sp. (*Ac*) (**b** SMF-HF-28, **c** SMF-HF-25, **d** SMF-HF-29, **e** SMF-HF-22, **f** SMF-HF-26). Scale bars are 3 mm

Sediment baffling

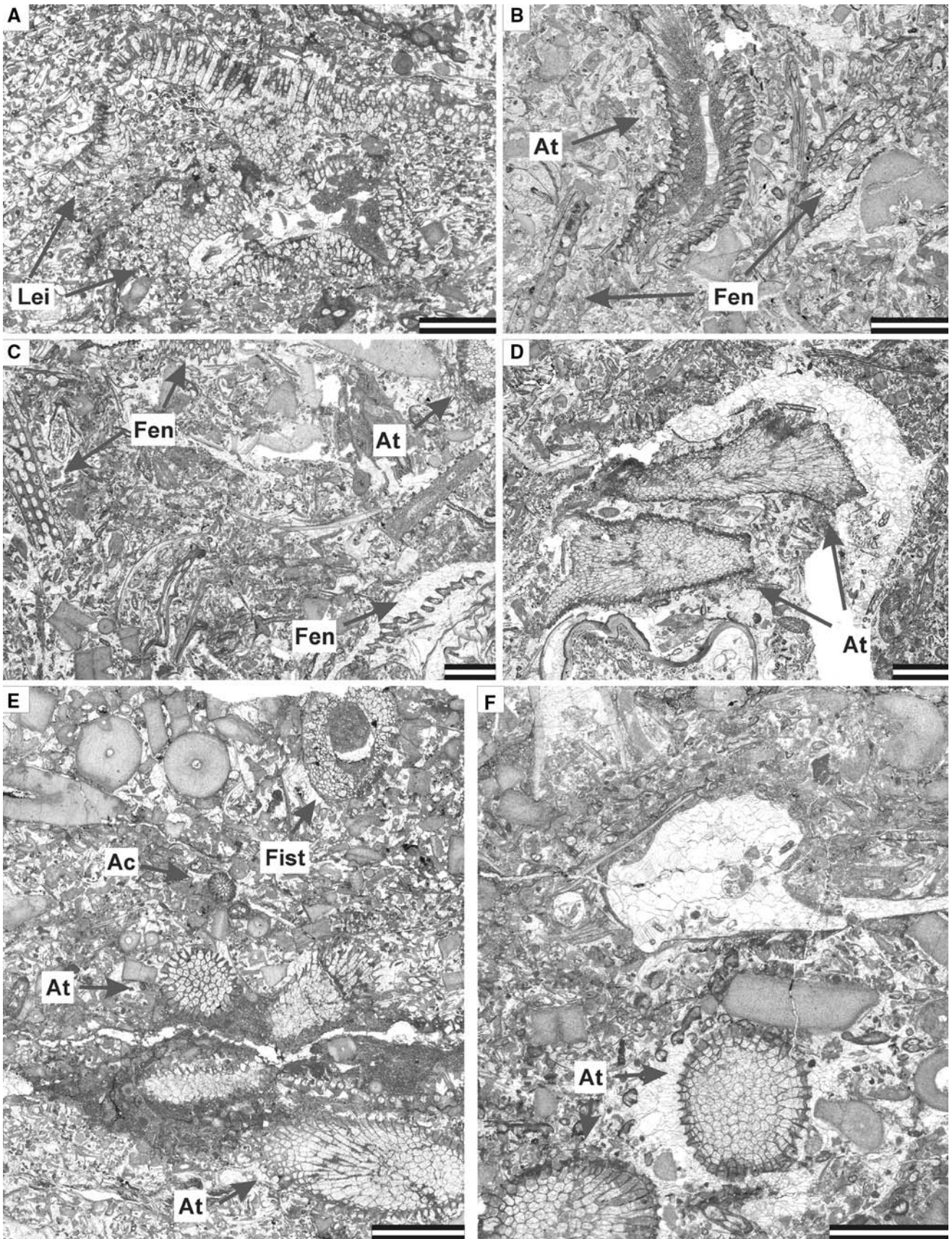
Large fenestrate colonies like *Reteporidra* and *Rectifenestella* (Fig. 4a, b) are known to be effective in trapping sediment (e.g., Troell 1962; McKinney et al. 1987; Christopher 1990). This is due to their net-like shape and also because of the activity of their polypides. Polypides create feeding currents that accelerate the sediment precipitation in the vicinity of the colony (McKinney et al. 1987; Fagerstrom 1987).

