Indigenous demosponge spicules in a late Devonian stromatoporoid basal skeleton from the Frasnian of Belgium)

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Short title: demosponge spicules in a Devonian stromatoporoid

We show the first record of a demosponge spicule framework in a single specimen of a Devonian stromatoporoid from the Frasnian of southern Belgium. The small sample (2.5 x 2 cm) is a component in a brecciated carbonate from a Frasnian carbonate mound in La Boverie Quarry 30 km east of Dinant. Because of the small size of the sample, generic identification is not confirmed, but the stromatoporoid basal skeleton is similar to the genus *Stromatopora*. The spicules are arranged in the calcified skeleton, but not in the gallery space, and are recrystallised as multicrystalline calcite. The spicules fall into two size ranges: 10 - 20 µm diameter and 500 - 2000 µm long for the large ones and between 5 to 15 µm and 50 to 100 µm for the small ones. In tangential section, the spicules are circular, they have a simple structure and no axial canal has been preserved. The large spicules are always monaxons, straight or slightly curved styles or strongyles. The spicules most closely resemble halichondrid/axinellid demosponge spicules, and are important rare evidence of the existence of spicules in Palaeozoic stromatoporoids, reinforcing the interpretation that stromatoporoids were sponges. The basal skeleton may have had an aragonitic spherulitic mineralogy. Furthermore, the spicules indicate that this stromatoporoid sample is a demosponge.

Keywords: Stromatoporoids, Devonian, demosponge spicules, Porifera, Frasnian

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Stromatoporoids were first described in Devonian rocks by Goldfuss (1826), with representatives through the geological record from Lower Ordovician to modern times (with gaps). Stromatoporoids are currently generally agreed to be hypercalcified sponges. Some authors (e.g. Stearn *et al.* 1999), have distinguished Palaeozoic stromatoporoids from Mesozoic forms, also called Mesozoic stromatoporomorphs. The latter were considered as a polyphyletic grouping of stromatoporoid-like organisms (Stearn *et al.* 1999; Stock 2001), but not belonging taxonomically in the class Stromatoporoidea (Stearn 2010). Since their first description, strong controversy has surrounded their taxonomic position and the stromatoporoids have been assigned to seven groups of organisms: foraminifers, sponges, scleractinians, bryozoans, hydrozoans, algae and cyanobacteria (Kazmierczak & Kempe 1990; Kazmierczak & Krumbein 1983; Kershaw 1998; Stearn 2010). The discovery of living calcified sponges showing similarities with stromatoporoids (Hartman & Goreau 1970) as well as the discovery of sponge spicules in Mesozoic stromatoporoids (Wood & Reitner 1988) led to the conclusion that stromatoporoids are Porifera. Vacelet (1985) and Reitner (1991) distributed stromatoporoid sponges into the Poriferan classes Calcarea and Demospongiae, on the basis of the form of their spicules or their absence. Spicules were identified in Mesozoic stromatoporoids (Wood 1987; Wood & Reitner 1986) and in Upper Carboniferous stromatoporoids (Wood *et al.* 1989), although, some authors do not consider these Upper Carboniferous specimens as stromatoporoids (e.g. Stearn 2010). Reitner (1992) also discussed whether or not the densely packed spherical structures ("cellular" *sensu* Stearn 1966) within the basal skeleton of the stromatoporid *Syringostroma* are comparable with aster microscleres known from the demosponge *Chondrilla*. Unfortunately the possible spicule remains are not perfectly preserved. Because spicules were not found in lower and middle Palaeozoic stromatoporoids, they were considered as aspiculate (Kershaw 1998; Stearn 2010; Stearn *et al.* 1999). However, in some modern sponges, even in taxa that contain spicules, the spicules can be corroded, or dissolved, or they do not become incorporated into the calcareous skeleton but remained free within the soft tissue and so dispersed on death (Wood 1990). Thus absence of spicules in fossil stromatoporoids may be due to non-preservation.

Since spicules were not identified in Palaeozoic stromatoporoids, the traditional taxonomy is based on the architecture of the calcified skeleton, now recognised as a secondary calcareous skeleton in modern sponges, so that the term stromatoporoid is regarded as a grade of organisation of a sponge skeleton. Because of widespread recognition of spicules in Mesozoic stromatoporoids and modern calcified demosponges, the taxonomic class Stromatoporoidea is considered by some authors to have no taxonomic validity and the mid-Palaeozoic fossils of stromatoporoid grade cannot be validly subdivided into taxonomic groups (Reitner 1991; Reitner & Wörheide 2002; Wood 1987; Wood *et al.* 1989).

In the Treatise Online of Invertebrate Palaeontology, the Palaeozoic fossils are defined by characteristic skeleton and lack of spicules and are considered as part of the Porifera. The similar forms of the Mesozoic Era are divided into those fossils with spicules that can be assigned to taxa of living sponges and the aspiculate group

that can be classified only on the basis of their calcareous basal skeleton as hypercalcified sponges (Stearn 2010).

In this paper we present a stromatoporoid specimen from the Frasnian (Upper Devonian) carbonate mounds in Belgium, showing numerous structures identified as spicules. After the detailed description of the specimen and of the spicules and spicule organization, we propose a comparison with other younger stromatoporoids bearing spicules. This spicule finding is the first record in a Devonian stromatoporoid and this sample is potentially highly significant in understanding their biology.

Material and method

The newly-discovered specimen was collected from the Frasnian carbonate mound succession in the La Boverie quarry, a single specimen in a stromatoporoid collection of 3079 specimens (collected in 2009, complete palaeoecological results and setting in Da Silva *et al.* 2011). The La Boverie quarry is located at the southeastern edge of the Dinant Synclinorium, 3 km north of Rochefort (Fig. 1A; Institut Géographique National Belge (IGN) map 59/3, Lambert coordinates: X= 212.000 and Y= 97.600). The Frasnian in southern Belgium is characterized by a succession of four mud mounds, which are in stratigraphic order: the Arche, La Boverie, Lion and Petit Mont mounds (Fig. 1B; Boulvain & Coen-Aubert 2006). The series of build-ups, including the Arche, La Boverie and Lion mounds, exposed in the quarry is nearly 300 m thick (Fig. 1B-C). The specimen described in this paper comes from the middle part of the Arche mound (lower part of the Middle Frasnian), from a brecciated level (Fig. 1C), containing centimetre to decimetre-sized broken pieces of stromatoporoids and tabulate corals (Fig. 2A). The occurrence of these brecciated levels is interpreted as related to a lowering of the sea-level leading to a reworking on the top of the mound and occurrence of these brecciated beds on the flank of the mound (Boulvain 2007). Thus the horizon is interpreted to be lateral to the mound body (Da Silva *et al.* 2010; 2011).

