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

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This paper records the first example of a demosponge spicule framework in a single specimen of a Devonian stromatoporoid from the Frasnian of southern Belgium. The small sample (2.5 × 2 cm) is a component in a brecciated carbonate from a 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 recrystallized as multi-crystalline calcite. The spicules fall into two size ranges: 10–20 μm diameter and 500–2000 μm long for the large ones and between 5–15 μm diameter and 50–100 μm length 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. ☐ *Demosponge spicules, Devonian, Frasnian, Porifera, stromatoporoids.*

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Stromatoporoids were first described in Devonian rocks by Goldfuss (1826) and are known to have representatives through the geological record, with gaps, from Early Ordovician to the Recent. Stromatoporoids are currently generally considered 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 to 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 & Krumbein 1983; Kazmierczak & Kempe 1990; 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 & Reitner 1986; Wood 1987) and in Upper Carboniferous stromatoporoids (Wood *et al.* 1989), although some authors do not consider these Upper Carboniferous specimens to be 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 stromatoporoid *Syringostroma* are comparable with aster micro-scleres known from the demosponge *Chondrilla*. Unfortunately, the possible

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spicule remains are not perfectly preserved. Because spicules were not found in Lower and Middle Palaeozoic stromatoporoids, they were considered aspiculate (Kershaw 1998; Stearn *et al.* 1999; Stearn 2010). Nevertheless, 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, the absence of spicules in fossil stromatoporoids may be due to non-preservation.

As spicules were not identified in Palaeozoic stromatoporoids, the traditional taxonomy is based on the architecture of the calcified skeleton, now recognized as a secondary calcareous skeleton in modern sponges, so that the term stromatoporoid is regarded as a grade of organization of a sponge skeleton. Because of the widespread recognition of spicules in Mesozoic stromatoporoids and modern calcified demosponges, the taxonomic class Stromatoporoidea is not considered by some authors to have taxonomic validity and the mid-Palaeozoic fossils of stromatoporoid grade cannot be validly sub-divided into taxonomic groups (Wood 1987; Wood *et al.* 1989; Reitner 1991; Reitner & Wörheide 2002).

In the *Treatise Online of Invertebrate Palaeontology* (Stearn 2010), the Palaeozoic stromatoporoid fossils are defined by their 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 article, 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 is the first record of spicules in a Devonian stromatoporoid and is potentially a highly significant to the understanding of stromatoporoid biology.

Materials and methods

The specimen described was collected from the Frasnian carbonate mound succession in the La Boverie quarry, in a stromatoporoid collection of 3079 specimens (collected in 2009, complete palaeoecological results and setting in Da Silva *et al.* 2011a). 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 stratigraphical 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). In the Central and Northern parts of the Frasnian belgian platform (Fig. 1B), biostromal and lagoonal facies dominate and are also rich in stromatoporoids (Da Silva *et al.* 2011b). The specimen described in this study 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 main mound body (Da Silva *et al.* 2010, 2011a).

The stromatoporoid sample containing spicules is a fragment measuring 2.5 × 2 cm, which is 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 (one tangential, one longitudinal and two oblique sections). The samples were examined under a normal light microscope, scanning electron microscope and cathodoluminescence (CL), the last offering the best images. The specimen, sample LBv54, 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