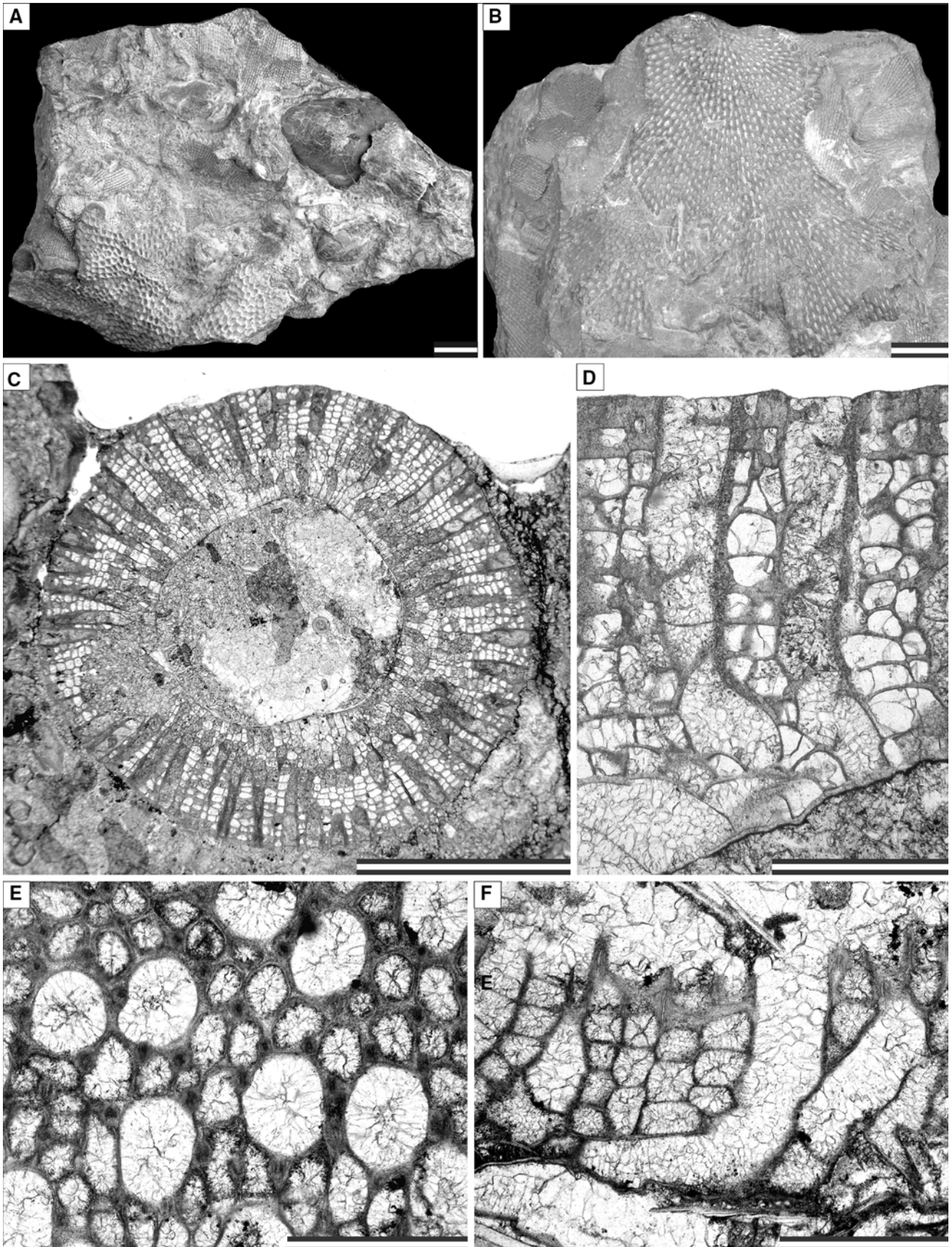
Sediment filling

All calcified bryozoan skeletons can contribute carbonate to reef sediment. In contrast with many other groups (e.g., gastropods, bivalves; Bathurst 1964), skeletons of bryozoans can persist a long time without being dissolved. Most Palaeozoic bryozoans had skeletons consisting of the low Mg calcite (Lowenstam 1963; Sandberg 1983; Boardman and Cheetham 1987; Taylor 1999), which is very stable to diagenetic alteration. Different genera contribute varying amounts of carbonate to the sediment. Large colonies of *Atactotoechus*, *Reteporidra*, *Rectifenestella* and *Fistuliphragma* contribute more carbonate to the reefs, whereas the rarer *Reteporidra*, ? *Speotrypa* and *Semicoscinium* contribute less. Small-sized bryozoan colonies can contribute significantly to the sediment volume if they occur in large numbers (Fig. 3e).

Discussion of the role of bryozoans in reefs

Bryozoans contribute to reef construction in different ways: as principal frame builders, accessory frame encrusters, sediment formers and sediment-movement inhibitors (Cuffey 1977), but generally bryozoan-dominated reef structures are small “patch reefs” or “reef knolls” (Cuffey 2006). Bryozoans rarely appear as principal frame builders, either alone or in conjunction with other organisms; an exception is a fossil reef from Vermont, USA, of Ordovician age (Pitcher 1964). These reefs are constructed by densely packed colonies of trepostomid bryozoans in upright growth position (Cuffey 1977). In Silurian reefs of Gotland, bryozoans accompanied by corals, produced small reef bodies on the flanks of the main reef complex (Fanterna type reefs, Manten 1971, p. 473). In Upper Permian Zechstein reefs, which reach about 100 m in thickness fenestrate bryozoans appeared in large