The stromatoporoid containing spicules is a piece 2.5 x 2 cm, surrounded by dolomitic and sparitic cements and is part of a stromatoporoid rudstone (Fig. 2A). Four thin sections were made from the small piece of stromatoporoid (1 tangential, 1 longitudinal and 2 oblique sections). The samples were examined under normal light microscope, scanning electron microscope and cathodoluminescence (CL), the latter offering the best images. The specimen, sample LBv52b, is held in Liège University (Belgium). Stromatoporoid terminology comes from the Treatise Online of Invertebrate Palaeontology (Webby 2010).

All La-ICPMS measurements were made with an ELAN DRC II ICP-MS from PerkinElmer SCIEX. This instrument is combined with a COMPex 110 ArF Excimer-Laser from Lambda Physik and an optical bench Geolas from Mikrolas. Furthermore a microscopic system from Zeiss with a movable X-Y-Z-table from Physiks Instrumente is attached. Intensities obtained by the ICP-MS instrument refer to counts per second. For the calculation into concentrations both an external and an internal standard are needed. As external standard the NIST-SRM 610 standard glass provided by the National Institute of Standards and Technology with the evaluated values by Jochum *et al.* (2011) was used. As internal standard a calcium concentration of 400000 ppm for pure carbonates was assumed. This value should not be regarded as exact, therefore the indicated concentrations should be regarded

as a close approximation. However, the ratios between the element values are realistic.

One thin section was investigated by Field Emission-SEM using a LEO 1530 Gemini (Zeiss) instrument at 3,8 kV. The sample was polished prior to etching with 5% EDTA-solution for 5 seconds to investigate micritic fabrics and blocky sparitic cements. Energy dispersive X-ray spectrometry (Oxford Instruments EDX) was performed on Au-coated samples using the same instrument operated at 15 kV.

Cathodoluminescence investigations were carried out with a Citl 8200 MK3A cold cathode mounted on a Zeiss Axiolab microscope. Micrographs were recorded at 15 kV voltage using a cooled SPOT-CCD camera. All facilities are hosted in the Geobiology laboratory at the University of Göttingen where the work was carried out.

Description of the specimen

The specimen shows the distinctive features of stromatoporoids such as pillars, laminae and dissepiments (Fig. 2B). The original external morphology of the stromatoporoid could not be determined because the specimen is a broken piece. However, we can eliminate a branching morphology. Elements of the stromatoporoid are relatively thick (about 0.5 mm) and the microstructure is finely cellular to melanospheric. In longitudinal section (Fig. 2B), the structure appears cassiculate, or as an alternation of zones slightly dominated by pachysteles followed by cassiculate-dominated zones or pachystrome-dominated zones. Pachysteles are columnar to spool-shaped, confined to an interlaminar space. Galleries are circular, and are cut by dissepiments, which are relatively abundant and slightly curved. In tangential section, the structure is labyrinthic. The specimen is relatively close to *Stromatopora* (?), as described by Stearn (1993, 2011) and Stearn *et al.* (1999) considering the skeleton structure (cassiculate with locally dominant pachysteles or pachystromes) and microstructure (melanospheric).

Two kinds of spicules are observed corresponding to two size ranges (Fig. 3). The spicules size range is between 10 to 20 µm wide and 500 to 2000 µm long for the large ones (which are conspicuous) and between 5 to 15 µm and 50 to 100 µm for the small ones. In tangential section, both kinds of spicules are circular (Fig. 4), they have a simple structure and no axial canal has been preserved probably due to diagenetic processes. The large and small ones are always monaxons, straight or slightly curved styles (Fig. 2D-E, 3, 4) or strongyles (Fig. 4C). The spicules are preserved as multi-crystalline calcite (5 to 20 µm crystals) and are strongly affected by diagenesis, resulting in a recrystallized structure (e.g. Fig. 2D-E; Fig. 5). They appear to be more concentrated in some areas than in others, which seems to be related to differential diagenetic alteration (Fig. 2B-C). The spicules are more clearly visible in normal light because they are more recrystallized and so are coarser. However, in areas where the spicules are not clearly visible in normal light, they are clearly observed in CL. Observations with backscatter mode in SEM show no density differences between the spicules and surrounding stromatoporoid skeleton, indicating a purely calcium carbonate composition for the spicules.

The spicules are organized as follows: they are commonly enclosed in the skeleton and do not enter the galleries therefore, they are intramural. They are relatively closely packed and arranged as (A) perpendicular network (Fig. 3) or (B)

plumose structures (low angle between them; Fig. 3-4). They are commonly parallel to both the pachystromes and the pachysteles.

The possibility that the spicule-shape structures could be microborings in the stromatoporoid basal skeleton is discounted because of the lack of deposited sediment, which would be expected if they are boreholes. Furthermore, the very regular and characteristic arrangement into the skeleton (plumose structure, intramural) is also a strong argument in favor of demosponge spicules and architecture. This discussion is important because some palaeontologists have described spicules from Devonian favositid tabulates (Kazmierczak 1984, 1991) which have been identified as various types of microborings. Chatterton *et al.* (2008) however, could convincingly demonstrate octocoral-like spicules from a Silurian favositid tabulate.

Type of basal skeleton

The basal skeleton of the new spicule-bearing stromatoporoid shows similarity to the genus *Stromatopora* as mentioned above. The microstructure of the basal skeleton is somewhat melanospheric, containing common round shaped dark spots ca. 100 µm across. This melanospheric structure may be a diagenetic pattern of a former spherulitic structure. The dark spots are presumably micritized cores of former spherulites. Similar patterns are also known from extant and fossil spherulitic coralline sponges, e.g. the “stromatoporoid” *Astrosclera* (Reitner 1992; Wörheide 1998) and *Stachyodes* (plate 1 in (Mistiaen 1991)). The investigated basal skeleton of the spicule-bearing stromatoporoid is diagenetically partly altered. The basal skeleton has a micritic texture and is now preserved in low-Mg calcite, based on EDX and La-ICPMS analyses (Fig. 6A). The micritic crystals have sizes around 1-3 µm and are subangular. Canals and other primary open spaces of the stromatoporoid are cemented by subangular sparitic (10-80 µm, mean value 50 µm) low-Mg calcite crystals. The former spicules are preserved also in a sparitic low-Mg calcite, however with smaller crystal sizes of ca. 10-20 µm. The later cements-, between the components of carbonate rudstone, are white euhedral sparitic Fe-rich dolomites. Very late diagenetic phases exhibit typical “sugar grained” brown euhedral Fe-rich dolomites (Fig. 6B) often related with framboidal pyrite, a product of microbial sulphate reduction, which has favoured the dolomitisation process (Vasconcelos *et al.* 1995).

