An Upper Ordovician sponge-bearing micritic limestone and implication for early Palaeozoic carbonate successions

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ABSTRACT

A potentially new type of non-reef sponge-bearing micritic limestone is reported from the Upper Ordovician Xiazhen Formation of south-eastern China. The sponges are preserved as incomplete skeletons that consist of curved bifurcated and trifurcated spicules embedded in dark micrite, and can only be recognized under a petrographic microscope. The characteristics of the spicule networks suggest that the sponges are probably belonging to demosponges. However, based on the absence of features such as desma, zygome, a distinct dermal layer, and a canal system, they are not considered to be lithistids. The majority of the sponges are found in a lime mudstone facies, together with some micritic portions of wackestone to grainstone facies, comprising approximately 13% of the 50-m thick micritic limestone successions. It is interpreted that the non-lithistid demosponges flourished on soft substrates over shallow marine carbonate platform. Such sponge-bearing carbonates are similar to spiculites and spongolites in terms of being a major constituent of the sedimentary rocks and their potential contribution as sediment producers, but affinity and modes of preservation of the Xiazhen sponges are significantly different to those of the spiculites and spongolites. In light of the present finding, it is suggested that non-lithistid demosponges may have been more widespread in early Palaeozoic non-reef carbonates than has previously been recognized, thus indicating the critical need for further detailed studies if we are to understand their distributions and sedimentological contributions.

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1. Introduction

Sponges, which may have appeared as far back as the Cryogenian, are widely accepted to be one of the oldest metazoans according to biomarker (Love et al., 2009) and molecular clock (Erwin et al., 2011) analyses. The oldest known genuine fossil sponges consist of spicules of demosponge (Reitner and Wörheide, 2002) or hexactinellid affinities (Brasier et al., 1997); definitive impressions of hexactinellid spicular networks are known from the latest Ediacaran (Gehling and Rigby, 1996). Demosponges and hexactinellid

sponges are often preserved as completely to partially preserved skeletons or scattered spicules, according to their preservation potential; the chance of preservation in sponges with rigid bodies containing articulated (lithistids; demosponges) or fused spicular skeletons (hexactinosids and lychniscosids; hexactinellids) is better than that of soft-bodied sponges (Pisera, 2006). In reefs, siliceous sponges with rigid skeletons have been important reef builders throughout the Phanerozoic (e.g., Klappa and James, 1980; Wendt et al., 1989; Brunton and Dixon, 1994; Olóriz et al., 2003; Hong et al., 2015) as well as Recent (Conway et al., 1991; Krautter et al., 2001). Rigid sponge skeletal remains in non-reef carbonate and clastic settings are relatively well documented from numerous deposits, such as from the Mesozoic carbonate and clastic successions of Europe (Zimmerle, 1991) and the Eocene clastic sequences of southern Australia (Gammon and James, 2001).

Remains of non-rigid siliceous sponges, e.g., non-lithistid demosponges and hexactinellids with isolated spicules, are commonly found throughout the Phanerozoic deposits in the form of scattered spicules and spiculites (e.g., Zimmerle, 1991, Table 1; Franseen, 2006, Table 4). During the early Palaeozoic, scattered spicule-bearing

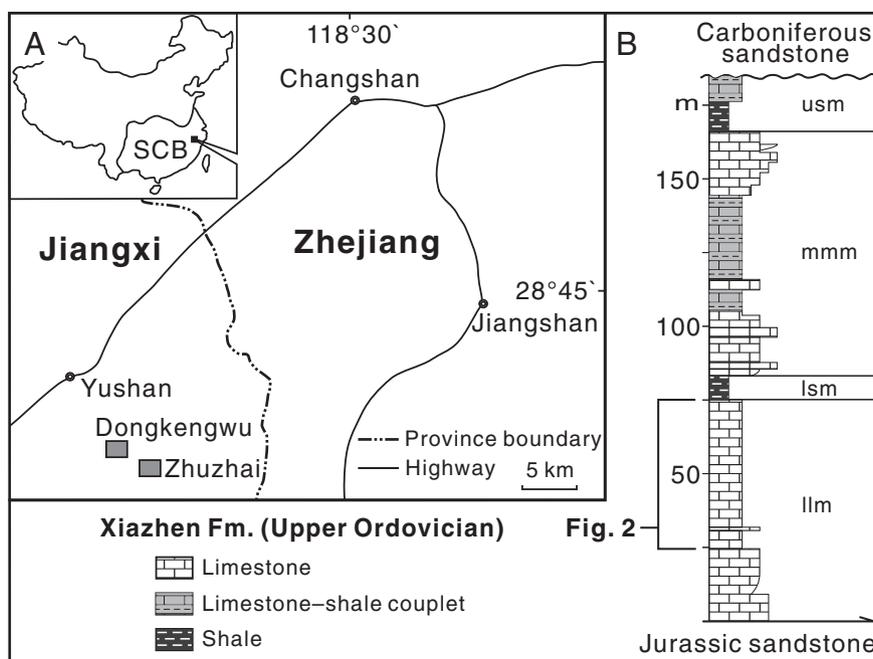* Corresponding author. Tel.: +82 2 3290 3180; fax: +82 2 3290 3189.
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Fig. 1. (A) Location of the study area near the border between Zhejiang and Jiangxi provinces, China. Two measured sections are located near Dongkengwu and Zhuzhai villages, 10 and 15 km southeast of Yushan, respectively. SCB = South China Block. (B) Simplified lithological column of the Xiazhen Formation. The formation at Zhuzhai is in fault contact with underlying Jurassic sandstone of the Linshan Group and is disconformably overlain by the Lower Carboniferous Yejiatang Formation (Zhang et al., 2007). llm = lower limestone member; lsm = lower shale member; mmm = middle mixed lithology member; usm = upper shale member.