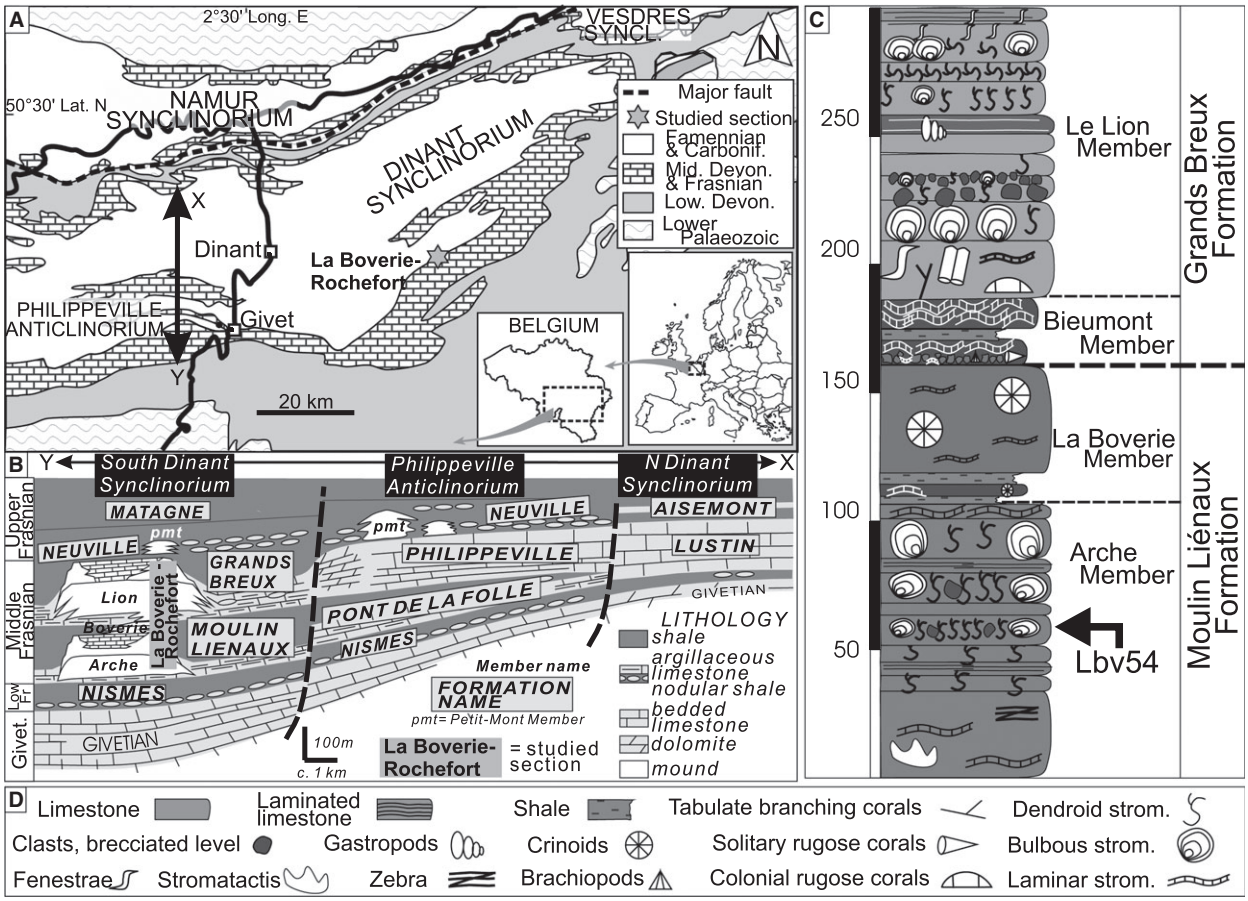

Fig. 1. Geological setting of the Frasnian of Belgium. A, geological map with outcrop location. B, north–south section of the Frasnian basin before Variscan deformation, with the La Boverie-Rochefort quarry stratigraphic extension mentioned (section X-Y from Fig. 1A). C, simplified lithological column of the 300 m succession from the La Boverie Rochefort section (detailed column in Da Silva *et al.* (2011a)) with formation and member names. The dark arrow indicates the stratigraphical position of the sample LBv54 where the spicules were found. D, legend for the lithological column in C.

standard, a calcium concentration of 400 000 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 s 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 micro-structure 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.*