Trace element analyses of the basal skeleton show a slight increase of bulk Sr values of around 400-500 ppm in comparison with the later cements, which exhibit values of only 200 ppm (Fig. 6C). Intriguing is the observation that the laser line analysis shows a strong variation of Sr values between 200 and 800 ppm. This pattern is explained by the melanospheric micritic basal skeleton and the cemented primary openings and spicule remains. The highest Sr values are related to the melanospheric basal skeleton. This pattern could be a relic of a primary aragonitic biomineralogy. Important are also the cathodoluminescence behaviour of the basal skeleton and the various cements, which support this assumption. The late dolomitic cements are non-luminescent except for some bright small spots. Also the diagenetic calcite crystals of the spicules are non-luminescent. The basal skeleton exhibits areas with bright CL and areas with weak CL; the latter are the melanospheric areas. The Mn values are generally low (100-600 ppm average); exceptions are strongly luminescent bright dolomite crystals with up to 3000 ppm Mn (Fig. 6D). High Mn

values within these crystals activate the luminescence (Vortisch 2011). However, within the basal skeleton Mn values are low (100-200 ppm) but negatively correlated with Sr, increased Sr means decreased Mn concentration.

The measured slight increase of Sr within the basal skeleton could indicate a primary aragonite skeleton. The melanospheric microstructure may be a diagenetic product of an original spherulitic structure.

Discussion

The discovery of demosponge spicules in a single sample emphasizes the sponge affinity of stromatoporoids, but because the sample is a single small fragment that limits the value of this sample for taxonomy of stromatoporoids. Kershaw's (1998) argument that the Palaeozoic stromatoporoid skeleton had validity at genus level is unaffected by this new discovery since the sponge cannot be readily identified from the spicules in this sample. Therefore the value of this sample is to reinforce the views that stromatoporoids were sponges. In order to relate the new sample to spicule-based sponge taxonomy the following discussion considers the relationship of this sample with other calcified sponges.

Comparison with existing stromatoporoid coralline sponges

Spicules were described in different genera of post Devonian stromatoporoids (Wood 1987; Wood & Reitner 1986; Wood *et al.* 1989) and some similarities can be highlighted. The combination of the two types of spicules (strongyle and style) and the spicule organization (plumoses or perpendicular) were also observed in the Upper Carboniferous halichondrid "*Newellia" mira* (Wood *et al.* 1989) (*Spongonewellia sensu* Özdikmen (2009)) and in the Lower Cretaceous halichondrid demosponge *Euzkadiella erenoensis* (Reitner 1987) (Fig. 7, Table 1). However, spicule size is an important difference between these post-Devonian examples and our Devonian sample. The small spicules observed in our Frasnian stromatoporoid (between 50 and 100 µm) are in the same size range as for *E. erenoensis* (between 75-105 µm) and for *S. mira* (60 and 120 µm), but the large spicules (500-2000 µm) are 10 times bigger than for *E. erenoensis* (between 105-250 µm) and for *S. mira* (115 and 150 µm). As observed in Fig. 7, the spicules and the whole stromatoporoid structure are actually larger.

Most of the Mesozoic stromatoporoids with intramural spicules are related to the Milleporellidae. *Dehornella crustans* Hudson 1960 acts as a good representative of Late Jurassic/Early Cretaceous spicule-bearing stromatoporoids with an axinellid-plumose arrangement of styles. Beside the Milleporellidae the Actinostromatomariicae (*Actinostromarianina lecompti* Hudson 1960) exhibit subtylostyle plumose arranged spicules in some samples. Other Mesozoic stromatoporoids are classified as Haplosclerida (*Stromatoacervochalina turnseki* Reitner 1992). For comparison, modern coralline demosponges with a stromatoporoid grade of basal skeleton are related to the Agelasidae (*Astrosclera willeyana* Lister 1900) or to the Haplosclerida (*Calcifibrospongia actinostromarioides* Hartman 1979) (for details see Reitner (1992); Wood (1987); Wood & Reitner (1986); Wörheide (1998)). Reitner (1992) regarded the Agelasida as a sister group to the Halichondrida, which emphasises the demosponge affinity of the specimen described in this paper.

Affinities to modern halichondrid demosponges

The classical taxonomy of the Halichondrida is based on spicule types and spicule architecture and was revised in the *Systema Porifera* - a large compilation on modern sponge taxonomy (Hooper & van Soest 2002) and includes the families Desmoxyidae, Halichondriidae, Dictyonellidae, Bubaridae, and Axinellidae. Characteristic spicules are styles, oxeas and strongyles, microscleres are normally missing with some exceptions. The main spicule architecture is plumoreticulate, irregular spicule bundles and also single megascleres. Ectosomal spicular skeletons of the Halichondrida are rare, often tangentially arranged or in bouquets of spicules. Axinellidae lack an ectosomal spicular skeleton. For the fossil record it is noticeable that the choanosomal spicular skeleton is basically plumoreticulate. The plumose spicule bundles are often interconnected by single spicules. The outer ectosomal spicular skeleton is normally not preserved. The spicule architecture of the Devonian stromatoporoid of this study exhibits close coincidence with the axinellid spicule architecture. Axinellids are characterised by a choanosomal skeleton often formed by ascending plumose spicule tracts horizontally connected by smaller spicules. Megascleres are oxeas, styles and curved styles. Microscleres are thin raphides in some taxa. Megascleres could reach lengths of 600-700µm and therefore large, average length is around 200-300µm. The type species *Axinella polypoides*, the genera *Auletta*, and *Phakellia* exhibit choanosomal spicule architecture which coincides well with the spicule-bearing fossil relatives from the Palaeozoic and Mesozoic (new Devonian stromatoporid, Carboniferous *S. mira*, Jurassic *Dehornella*, Cretaceous *E. erenoensis*, and others).

However, recent molecular phylogenetic investigations have shown that the taxon Halichondria Gray 1867 is not a monophyletic grouping as traditionally established (Erpenbeck *et al.* 2006; Erpenbeck *et al.* 2005; Erpenbeck *et al.* 2012; Morrow *et al.* 2012). Unfortunately, Halichondrids lack synapomorphic characters like characteristic microscleres and the definitions of the families are mainly based on the absent of characters. Spicule types and architectures are more plesiomorphic characters and therefore not suited for phylogenetic analyses. The Axinellida/Halichondrida which are most applicable to this study, are part of different phylogenetic groups and non-monophyletic (Alvarez *et al.* 2000; Erpenbeck *et al.* 2012; Gazave *et al.* 2010; Morrow *et al.* 2012; Uriz *et al.* 2003). These studies have re-classified the demosponges (Wörheide *et al.* 2012). Except for the type species *Axinella polypoides*, other species with axinellid plumoreticulate spicule arrangement are now related to the Agelasidae.