limestones were widespread in shallow to deeper subtidal conditions around the world, but completely or partially preserved skeletons of non-rigid sponges were rare (Carrera and Rigby, 1999, 2004; Carrera and Botting, 2008; Muir et al., 2013). In this study, we report on a new type of sponge-bearing non-reef micritic limestone from the Xiazhen Formation (Upper Ordovician), south-eastern China, in which the incomplete skeletons of numerous non-lithistid demosponges embedded in micrite were found. This study aims to document the sponges preserved in the micritic limestone and to provide additional information on sponge distribution patterns during the early Palaeozoic.

## 2. Geologic setting and methods

The Xiazhen Formation of south-eastern China (Fig. 1A) is a mixed carbonate–siliciclastic fossil-rich deposit that contains stromatoporoids, corals, brachiopods, calcareous algae, calcimicrobes, trilobites, and molluscs (Zhan et al., 2002; Li et al., 2004; Zhang et al., 2007; Lee et al., 2012; Lee, 2013). The formation, which occurs as a thrust-faulted inlier resting on top of Jurassic strata (Fig. 1B), has been correlated with its seaward equivalents, the Sanjushan Formation and the outer-shelf clastic deposits of the Changwu Formation (Zhan et al., 2002; Li et al., 2004). Although no definitive index fossils have been found in the Xiazhen Formation, it has been estimated to be of the late Katian (middle Ashgill) age, based on graptolites from the Changwu Formation (Zhang et al., 2007). The Xiazhen Formation has been interpreted as tidal flat to lagoonal deposits that were deposited on the Zhe-Gan Platform, along the northern margin of the Cathaysian Oldland (e.g., Li et al., 2004). The present study adopts the stratigraphy of the Xiazhen Formation recently revised by Lee et al. (2012), in which the following members are recognized in ascending order: a lower limestone member, a lower shale member, a middle mixed lithology member, and an upper shale member (Fig. 1B).

Two stratigraphic sections in the lower limestone member were measured and correlated at a scale of 1:20, supplemented by 420 samples with an average vertical interval of 25 cm (Fig. 2). To describe the carbonates, we implemented the ichnofabric index concept (sensu Droser and Bottjer, 1986), which is a semi-quantitative measurement of bioturbation perpendicular to bedding (Droser and Bottjer, 1986, 1993). Sedimentary facies were classified in the field on the basis of sedimentary textures, fossil contents, and sedimentary structures (Table 1). The extent of sponge remains was calculated from the cumulative areal coverage of spicule networks in 184 thin sections, including 90 standard (28 × 48 mm) and 94 large-format (54 × 76 mm) thin sections cut perpendicular to bedding (Fig. 2).