◀ **Fig. 4** **a, b** Rock samples with large fragments of fenestellid bryozoans. *Scale bars* 10 mm. **c, d** *Fistuliphragma* sp. **c** Transverse section of a tubular colony (SMF-HF-24), *scale bar* 3 mm. **d** Longitudinal section (SMF-HF-27), *scale bar* 0.5 mm. **e, f** *Leioclema* sp., encrusting colony: **e** tangential section, **f** longitudinal section; *scale bars* 0.5 mm (SMF-HF-21)

quantities. However, they were not principal frame builders. This role was filled by algae and microbial mats which triggered a fast synsedimentary lithification and produced wave-resistant reefs (Kerkmann 1967). Similar accumulation patterns have been described by Antoshkina (1996) in Ordovician reefs of the Urals. However, accessory frame encrusting roles involve bryozoans growing upon or within reefal frameworks constructed earlier by other frame-building organisms. In this way, bryozoans play a role of “venerers of dead reefs” (Cuffey 1977). After the principal frame builder such as corals are killed by severe conditions, bryozoans can overgrow dead reef building organism as a “veneer”. Examples of such reefs veneered by cheilostome bryozoans are known from the Miocene of the Black Sea (Martin 1943). More commonly, bryozoans appear in living and fossil reefs as crypto fauna, producing considerable biomass. Their roles in this concept are reduced to hidden encrusters, cavity dwellers, and cavity fillers (Cuffey 1977; Fagerstrom 1994). Due to their relative independence from daylight to small sizes, bryozoans inhabit the free space between framebuilders and other reef dwellers. Based on their variety of growth forms bryozoans can stabilize loose or movable sediments. Sometimes they appear as active sediment binders consolidating sediment grains to larger components by encrusting. Such examples are known from bryozoan patch reefs in the Middle Ordovician of North America (Ross 1981). Other examples of compact crust mounts have been reported by Cuffey and Taylor (1989) and Cuffey et al. (1991). In some Palaeozoic reefs, bryozoans acted as sediment stabilizers (e.g., Cuffey 1970, 1977; McKinney et al. 2001) similar to those described from the Sabkhat Lafayrina reef complex.