The most recent results and interpretations of the taxon Halichondrida make it very difficult to integrate fossil data within the modern phylogenetic framework. For this reason it seems more convincing to follow the classical taxonomic framework based on the revision published by (Hooper & van Soest 2002). In any case the Devonian spicule-bearing stromatoporoid exhibits a spicular architecture and spicule types which are characteristic for the Axinellida *sensu lato*. One type of the megascleres of the new type is very large. However, within the modern Axinellida large megascleres (up to 800µm) also occur. More important for phylogenetic interpretations is the plumoreticulate choanosomal spicule architecture. This is the first observation of complex halichondrid/axinellid spicule architecture in the fossil record of the halichondrid-type demosponges, and also the first occurence of a sponge spicule-bearing coralline demosponge. Intramural spicules within

Archaeocyaths are probably of allochthonous origin (Debrenne & Reitner 2001; Reitner & Mehl 1995).

The spicule arrangements of the halichondrids and the new Devonian type are very similar to the Carboniferous *Spongonewellia*, the Jurassic Milleporellidae (*Dehornella* div.sp.) and the Aptian *Euzkadiella*. However, the types of the basal skeletons differ. The Devonian stromatoporoid may have possessed a spherulitc, aragonitic basal skeleton, in contrast to the Carboniferous *Spongonewellia* which developed a simple micritic, probably aragonitic basal skeleton. Most of the Mesozoic stromatoporoids, have developed Mg-calcite basal skeletons. The Milleporellidae are characterised by a typical "water jet" arrangement of the calcite crystals, *Euzkadiella* shows a spherulitic Mg-calcite (Reitner 1987; Wood 1990; Wood & Reitner 1986). Based on biomineralisation studies on modern coralline sponges it is known that the basal skeleton formation is enzymatically controlled by the sponge (e.g. Jackson *et al.* 2011; Jackson *et al.* 2007). However, the stable carbon isotope analyses of the basal skeletons of modern coralline sponges clearly show a formation close to seawater equilibrium (Böhm *et al.* 2002; Haase-Schramm *et al.* 2003). The basal skeletons are highly convergent and have only phylogenetic significance on very low taxonomic level (Reitner 1992).

Conclusions

1. The new findings of intramural demosponge spicules within the basal skeleton of a Frasnian stromatoporoid (probably *Stromatopora* sp.) supports the interpretation that mid-Paleozoic stromatoporoids are hypercalcified demosponges. These are the oldest intramural demosponge spicules in the fossil record up to now and also the first record of a complex axinellid/halichondrid spicule architecture.

2. Spicule types and spicule architecture are comparable with the taxon *Axinella sensu lato*. Using the classical taxonomy based on the revision in Systema Porifera (Hooper & van Soest 2002) the new type is classified as member of the Halichondrida. The younger representatives of spicule-bearing stromatoporoids (*Spongonewellia*, *Dehornella, Euzkadiella*) were also classified as axinellid/halichondrid demosponges. For comparison, the modern coralline sponges with a stromatoporoid basal skeleton are classified in closely related demosponge group of Agelasidae (*Astrosclera*) and Haplosclerida (*Calcifibrospongia*).

3. The type of the basal skeleton of the new spicule-bearing stromatoporoid is difficult to evaluate. Geochemical and electron microscopic investigations show diagenetic overprinting. The melanospheric microstructure is interpreted as primary spherulitic. The relative high Sr amounts of the basal skeleton suggests primary aragonitic mineralogy.

4. The discovery of this sample reinforces the view of some workers that Stromatoporoidea is not a valid taxonomic unit.

5. The stromatoporoid basal skeleton type represents a special type of sponge tissue organisation.

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Figure Legends

Fig. 1. Geological setting of the Frasnian of Belgium. A. Geological map with outcrop location. B. North-South section of the Frasnian basin before Variscan deformation, with section location (section X-Y from Fig. 1A). C. Simplified lithological column (detailed column in Da Silva *et al.* (2011) with formation and member names. The dark arrow indicates the stratigraphic position of the sample LBv52b where the spicules were found. D. Legend for the lithological column in C.

Fig. 2. Sample LBv52b, general view of the sample and the spicules. A. Polished sample, stromatoporoid and tabulate coral (centimeter size) rudstone with a sparitic and dolomitic cement. The stromatoporoid with spicules is framed (centre left) and this frame corresponds to the picture C; B. Longitudinal section in the stromatoporoid characterized by a thick wall structure; with the dominance of the pachystele elements in the lower part, left side corner and with the dominance of the pachystrome elements in the upper part, left side corner; C. Oblique almost tangential section, showing the link between the spiculate network and the whole specimen; D. Enlargement of Figure C (white framed area in C), the white arrows point to the spicules; E. Curved spicule (white arrow), following the skeleton structure and lying entirely within the skeleton.

Fig. 3. Organization of the spicules. Large intermural spicules organized as a perpendicular network, with numerous small spicules, and showing local organization of the spicules in plumules. A-B. Cathodoluminescence micrograph and corresponding sketch; C. Normal light picture; D. Sketch of the spicule arrangement.