3. Results

3.1. Xiazhen sponge remains

Xiazhen sponges, which are preserved as networks composed of microspar embedded within micrite and tentatively regarded as spicule networks, were identified in 43% of the samples collected from the lower limestone member (Fig. 2). The networks are not visible in outcrop surfaces or on slabs (Fig. 3A), but only recognizable in thin sections (Fig. 3B); they are a few millimetres to several centimetres across, and often change gradationally from well-preserved networks to micrite without any distinct boundaries (Fig. 4C, D). On the other hand, sponge remains were not found after treating the specimens with acid. The networks are composed of "spicules" 35–50 μm in diameter and 60–200 μm in length. The spicules are often curved, bifurcated or trifurcated, and the spicule rays are mostly at non-perpendicular angles to one another (Fig. 3C). Each spicule shows smooth outline with relatively uniform diameter, including intersecting points. Most of the networks display irregularly shaped outlines in cross sections, whereas some circular to ellipsoidal forms of less than 1 cm in diameter also
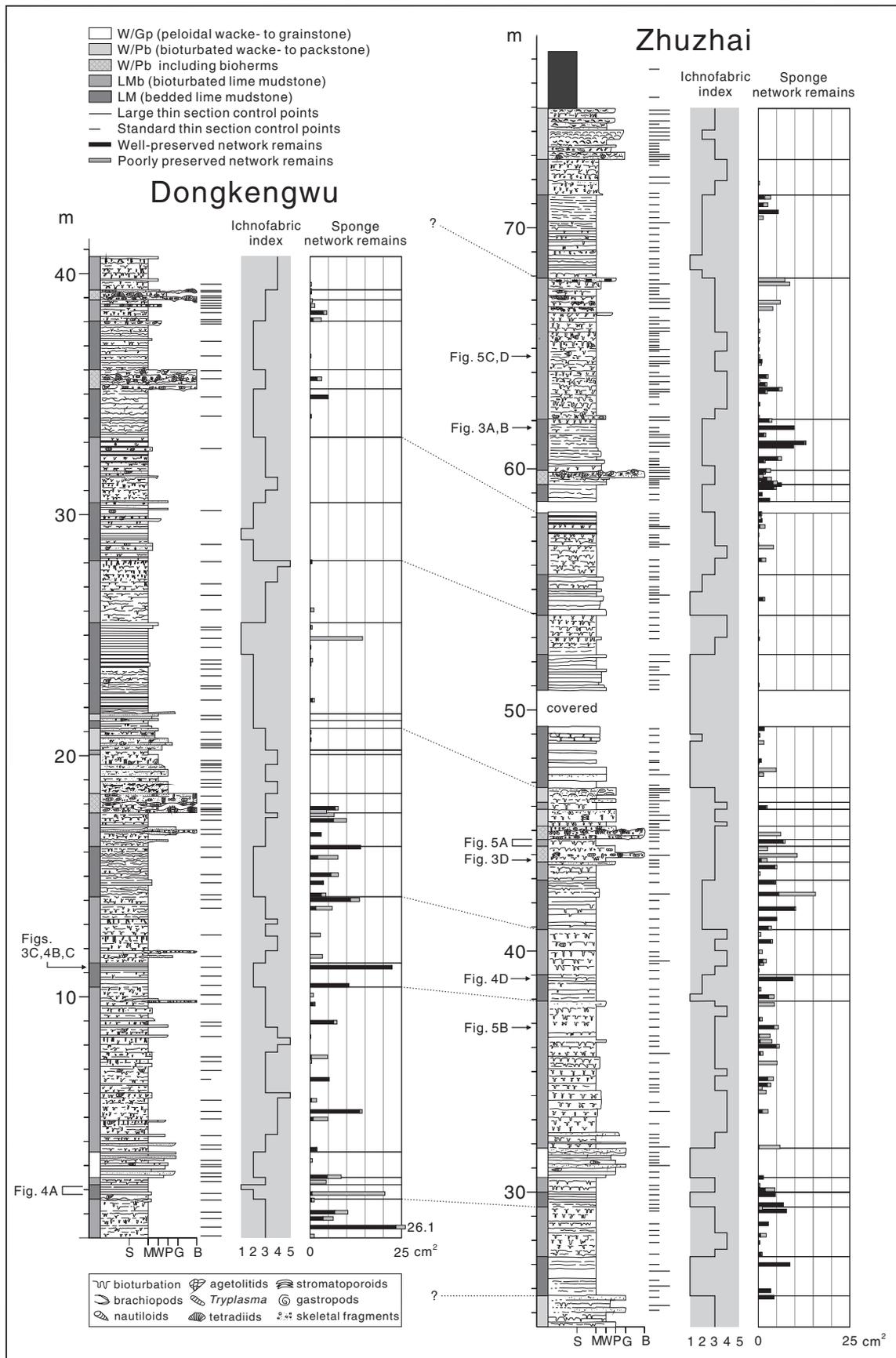
Fig. 2. Lithological logs of the middle to upper parts of the lower limestone members at Dongkengwu and Zhuzhai. See Kwon et al. (2012) for the 25-m-thick lowermost part of the member at Zhuzhai. Sponge occurrences and their areas, as measured from thin sections, are marked on the right side of the columns. S = shale; M = lime mudstone; W = wackestone; P = packstone; G = grainstone; and B = boundstone.

Table 1
Sedimentary facies of the lower limestone member of the Xiazhen Formation.