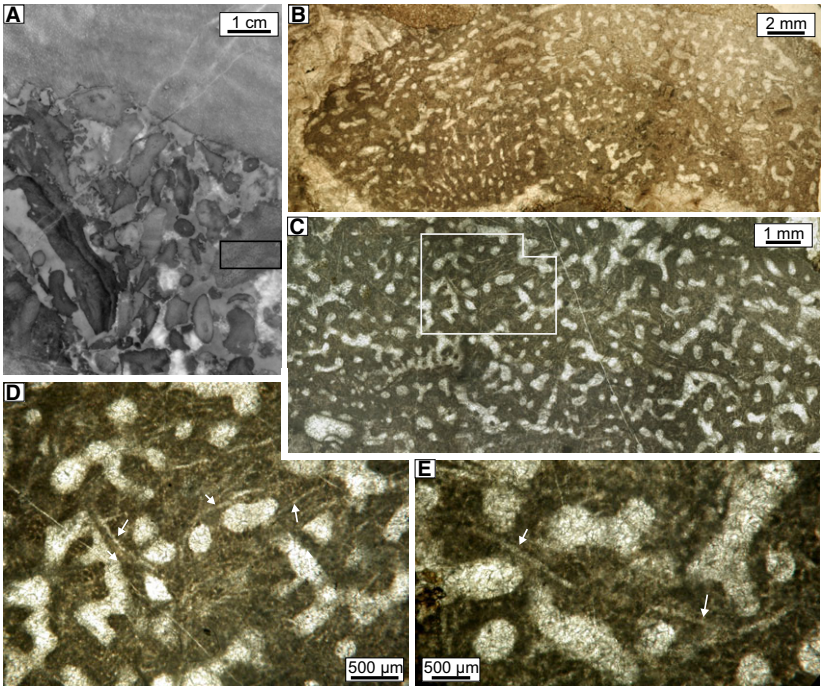

Fig. 2. Sample LBv54, general view of the sample and the spicules. A, polished sample, stromatoporoid and tabulate coral (centimetre size) rudstone with a sparitic and dolomitic cement. The stromatoporoid with spicules is framed (centre right), and this frame corresponds to the picture C. B, longitudinal 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.

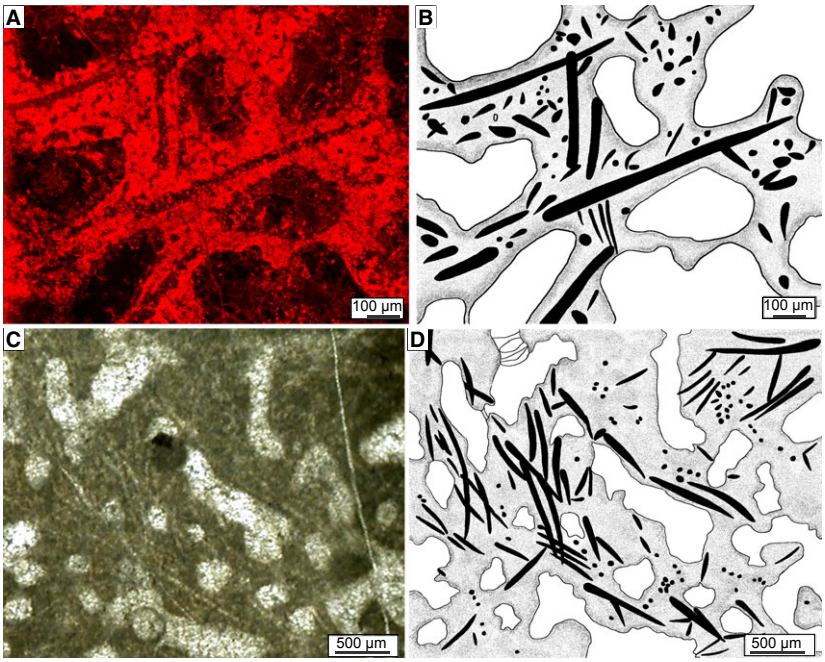

Fig. 3. Organization of the spicules in different zones of the specimen LBv54. Large intermural spicules organized as a perpendicular network, with numerous small spicules, and showing local organization of the spicules in plumules. A, B, cathodoluminescence micro-graph and corresponding sketch. C, normal light picture, zone with a plumose network. D, sketch of the spicule arrangement, showing the plumose network, the two sizes of spicules and the fact that they lie entirely within the skeleton.

(1999) considering the skeleton structure (cassiculate with locally dominant pachysteles or pachystromes) and micro-structure (melanospheric).

Two kinds of spicules are observed corresponding to two size ranges (Fig. 3). The spicule size range is between 10–20 μm wide and 500–2000 μm long for the large ones (which are conspicuous) and between 5–15 μm wide and 50–100 μm long 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 (Figs 2D, E, and 3 and 4) or strongyles (Fig. 4C). The spicules are preserved as multicrystalline calcite (5–20 μm crystals) and are strongly affected by diagenesis, resulting in a recrystallized structure (e.g. Figs 2D, E and 5). They appear to be more concentrated in some areas than in others, which seem 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.