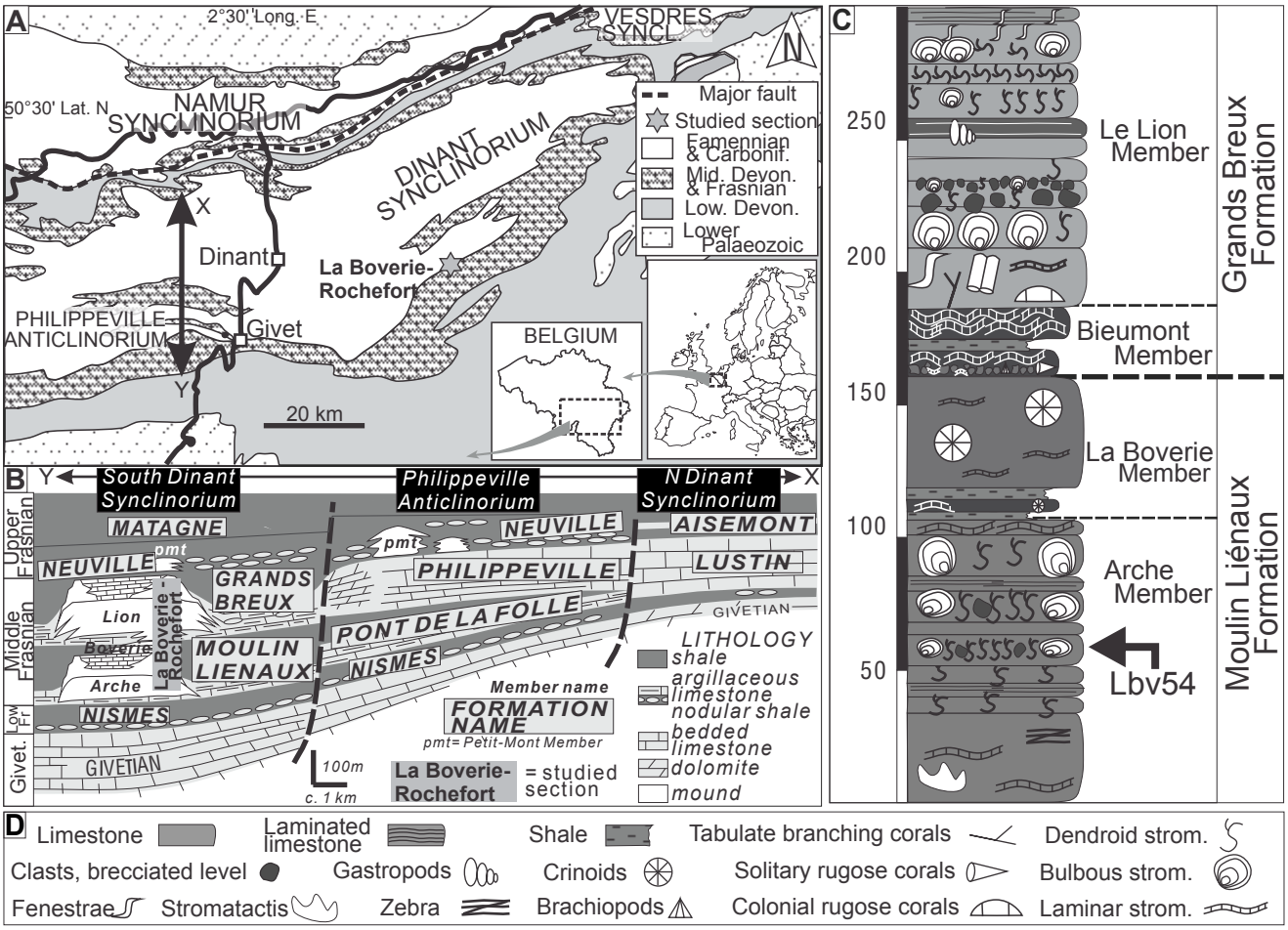
Fig. 4. Cathodoluminescence micrographs, organization of the spicules and shape. A-B. On these sections, most of the spicules are cut transversally, with only a few spicules with a longitudinal section. C. Spicules with strongyle shape, with a low angle between them. D. Normal light picture, Plumose arrangement, the spicules are organized with a low angle between them. E. Spicules organized in “bouquet” in a tangential view. F. 3D representation of the spicular arrangement, reconstruction after the micrographs D and E.

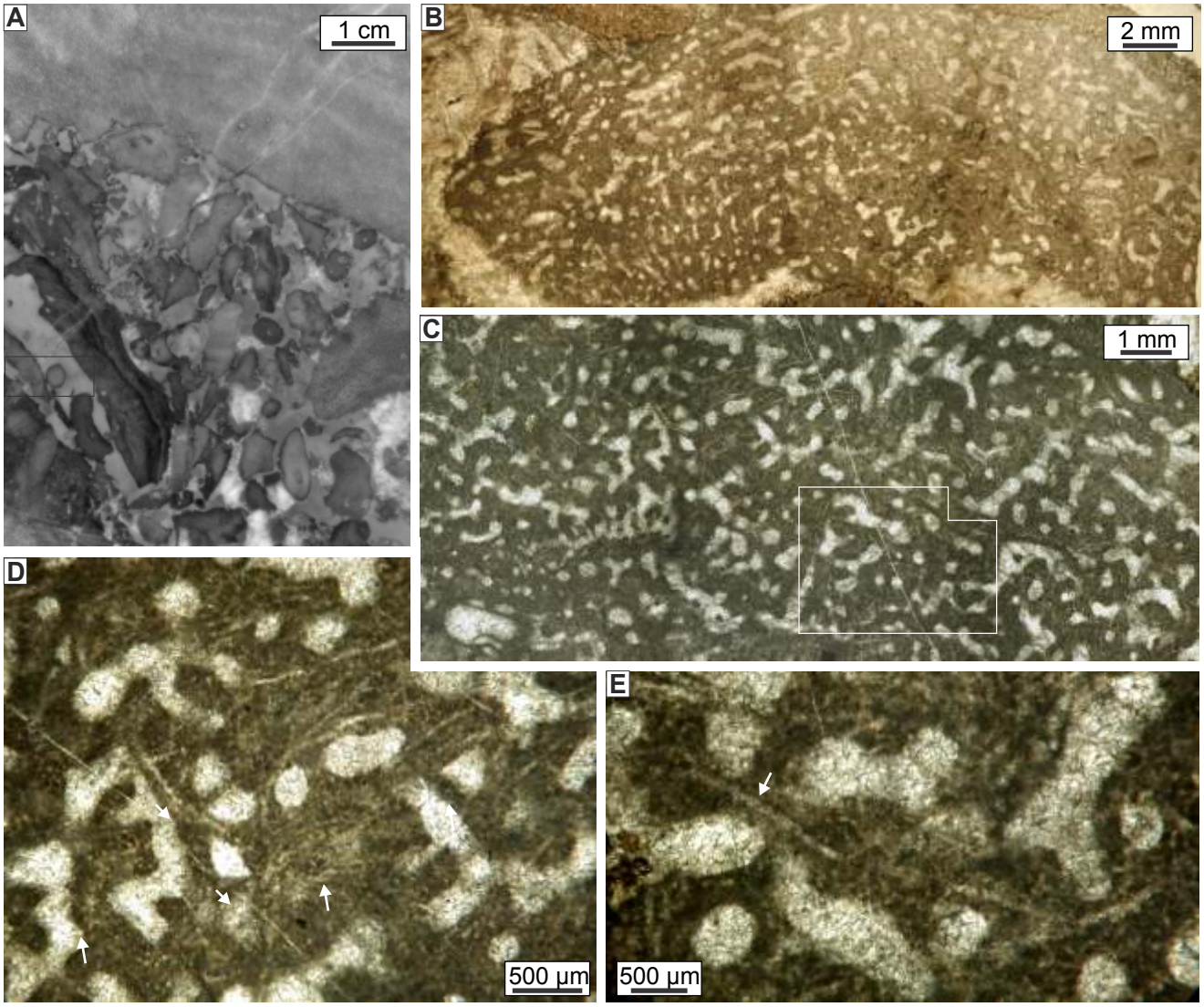
Fig. 5. SEM pictures of the spicules. A. Tangential circular section of a large spicule. B. Spicules in tangential section (white arrow) and in longitudinal section (black arrows) composed of coarse crystals.