Facies	Description		Ichnofabric index	Proportion of specimens containing sponge remains	Interpretation
	Outcrop	Thin section			
Lime mudstone (LM)	Thinly bedded (<10 cm) grey lime mudstone bounded by stylolites or dissolution seams. Occasional intercalation of fossil layers (<1 cm) composed of gastropods, bivalves, and nautiloids. Isolated burrows gradationally increase toward LMb facies. Thickness: 0.5–5.5 m	Homogeneous dark grey micrite with abundant sponge spicule networks	1–2	58/105 (55%)	Deposition under low-energy conditions
Bioturbated lime mudstone (LMb)	Massive bedded grey (>20 cm) lime mudstone with extensive bioturbation and rare erosional surfaces. Mottled and bifurcating sub-horizontal to vertical tube-shaped burrows (>5 cm in depth), resembling *Thalassinoides*. Rare highly bioturbated (i.i., 5) zones. Occasional intercalation of fossil layers (<1 cm) composed of ostracods, gastropods, bivalves, nautiloids, and rare rugose corals. Thickness: 0.2–6 m	Micrite containing abundant burrows filled with lighter grey micritic dolomite. Sponge spicule networks are common within dark grey micrite	3–4 (5)	100/143 (70%)	Deposition under low-energy conditions with common burrowing organisms
Bioturbated wacke- to packstone (W/Pb)	Massive skeletal wackestone to packstone with common burrows. Commonly intercalated with thin lenticular skeletal beds with sharp erosional bases. Occasional cm- to dm-scale buildups composed of tabulate (agetolitid) and rugose (*Tryplasma*) corals, tetradiids, calcimicrobes, and stromatoporoids (*Clathrodictyon*). Thickness: 0.3–2 m	Common occurrences of gastropods, bivalves, nautiloids, calcimicrobes, bryozoans, trilobites, ostracods, *Amsassia*, corals, tetradiids, and brachiopods. Sponge spicule networks are rare	3–4	21/85 (25%)	Deposition under normal marine and shallow subtidal conditions
Peloidal wacke- to grainstone (W/Gp)	Cross-laminated or graded and thinly bedded (0.5–10 cm) dark grey peloidal wackestone to grainstone with common fenestral fabrics. Often associated with hemispherical stromatolites occurring on top of peloidal grainstone beds. Thickness: 0.3–2 m	Sets of graded laminae with erosional bases composed of graded grainstone to wackestone. Common peloids, aggregates, rounded intraclasts, superficial ooids, and ostracods. Rare oncoids, calcimicrobes (*Ortonella*), mollusc fragments, and sponge spicule networks	1–2	5/85 (6%)	Deposition under shallow subtidal to intertidal conditions

occur but rarely (Fig. 4D). The sponge remains can be further subdivided into well- and poorly preserved networks. Well-preserved networks are composed of regularly spaced spicules (Fig. 3B, C), whereas poorly preserved networks are characterized by indistinct or distorted networks that retain only partially connected spicules (Fig. 3D). Discrete canal systems or dermal spiculation are not recognized. Most of the sponge network remains described in this study are not encrusted either by other organisms, or by each other. Loose spicules are rare to absent in micritic carbonate succession of the lower limestone member.

Based on the bifurcated and trifurcated features of the spicules, the spicule networks are not considered to be hexactinellid sponges (with six-rayed spicules, or four-rayed in plan view), calcareous sponges (with triaxons, or three-rayed in plan view), or octactines (six-rayed in plan view). The absence of scattered monaxial and tetraxial spicules near the spicule networks indicates that the sponges are not demosponges with loosely connected skeletons (e.g., monaxonids or choristids). The Xiazhen sponge remains also lack convincing features such as interlocking megascleres with an irregular warty form (desma), hypertrophic terminals that lock the spicules together into a rigid skeleton (zygome), and distinct dermal layers and canal systems, all of which are diagnostic characteristics of lithistid demosponges (Pisera and Lévi, 2002; Reid, 2003; Finks and Rigby, 2004). Recently similar structures are reported from Devonian and Triassic reefs and interpreted to be keratosan sponges, which are non-spicular demosponges composed of a network of spongins based on three-dimensional reconstructions (Luo

and Reitner, 2014). Even though "spicules" in this study are open to be reconsidered as fibrous spongin networks, it is not possible to test this idea on the current material, because three-dimensional reconstruction of such small structures cannot be done from thin sections. In any case, overall characteristics of the Xiazhen sponge remains suggest that they are most probably a type of non-lithistid demosponge, although further taxonomic inferences are not possible at present.