Fossil reef structures have been variously reconstructed (Copper 1989, 2002, cum lit.), but have not been fully considered in the light of interactions between skeletal organisms, microbialites, and community successions of reef builders (Adachi et al. 2006). These complex biotic interrelationships are still poorly understood even in Devonian reefs; however, this excellent reef complex provides the opportunity for more detailed studies.

Conclusions

The Middle Devonian Sabkhat Lafayrina reef complex in Western Sahara represents one of the most prominent Middle Devonian reef structures in northern Africa. The com-

plex belongs to the fourth reef cycle in the Uein Terguet area. The occurrence of bryozoans is mainly associated with crinoidal limestones, and to a lesser extent with stromatoporoid bindstones in different units in the basal part of the reef complex. Based on the diverse fauna, bryozoans grew in optimum conditions either at the sediments surfaces or within the reefal framework.

Although bryozoans are not primary reef builders in Devonian reefs, they sometimes played other important roles within the reefs. In the Middle Devonian reefs in Sabkhat Lafayrina, Western Sahara, bryozoans appeared in pioneer communities, playing roles as sediment stabilizers, sediment bafflers, and sediment fillers. Bryozoans stimulated the initial phase of reef growth, providing suitable growth substrates and/or stabilizing unconsolidated substrates for the main reef-building organisms. These organisms may be useful for palaeoecological and palaeoenvironmental reconstructions.

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References

- Adachi N, Ezaki Y, Pickett JW (2006) Marked accumulation patterns characteristic of Lower Devonian stromatoporoid bindstone: palaeoecological interactions between skeletal organisms and microbes. *Palaeogeogr Palaeoclimatol Palaeoecol* 231:331–346. doi:10.1016/j.palaeo.2005.09.002
- Antoshkina AL (1996) Ordovician reefs of the Ural Mountains, Russia—a review. *Facies* 35:1–7. doi:10.1007/BF02536954
- Bathurst RGC (1964) The replacement of aragonite by calcite in the molluscan shell wall. In: Imbrie J, Newell ND (eds) *Approaches to paleoecology*. Wiley, New York, pp 357–376
- Boardman RS, Cheetham AH (1987) Phylum Bryozoa. In: Boardman RS, Cheetham AH, Rowell AJ (eds) *Fossil invertebrates*. Blackwell, Oxford, pp 497–549
- Christopher CC (1990) Late Mississippian *Girvanella*-bryozoan mud mounds in southern West Virginia. *Palaios* 5:460–471. doi:10.2307/3514838
- Copper P (1989) Enigmas in Phanerozoic reef development. In: Jell PA, Pickett JW (eds) *Fossil Cnidaria*. *Mem Assoc Austral Palaeont* 8:371–385
- Copper P (2002) Silurian and Devonian reefs: 80 million years of global greenhouse between two ice ages. In: Kiessling W, Flügel E, Golonka J (eds) *Phanerozoic reef patterns*, *SEPM Spec Publ* 72:181–238
- Cowen R, Rider J (1972) Functional analysis of fenestellid bryozoan colonies. *Lethaia* 5:145–164, doi:10.1111/j.1502-3931.1972.tb00848.x
- Cuffey RJ (1970) Bryozoan-environment interrelationships—an overview of bryozoan paleoecology and ecology. *Pennsylvanian State Univ Earth Mineral Sci Bull* 39:41–45, 48