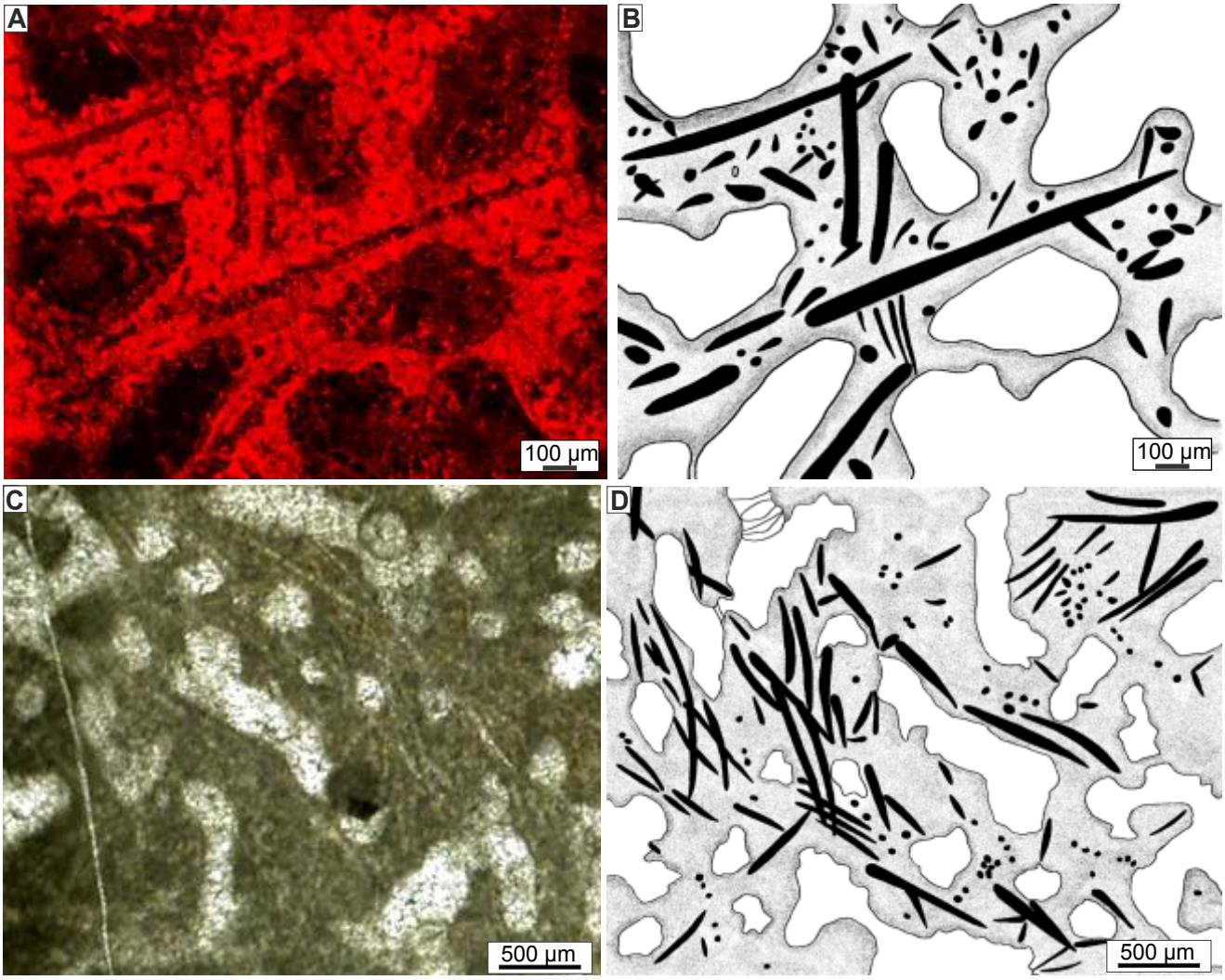
Fig. 6. Mg, Fe, Sr and Mn concentration along a transect on the LBv52b sample. Cutting through a dolomitic cement (0-5000 and 22000-25000 µm) with a higher Mg (A), Fe (B) and Mn (D) concentration and then the spicule bearing specimen (10000-22000 µm), with a higher Sr concentration (C).