3.2. Sponge distribution by facies

3.2.1. Thinly bedded lime mudstone (LM) facies

The LM facies is composed of sporadically burrowed grey lime mudstone beds less than 10 cm in thickness (Fig. 4A) and associated with either a bioturbated lime mudstone (LMb) or bioturbated wackestone to packstone (W/Pb) facies (Fig. 2). Each bed is typically bounded by dolomitized laminae or dissolution seams (Fig. 4B), with rare intercalations of thin skeletal laminae composed of whole or partly fragmented fossils. The sponge remains occur in more than half (55%; 58/105) of the LM facies thin sections, although they do not occur evenly throughout the facies (Fig. 2). Most network remains embedded within dark micrite show irregular outline with indistinct boundary (Fig. 4C, D), and about two-thirds of the circular to ellipsoidal-shaped networks (64%; 27/42) are found in this facies (Fig. 4D). The LM facies is characterized by the highest areal coverage of networks in total thin section area (282.6 cm^2; 16.7%) among all described facies. The percentage of
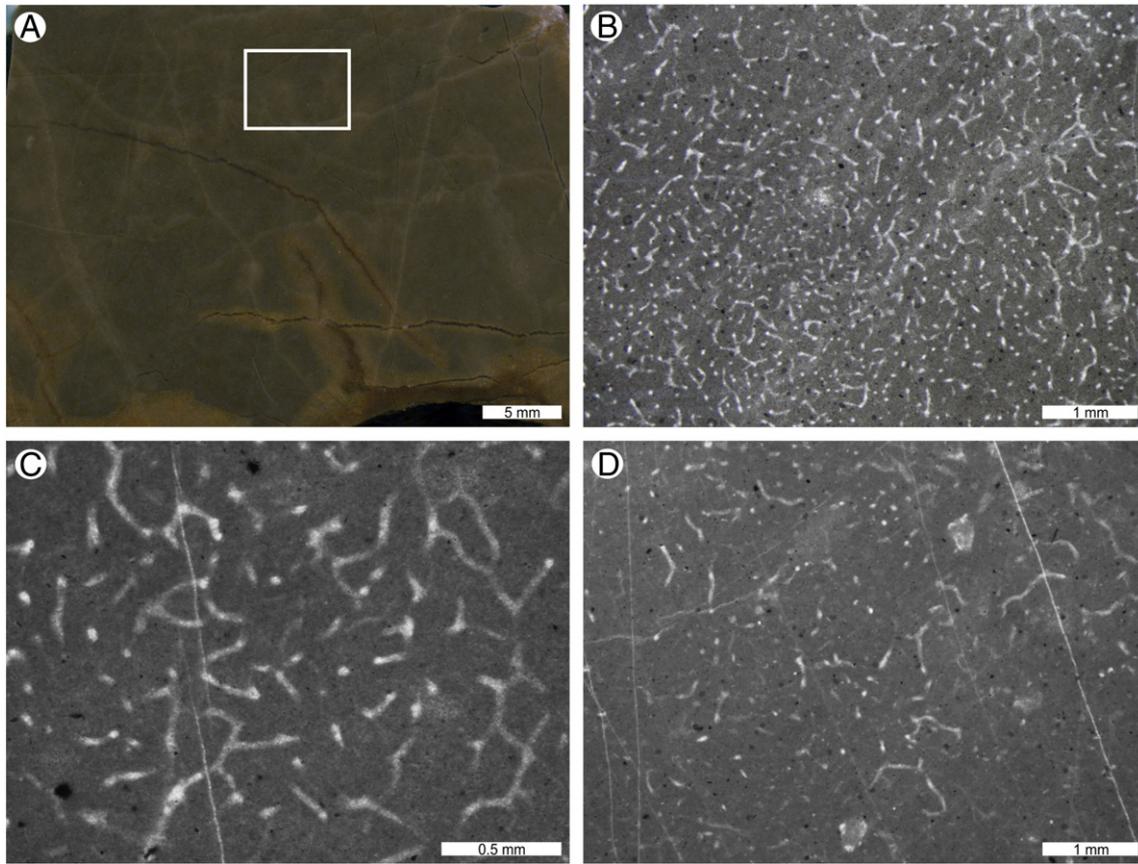
Fig. 3. Characteristic skeletal remains of Xiazhen non-lithistid demosponges. (A) Polished slab of lime mudstone. Note that the sponge skeletal remains are not visible on the slab surface. (B) Photomicrograph of thin section prepared from the rectangular area in A, showing well-preserved spicule networks with regular spacing. (C) Photomicrograph of well-preserved spicule networks consisting of spicules with similar diameters. Note the absence of desma with articulation (zygomes). (D) Poorly preserved spicule network, partially retaining bifurcated spicules.

well-preserved networks relative to the total area of networks (median = 76%) is distinctively higher than that in other facies.

3.2.2. Bioturbated lime mudstone (LMb) facies

The LMb facies consists of massive bedded (>20 cm) grey micritic limestone; burrows are common and are filled with light grey micrite or dolomitic micrite (Fig. 5A). Thin fossiliferous layers, with or without sharp erosional bases, are occasionally intercalated. The sponges of the LMb facies are found in more than two-thirds (70%; 100/143) of the thin sections (Fig. 2). The spicule networks are mostly irregular in shape, and circular to ellipsoidal networks are less common (31%; 13/42) than in the LM facies. The network remains are not observed in areas adjacent to burrows (Fig. 5B), and in highly bioturbated areas they are commonly preserved as small and irregular patches of poorly preserved networks (Fig. 5C, D). In this facies, spicule networks (311.7 cm^2) occupy 11.5% of total thin section area, but the percentage of well-preserved spicule networks relative to the total area of spicule networks (median = 30%) is much lower than that of the LM facies.

3.2.3. Bioturbated wackestone to packstone (W/Pb) and peloidal wackestone to grainstone (W/Gp) facies

The bioturbated wackestone to packstone (W/Pb) and peloidal wackestone to grainstone (W/Gp) facies occur mostly in the lower part of the lower limestone member (see Kwon et al., 2012, Fig. 1C) and are sporadically interbedded with beds of LM and LMb facies in the middle to upper parts of the member (Fig. 2). The W/Pb facies