- Cuffey RJ (1977) Bryozoan contributions to reefs and bioherms through geologic time. *Stud Geol (Tulsa)* 4:181–194
- Cuffey R (2006) Bryozoan-built reef mounds—the overview from integrating recent studies with previous investigations. In: Scholz J, Taylor PD, Vavra N (eds) *Contributions to bryozoology: a tribute to Ehrhard Voigt (1905–2004)*. Courier Forschungsinstitut Senckenberg 257:35–48
- Cuffey RJ, Taylor JF (1989) Altoona bryozoan-coral-stromatoporoid reef, uppermost Silurian, Pennsylvania. *Can Soc Petr Geol Mem* 13:296–298
- Cuffey RJ, Gooden-Seay JA, Heckel PH (1991) Incipient bryozoan reef-mounds in the upper Pennsylvanian of south-eastern Kansas (USA). *Soc Sci Nat l'Ouest de la France Bull Mem HS* 1:109–120
- Dumestre A, Illing LV (1967) Middle Devonian reefs in Spanish Sahara. In: Oswald DH (ed) *International Symposium on the Devonian System*. Alberta Soc Petroleum Geol 1:333–350
- Ernst A, Schroeder S (2007) Devonian bryozoans of Rhenish Slate Massif. *Neues Jahrb Geol Palaontol Abh* 246(2):205–233. doi:10.1127/0077-7749/2007/0246-0205
- Fagerstrom JA (1987) *The evolution of reef communities*. Wiley, New York, 600 p
- Fagerstrom JA (1994) The history of Devonian-carboniferous reef communities: extinctions, effects, recovery. *Facies* 30:177–192. doi:10.1007/BF02536896
- Flajs G, Hüssner H (1993) A microbial model for the lower Devonian stromatactis mud mounds of the Montagne Noire (France). *Facies* 29:179–193. doi:10.1007/BF02536928
- Flajs G, Hüssner H, Vigener M (1996) Stromatactis mud mounds in the Upper Emsian of the Montagne Noire (France): formation and diagenesis of stromatactis structure. In: Reitner J, Neuweiler F, Gunkel F (eds) *Global and regional controls on biogenic sedimentation. I. Reef evolution*. Research Reports. Göttinger Arb Geol Paläont Sb2:345–348
- Golonka J (2002) Plate tectonic maps of the Phanerozoic. *SEPM Spec Publ* 72:21–75
- Hageman SK, Bock PE, Bone Y, McGowan B (1998) Bryozoan growth habits: classification and analysis. *J Palaeontol* 72(3):418–436
- Hedinger AS (1989) Allstones creek reef (Frasnian), Alberta. In: Geldsetzer HHJ, James NP, Tebbutt GE (eds) *Reefs, Canada and adjacent area*. Canadian Society of Petroleum Geologists. Memoir 13:454–456
- Hollingworth NTJ, Tucker ME (1987) The Upper Permian (Zechstein) Tunstall reef of North East England: palaeoecology and early diagenesis. In: Peryt TM (ed) *The Zechstein facies in Europe*. Lecture Notes in Earth Sciences 10:23–50
- Jansen U, Bensaid M, Birenheide R, El Hassani A, Königshof P, Plodowski G et al (2006) Middle Devonian reefs in the Western Sahara. *Actes de la première Rencontre sur la Valorisation et la Préservation du Patrimoine Paléontologique*, pp 105–107
- Kerkmann K (1967) Zur Kenntnis der Riffbildungen in der Werraserie des thüringischen Zechsteins. *Freib Forschungsh C* 213:123–144
- Königshof P, Kershaw S (2006) Growth forms and palaeoenvironmental interpretation of stromatoporoids in a Middle Devonian reef, southern Morocco (West Sahara). *Facies* 52:299–306. doi:10.1007/s10347-005-0041-1
- Lowenstam HA (1963) Biological problems relating to the composition and diagenesis of sediments. In: Donnelly TW (ed) *The earth sciences: problems and progress in current research*. University of Chicago Press, Chicago, pp 137–195
- Manten AA (1971) Silurian reefs of Gotland. *Dev Sedimentol* 13:1–539. doi:10.1016/S0070-4571(08)70394-7
- Martin GPR (1943) Zur Kenntnis der tertiären Bryozoenriffe (Sarmat) auf der Halbinsel Kertsch. *Z Dtsch Geol Ges* 95:133–137