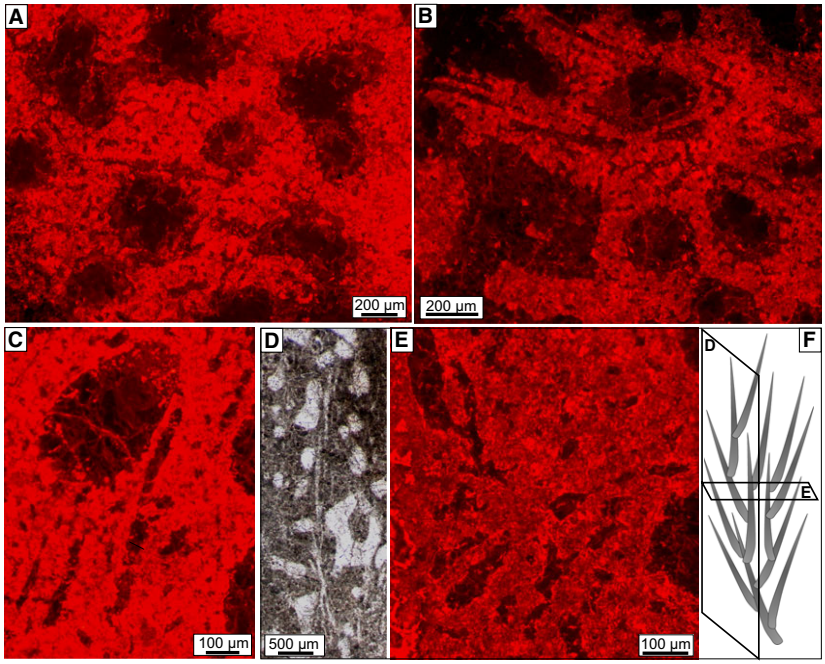

Fig. 4. Cathodoluminescence micro-graphs, organization of the spicules and shape (Specimen LBv54). A, B, on these sections, most of the spicules are cut transversally, with only a few spicules with a longitudinal section. C, spicules with strongyle shape, with a low angle between them. D, normal light picture, plumose arrangement, the spicules are organized with a low angle between them. E, spicules organized in a 'bouquet' in a tangential view. F, 3-D representation of the spicular arrangement, reconstruction after the micro-graphs D and E.

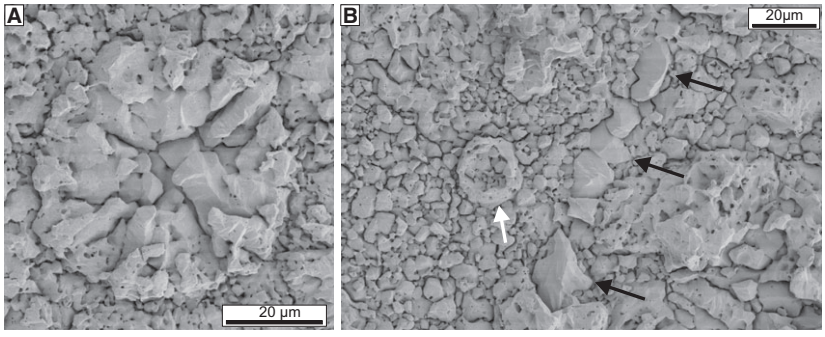

Fig. 5. SEM pictures of the spicules (Specimen LBv54). A, tangential circular section of a large spicule. B, spicules in tangential section (white arrow) and in longitudinal section (black arrows) composed of coarse crystals.

The spicules are organized as follows. They are commonly enclosed in the skeleton, and as they do not enter the galleries, they are intramural. The spicules are relatively closely packed and arranged as either a perpendicular network (Fig. 3) or as plumose structures (low angle between them; Figs 3 and 4). They are commonly parallel to both the pachystromes and the pachysteles.

The possibility that the spicule-shape structures could be micro-borings 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 favour 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 subsequently identified as various types of micro-borings. However, Chatterton *et al.* (2008) convincingly demonstrated 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 micro-structure of the basal skeleton is somewhat melanospheric, containing common, round, 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, for example, the 'stromatoporoid' *Astrosclera* (Reitner 1992; Wörheide 1998) and *Stachyodes* (plate 1 in Mistiaen 1991). The investigated basal skeleton of the spicule-bearing stromatoporoid is partly altered diagenetically. 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 sub-angular. Canals and other primary open spaces of the stromatoporoid are cemented by sub-angular 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 dolomitization process (Vasconcelos *et al.* 1995).