consists of massive skeletal wackestone to packstone, and mottled burrows are common (Fig. 6A). Coarse skeletal layers with sharp erosional bases are commonly intercalated within the facies. Carbonate buildups composed of corals, tetradiids, calcimicrobes and stromatoporoids occur locally (Fig. 2). The W/Gp facies, which consists of thin-bedded limestone with common fenestrae and scarce bioturbation, is characterized by sets of graded laminae composed of peloidal grainstone to wackestone (Fig. 6B). Hemispherical stromatolites occurring on top of peloidal grainstone beds are cyclically associated with the facies in the lower part of the member (Fig. 6B). A small number of specimens of the W/Pb facies (25%; 21/85) and W/Gp facies (6%; 5/85) contains irregularly shaped and poorly preserved spicule networks (Fig. 6C, D) surrounded by dark grey micrite, and their proportions in total area of thin sections are 2.3% (48.8 cm^2) in W/Pb and 0.8% (14.8 cm^2) in W/Gp facies, respectively. The proportion of well-preserved spicule networks relative to the total area of spicule networks is relatively high in the W/Gp facies (median = 15.7%), but those in the W/Pb facies (median = 6.4%) are lowest among all of the described facies.

3.3. Interpretation

Based on the examination of thin sections, it is calculated that approximately 8% of rock volume in the lower limestone member is composed of the sponge remains and the value can be further increased up to 13% in the 50 m-thick middle to upper part of the member (Fig. 2), where LM and LMb facies are dominant (Fig. 7). The occurrence of
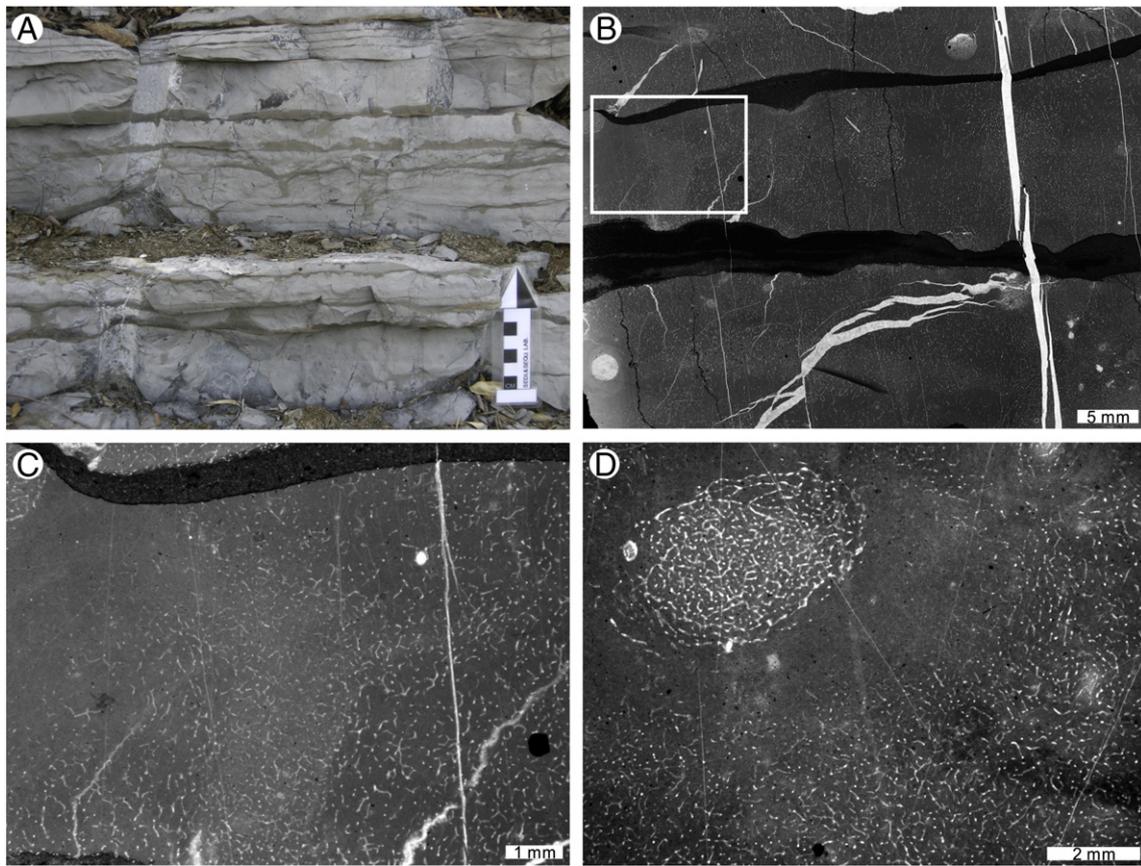
Fig. 4. Sponge remains from LM facies. (A) Photograph of thinly bedded grey lime mudstone bounded by dissolution seams. Note that there is no discernible sponge remains in outcrop surface. (B) Photomicrograph of lime mudstone facies with spicule networks and dissolution seams. (C) Photomicrograph of rectangle in B. Note the gradational change from spicule networks to the surrounding micrite without any discernible boundary. (D) Photomicrograph of rare ellipsoidal-shaped spicule networks with semi-concentric arrangement of spicules. Note that the outer boundary of these forms are relatively well defined in contrast to that of surrounding spicule networks.

sponge spicule networks in all of the described facies, albeit in different proportions, indicates that these sponges were able to adapt and colonize soft substrates over a wide spectrum of shallow marine environments.