- McKinney FK (1981) Planar branch systems in colonial suspension feeders. *Paleobiology* 7:344–354
- McKinney FK (1986) Evolution of erect marine bryozoan faunas: repeated success of unilaminar species. *Am Nat* 128:795–809. doi:10.1086/284606
- McKinney FK, Jackson JBC (1989) *Bryozoan evolution*. Unwin Hyman, Boston, 238 pp
- McKinney FK, Kříž J (1986) Lower Devonian Fenestrata (Bryozoa) of the Prague Basin, Barrandian Area, Bohemia, Czechoslovakia. *Fieldiana Geol NS* 15:1–90
- McKinney FK, McKinney MJ, Listokin MRA (1987) Erect bryozoans are more than baffling: enhanced sedimentation rate by a living unilaminar branched bryozoans and possible implications for fenestrata bryozoan mudmounds. *Palaio* 2:41–47. doi:10.2307/3514571
- McKinney FK, Webb F, McKinney MJ (2001) Middle Ordovician infratidal bryozoan-dominated microreefs (Bowen Formation), southwestern Virginia, USA. *Mem Sci Geol* 53:125–137
- Paul J (1996) Stromatolite reefs of the Upper Permian Zechstein Basin. In: Reitner J, Neuweiler F, Gunkel F (eds) *Global and regional controls on biogenic sedimentation. I. Reef evolution*. Research Reports. Göttinger Arb Geol Paläont Sb2:371–375
- Pitcher M (1964) Evolution of Chazyan (Ordovician) reefs of eastern United States and Canada. *Bull Can Pet Geol* 12:632–691
- Ross JRP (1981) Ordovician environmental heterogeneity and community organization. In: Gray J, Boucot AJ, Berry WBN (eds) *Communities of the past*. Hutchinson Ross, Stroudsburg, pp 1–33
- Sandberg PA (1983) Ultrastructure and skeletal development in cheilostome bryozoans. In: Boardman RS, Cheetham AH, Blake DB, Utgaard J, Karklins OL, Cook RL, Sandberg PA, Lutaud G, Wood TS (eds) *Treatise on invertebrate paleontology, Part G (1): Bryozoa (revised)*. Geol Soc of America/University of Kansas Press, Lawrence, pp 238–286
- Scotese CR (2003) PALEOMAP project. Available from: <http://www.scotese.com >
- Sepkoski JJ Jr (1993) Ten years in the library: new paleontological data confirm evolutionary patterns. *Paleobiology* 19:43–51
- Scholz J, Ernst A, Batson P, Königshof P (2005) Bryozoenriffe. *Denisia* 16:247–262
- Smith DB (1981) Bryozoan-algal patch-reefs in the Upper Permian Lower Magnesian limestone of Yorkshire, Northeast England. Marine palaeoenvironmental analysis from fossils. *Geol Soc Lond Spec Publ* 83:187–202
- Taylor PD (1979) The inference of extrazooidal feeding currents in fossil bryozoan colonies. *Lethaia* 12(1):47–56. doi:10.1111/j.1502-3931.1979.tb01241.x
- Taylor PD (1999) Bryozoa. In: Savazzi E (ed) *Functional morphology of the invertebrate skeleton*. Wiley, Chichester, pp 623–646
- Troell AR (1962) Lower Mississippian bioherms of southwestern Missouri and northwestern Arkansas. *J Sediment Petrol* 32:629–644
- Vermeij GJ (1987) *Evolution and escalation: an ecological history of life*. Princeton University Press, Princeton, p 527
- Wendt J, Kaufmann B (2006) Middle Devonian (Givetian) coral-stromatoporoid reefs in West Sahara (Morocco). *J Afr Earth Sci* 44:339–350. doi:10.1016/j.jafrearsci.2005.11.025
- Wood R (1999) *Reef evolution*. Oxford University Press, New York, 414 p
- Wyse Jackson PN (2006) Bryozoa from Waulsortian buildups and their lateral facies (Mississippian, Carboniferous) in Belgium and Ireland. In: Scholz J, Taylor PD, Vavra N (eds) *Contributions to bryozoology: a tribute to Ehrhard Voigt (1905–2004)*. Courier Forschungsinstitut Senckenberg 257:149–160