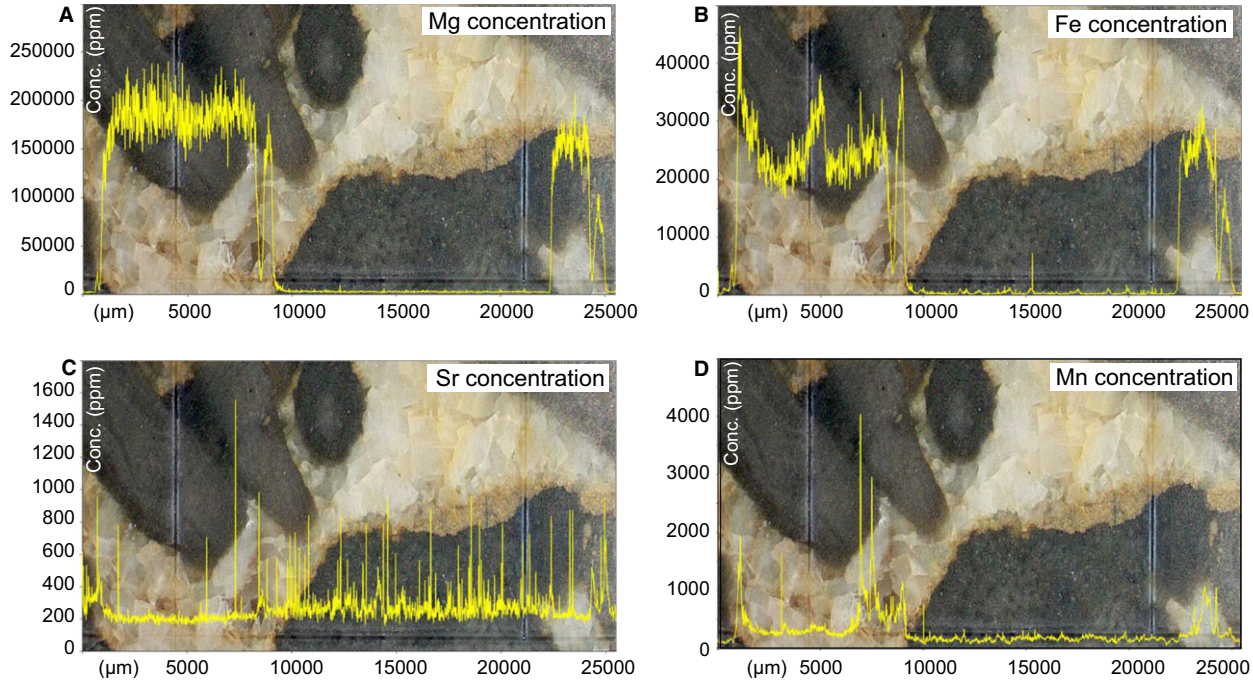

Fig. 6. Mg, Fe, Sr and Mn concentration along a transect on the LBv54 sample. Cutting through a dolomitic cement (0–10000 and 22 000–25 000 μm) with a higher Mg (A), Fe (B) and Mn (D) concentration and through the spicule-bearing specimen (10 000–22 000 μm), with a higher Sr concentration (C).

Trace element analyses of the basal skeleton show a slight increase in 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 in 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 (CL) behaviour of the basal skeleton and the various cements, which supports this assumption. The late dolomitic cements are non-luminescent except for some small bright 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 in Sr within the basal skeleton could indicate a primary aragonite skeleton. The melanospheric micro-structure may be a diagenetic product of an original spherulitic structure.

Discussion

The discovery of demosponge spicules emphasizes the sponge affinity of stromatoporoids, but because the sample is a single small fragment, this limits the value of this sample in determining the taxonomy of stromatoporoids. Kershaw's (1998) argument that the Palaeozoic stromatoporoid skeleton had taxonomic validity at genus level is unaffected by this new discovery, as 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. 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 & Reitner 1986; Wood 1987; 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 (plumose or perpendicular) was 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 (50–100 μm) are in the same size range as for *E. erenoensis* (75–105 μm) and for *S. mira* (60–120 μm), but the large spicules (500–2000 μm) are ten times bigger than those of *E. erenoensis* (between 105–250 μm) and *S. mira* (115–150 μm). As observed in Figure 7, the spicules and the whole stromatoporoid structure are actually larger.