Predominant occurrences of sponges in the LM (16.5%) and LMb (11.5%) facies suggest that the sponges probably favoured quiet muddy substrates devoid of other sessile organisms, as compared with common occurrences of stromatolites and other sessile organisms including corals, stromatoporoids, and calcimicrobes in W/Gp and W/Pb facies, respectively. The sponges are most probably preserved at or close to their position of growth, as there is no evidence of transportation. On the other hand, relatively infrequent occurrence of sponge remains in the W/Pb (2.3%) and W/Gp (0.8%) facies, which contain numerous other fossils, implies that the sponges were less well adapted to environments in which other organisms occupied or of higher energy conditions.

Variations in well- to poorly preserved spicule networks would have resulted from the preservational biases, rather than post-mortem disarticulation, as sedimentary facies rich in disarticulated spicules are not present in the succession. In addition, the preservation of sponge spicule networks might also have been related to the degree of bioturbation, since proportion of sponge network remains is higher in LM than LMb facies. It is suggested that the sponges would have been destroyed by burrowing organisms prior to the lithification. The absence of network remains immediately adjacent to burrows and the high ratio of well-preserved networks in the LM facies (median = 76%) collectively supports the interpretation (Fig. 7).

In summary, the widespread occurrence of partial sponge remains in the Xiazhen micritic limestone indicates the presence of extensive sponge meadows that developed in quiet depositional environments, which were partly destroyed by bioturbations. The sponges were also present in other environments, but in such cases, they were suppressed by other organisms and/or higher energy conditions. As the Xiazhen sponge remains occur in nearly half of the micritic carbonates sampled, the sponges must have been one of the most dominant components of the succession, and were therefore potentially important contributors to the sediment column.

4. Discussion

Micritic carbonates widely deposited in early Palaeozoic mixed carbonate–clastic successions, including inner shelf, deeper subtidal ramp and slope conditions (e.g., Semeniuk, 1973; Bova and Read, 1987; Osleger and Read, 1991; Lavoie, 1995; Álvaro and Vennin, 1997; Keller et al., 1998; Elrick and Snider, 2002). Early Palaeozoic siliceous sponges are ubiquitous in these various marine environments (Carrera and Rigby, 1999, 2004; Pisera, 2006; Carrera and Botting, 2008; Muir et al., 2013). In some cases, vast amount of sponges comprise significant volume of the successions, interpreted as sponge meadows on soft substrates (Álvaro and Vennin, 1997; Clausen and Álvaro, 2006). These sponges, however, were mostly preserved as spicules that disintegrated after death and dispersed on the seafloor, and differentiated from the Xiazhen sponges. Although early Palaeozoic lithistid sponges retained their spicular skeletons (Carrera and Rigby, 1999, 2004; Pisera, 2006;
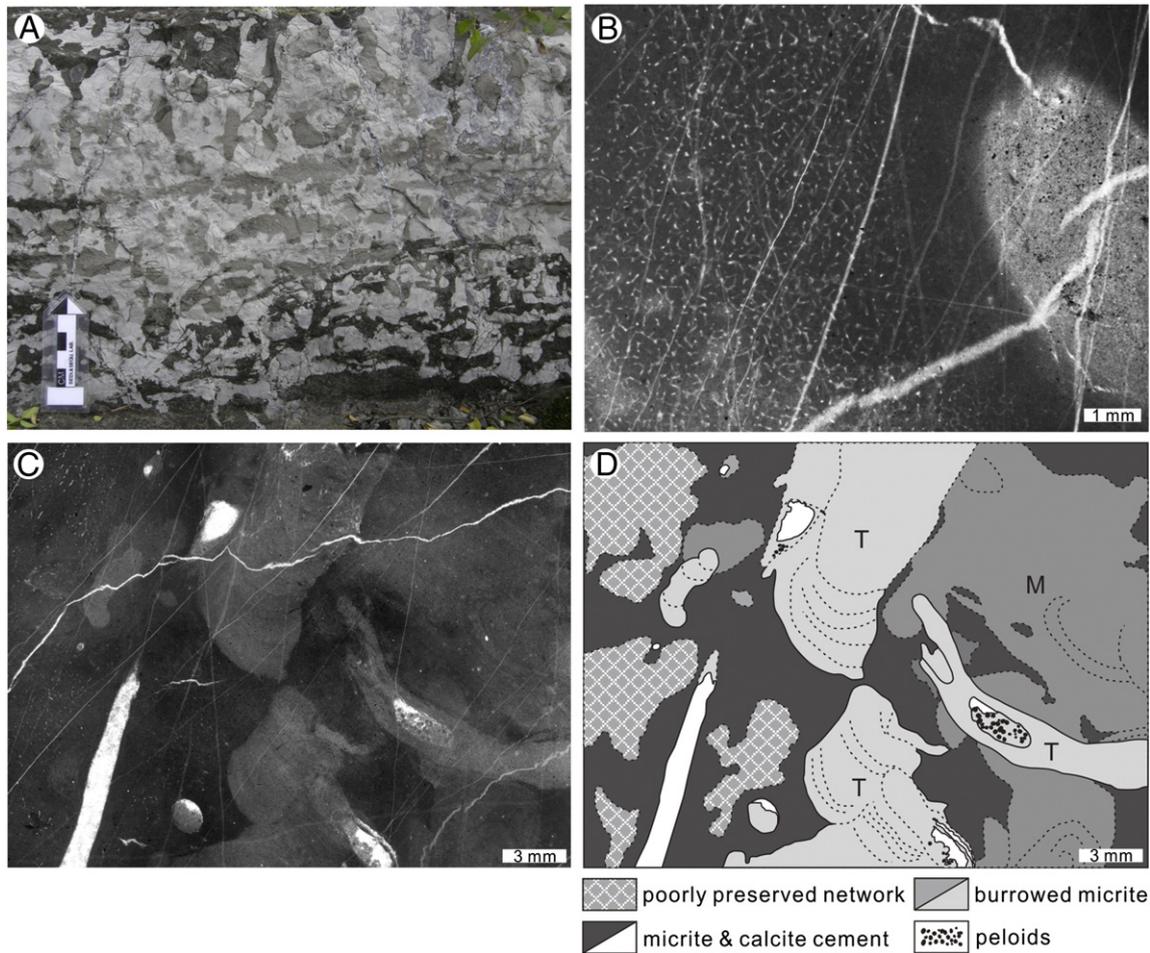
Fig. 5. Sponge remains from LMb facies. (A) Photograph of massive bedded lime mudstone with mottled burrows (i.i., 3). (B) Photomicrograph of sponge network remains within dark micrite. Sponges are not preserved near burrows. (C and D) Photomicrograph and shaded tracing of highly bioturbated micrite. Mottled burrows (M) are overprinted by tube-shaped burrows (T) filled with light grey micrite, peloids, scattered spicules and cement. Note occurrence of poorly-preserved spicule networks in dark grey micrite toward upper left side.