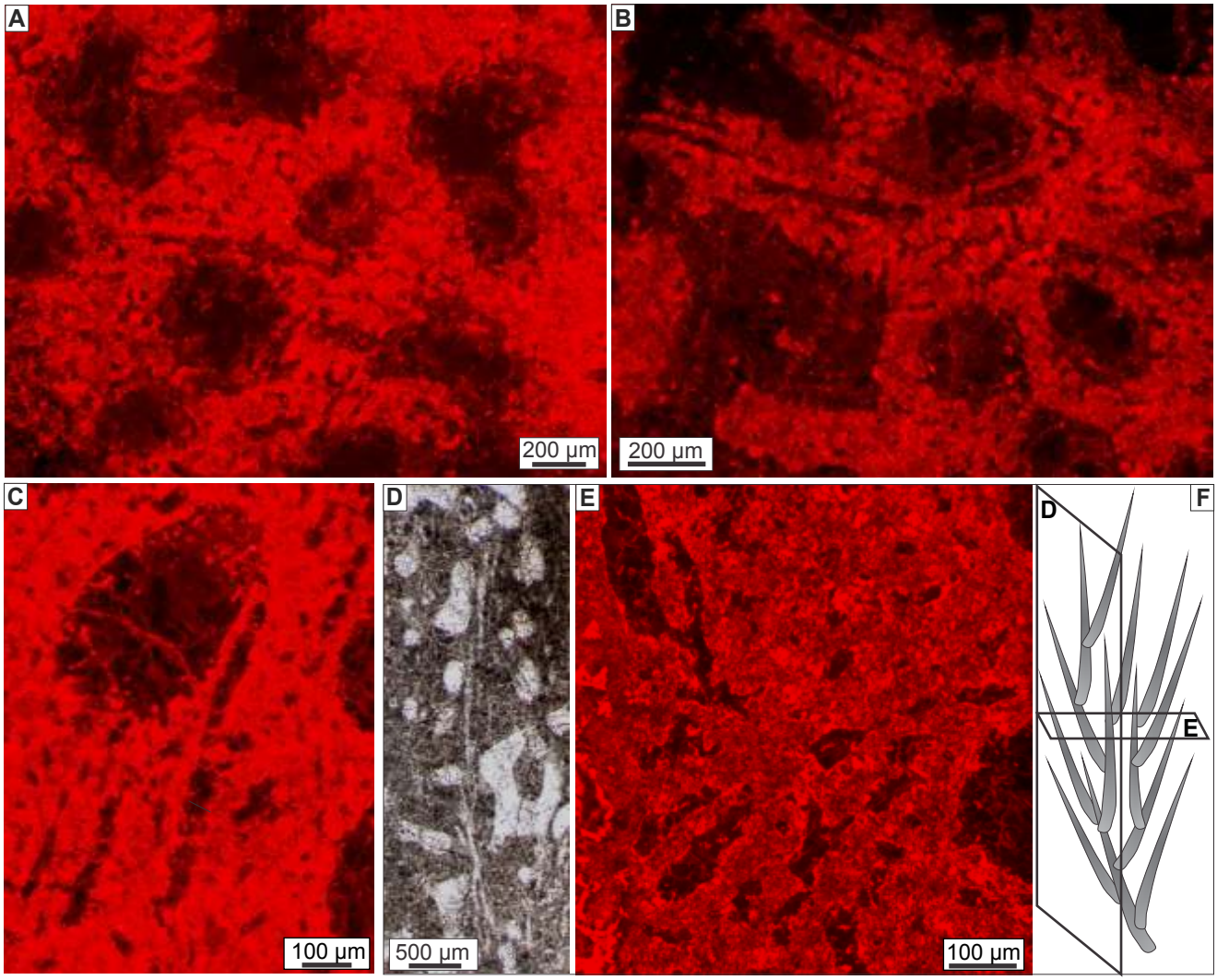
Fig. 7. Comparison of “*Newellia mira”* (Wood *et al.* 1989) and *Euzkadiella erenoensis* (Reitner 1987) with the specimen from this paper. Scale bar is 100 µm. The type of spicules and their arrangement is relatively similar but their size is strongly different with spicules 10 times bigger in our specimen.

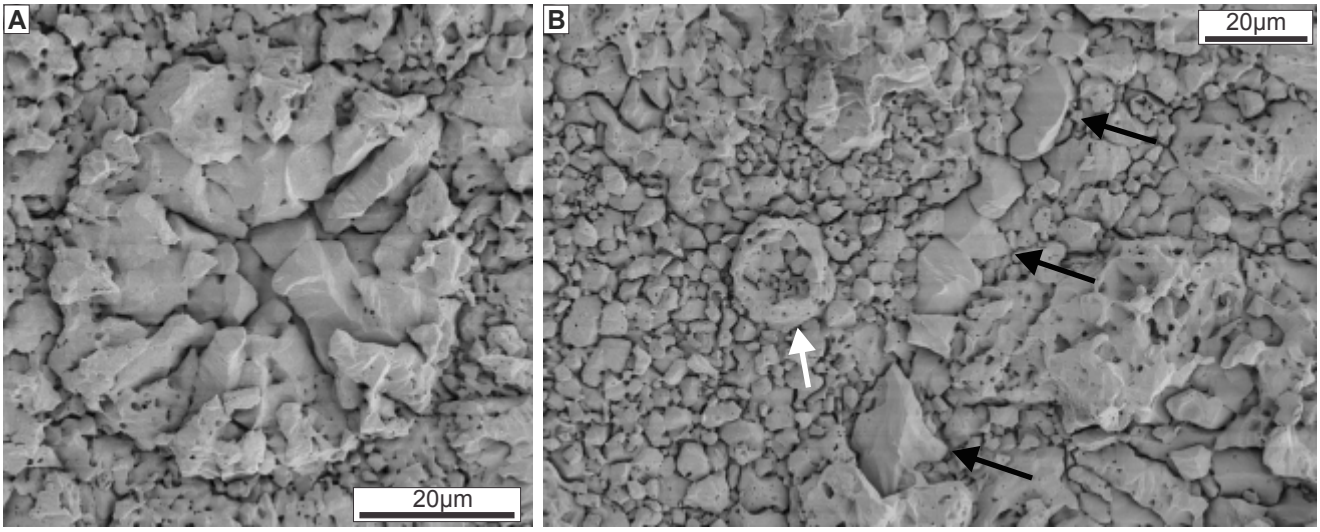
Table 1. Comparison of characteristic features from “*Newellia” mira* (Wood *et al.* 1989) and *Euzkadiella erenoensis* (Reitner 1987) with the specimen from this paper.