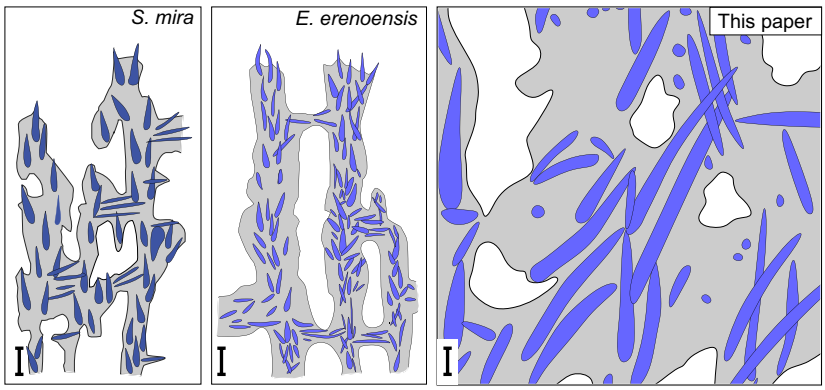

Fig. 7. Comparison of '*Newellia*' *mira* (Wood *et al.* 1989) and *Euzkadiella erenoensis* (Reitner 1987) with the specimen from this study (LBv54). Scale bar is 100 μm. The type of spicules and their arrangement is relatively similar, but their size is strongly different with spicules ten times larger 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.

Species		*Newellia mira*	*Euzkadiella erenoensis*	Specimen from this paper
Age		Upper Carboniferous	Lower Cretaceous	Middle Frasnian
Locality		Kansas, USA	Ereno, Spain	La Boverie, Belgium
Calcareous skeleton	External morphology	Massive nodular, encrusting	?	?
	Micro-structure	?	?	Melanospheric
Spicular data	Type of spicules	Style, Sub-tylostyle strongyle	Sub-tylostyle Strongyle style	Sub-tylostyle Strongyle style
	Distribution	Intramural plumules or perpendicular	Intramural plumules	Intramural plumules or perpendicular
	Present mineralogy	Calcite	Calcite	Calcite
	Size: L. (μm)	110–150 or 60–120	75–105 or 105–250	20–100 or 500–2000
	Size: D. (μm)	10–15 or 5–10		5–15 or 10–20
References		Wood *et al.* 1989;	Reitner 1987	This paper

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 sub-tylostyle 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 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 emphasizes the demosponge affinity of the specimen described in this paper.

Affinities to modern halichondrid demosponges

The classic taxonomy of the Halichondrida based on spicule types and spicule architecture, 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, and micro-scleres 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 lacks an ectosomal spicular skeleton. In 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 characterized by a choanosomal skeleton often formed by ascending plumose spicule tracts horizontally connected by smaller spicules. Megascleres are oxeas, styles and curved styles. Micro-scleres are thin raphides in some taxa. Megascleres could reach lengths of 600–700 μm, and therefore, large, average length is around 200–300 μm. 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.* 2005, 2006, 2012; Morrow *et al.* 2012). Unfortunately, halichondrids lack synapomorphic characters like characteristic micro-scleres, and the definitions of the families are mainly based on the absence of characters. Spicule types and architectures are more plesiomorphic characters and therefore not suited for phylogenetic analyses. The Axinellida/Halichondrida that are most applicable to this study are part of different phylogenetic groups and non-monophyletic (Alvarez *et al.* 2000; Uriz *et al.* 2003; Gazave *et al.* 2010; Erpenbeck *et al.* 2012; Morrow *et al.* 2012). These studies have reclassified 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 classic 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 800 μm) also occur. More important for phylogenetic interpretations is the plumoreticulate choanosomal spicule architecture observed in the sample LBv54 of this study. This is the first observation of complex halichondrid/axinellid spicule architecture in the fossil record of the halichondrid-type demosponges and also the first occurrence of a sponge spicule-bearing coralline demosponge. Intramural spicules within archaeocyaths are probably of allochthonous origin (Reitner & Mehl 1995; Debrenne & Reitner 2001).

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 spherulitic, 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 characterized by a typical 'water jet' arrangement of the calcite crystals, and *Euzkadiella* shows a spherulitic Mg calcite (Wood & Reitner 1986; Reitner 1987; Wood 1990). Based on biomineralization studies on modern coralline sponges, it is known that the basal skeleton formation is enzymatically controlled by the sponge (e.g. Jackson *et al.* 2007, 2011). However, 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 at a very low taxonomic level (Reitner 1992).

Conclusions

The following conclusions can be made.

1. The new finds of intramural demosponge spicules within the basal skeleton of a Frasnian stromatoporoid (probably *Stromatopora* sp.) support the interpretation that mid-Palaeozoic 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 into 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 micro-structure 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 organization.

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