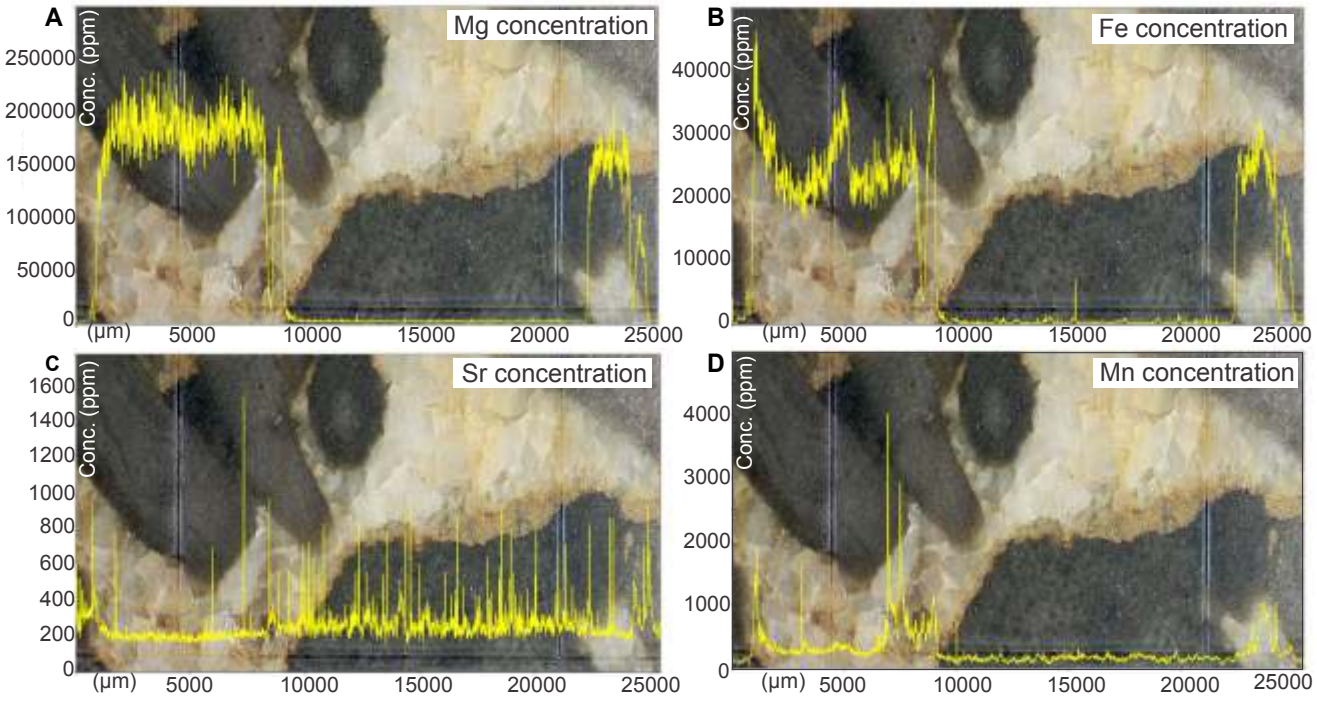

A
2°30' Long. E
50°30' Lat. N
NAMUR SYNCLINORIUM
DINANT SYNCLINORIUM
VESDRES SYNCL.
N
X
Y
Dinant
La Boverie-Rochefort
Givet
PHILIPPEVILLE ANTICLINORIUM
20 km
BELGIUM
Major fault
Studied section
Famennian & Carbonif.
Mid. Devon. & Frasnian
Low. Devon.
Lower Palaeozoic
B
South Dinant Synclinorium
Philippeville Anticlinorium
N Dinant Synclinorium
Upper Frasnian
Middle Frasnian
Low Fr
Givet.
MATAGNE
NEUVILLE
pmt
GRANDS BREUX
Lion
Boverie
Arche
La Boverie - Rochefort
MOULIN LIENAUX
NISMES
PONT DE LA FOLLE
PHILIPPEVILLE
AISEMONT
LUSTIN
GIVETIAN
100m
c. 1 km
Member name
FORMATION NAME
pmt= Petit-Mont Member
La Boverie-Rochefort = studied section
LITHOLOGY
shale
argillaceous limestone
nodular shale
bedded limestone
dolomite
mound
C
250
200
150
100
50
Le Lion Member
Bieumont Member
La Boverie Member
Arche Member
Lbv54
Grands Breux Formation
Moulin Liénaux Formation
D
Limestone
Laminated limestone
Shale
Tabulate branching corals
Dendroid strom.
Clasts, brecciated level
Gastropods
Crinoids
Solitary rugose corals
Bulbous strom.
Fenestrae
Stromatactis
Zebra
Brachiopods
Colonial rugose corals
Laminar strom.

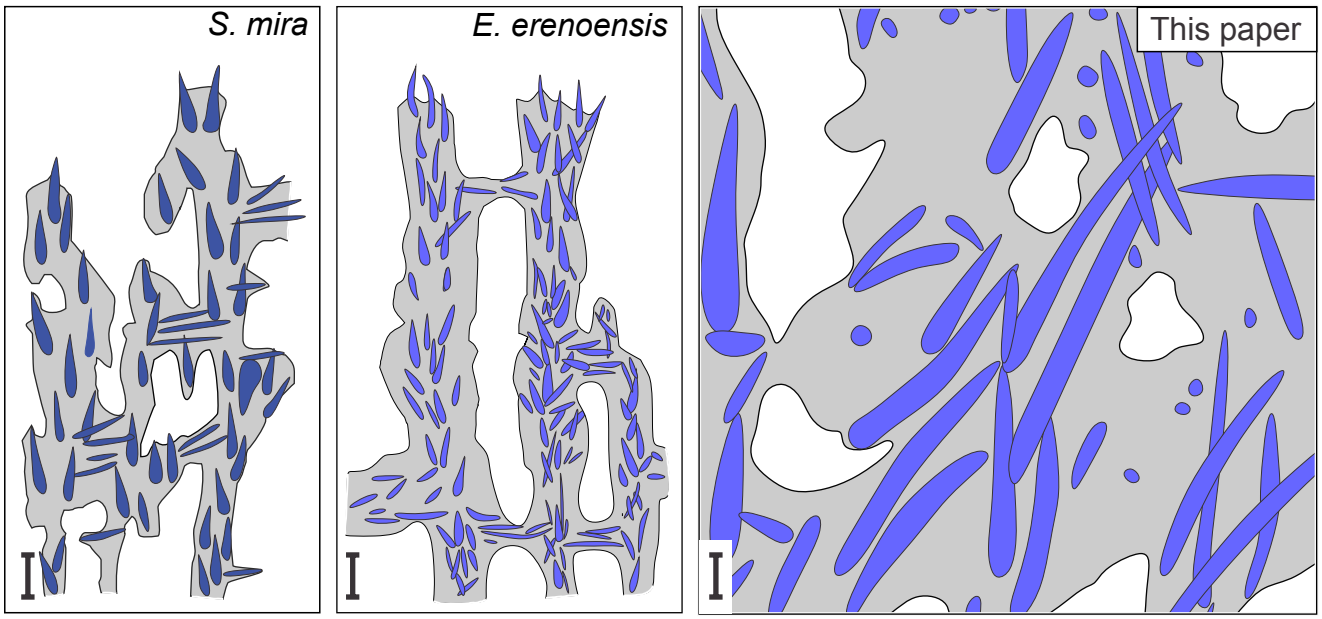

A
1 cm
B
2 mm
C
1 mm
D
500 µm
E
500 µm


A
100 µm
B
100 µm
C
500 µm
D
500 µm


A
200 µm
B
200 µm
C
100 µm
D
500 µm
E
100 µm
F
D
E


A
20μm
B
20μm


A
Mg concentration
Conc. (ppm)
250000
200000
150000
100000
50000
0
(µm)
5000
10000
15000
20000
25000
B
Fe concentration
Conc. (ppm)
40000
30000
20000
10000
0
(µm)
5000
10000
15000
20000
25000
C
Sr concentration
Conc. (ppm)
1600
1400
1200
1000
800
600
400
200
0
(µm)
5000
10000
15000
20000
25000
D
Mn concentration
Conc. (ppm)
4000
3000
2000
1000
0
(µm)
5000
10000
15000
20000
25000


S. mira
E. erenoensis
This paper