Carrera and Botting, 2008; Muir et al., 2013), they were not important sediment contributors within non-reef carbonate environments.

Sponges preserving their spicular skeletons began to constitute integral portion of sedimentary successions since the Mesozoic, forming spongolites (Zimmerle, 1991; Pisera, 2006). These spongolites are comparable to the Xiazhen sponge-bearing micritic carbonates in terms of their high proportion within sedimentary rocks, being significant sediment contributors. The prominent components of Mesozoic spongolites are rigid-bodied siliceous sponges, such as the lithistids, hexactinosids, and lychniscosids that are preserved as fragmented skeletal remains with discernible outlines (Zimmerle, 1991; Pisera, 2006), which were encrusted mainly by microbialites and/or to a lesser extent by serpulids, bryozoans, and foraminifera; they were also frequently bored, indicating early lithification of the sponge skeletons (Deusch et al., 1991; Pisera, 1991; Rosales et al., 1995; Olóriz et al., 2003; Reolid, 2007). These spongolites are associated with thinly bedded or nodular limestones which formed in low-energy conditions in lagoons, slope and basin environments (Trammer, 1982, 1991; Brachert, 1991; Deusch et al., 1991; Pisera, 1991, 1997; Rosales et al., 1995; Olóriz et al., 2003; Reolid, 2007).

The current study is the first report of numerous sponge skeleton-bearing lime mudstone succession in the early Palaeozoic, thus emphasizing that, in addition to the records of siliceous sponges in ancient reefs and mud mounds (Bourque and Boulvain, 1993; Reitner, 1993; Reitner and Neuweiler, 1995), skeletal remains of sponges may have been much more widespread in non-reef carbonates than previously recognized (Warnke, 1995; Neuweiler et al., 2007). Sponge remains similar to those of the Xiazhen Formation have been reported from middle to late Cambrian (Hong et al., 2012; Lee et al., 2014) and Early Ordovician (Hong et al., 2014, 2015) reefs. In addition, similar non-lithistid skeletal remains are found from limestone-shale couplets of the middle Cambrian Gushan Formation (Fig. 8A) (Shandong Province, China) and late Cambrian Hwajeol Formation (Taebaeksan Basin, Korea), as well as lime mudstone to bioclastic packstone of the Middle Ordovician Yeongheung Formation (Taebaeksan Basin, Korea) (Fig. 8B). Considering the high proportion of sponges within the Xiazhen micritic limestone, the occurrence of similar sponges from the early Palaeozoic reefs and the Gushan, Hwajeol and Yeongheung formations, and the difficulty of recognising them in the field, we postulate that similar sponges could have been widely distributed in early Palaeozoic micritic carbonates. It is possible that their abundance and distribution have long been overlooked and underestimated, even though such sponges may have been one of the key contributors to carbonate sediment production in the early Palaeozoic.

5. Conclusions

We report the presence of numerous partial skeletal remains of probable non-lithistid demosponges from a 50-m-thick micritic limestone succession in the Upper Ordovician Xiazhen Formation.
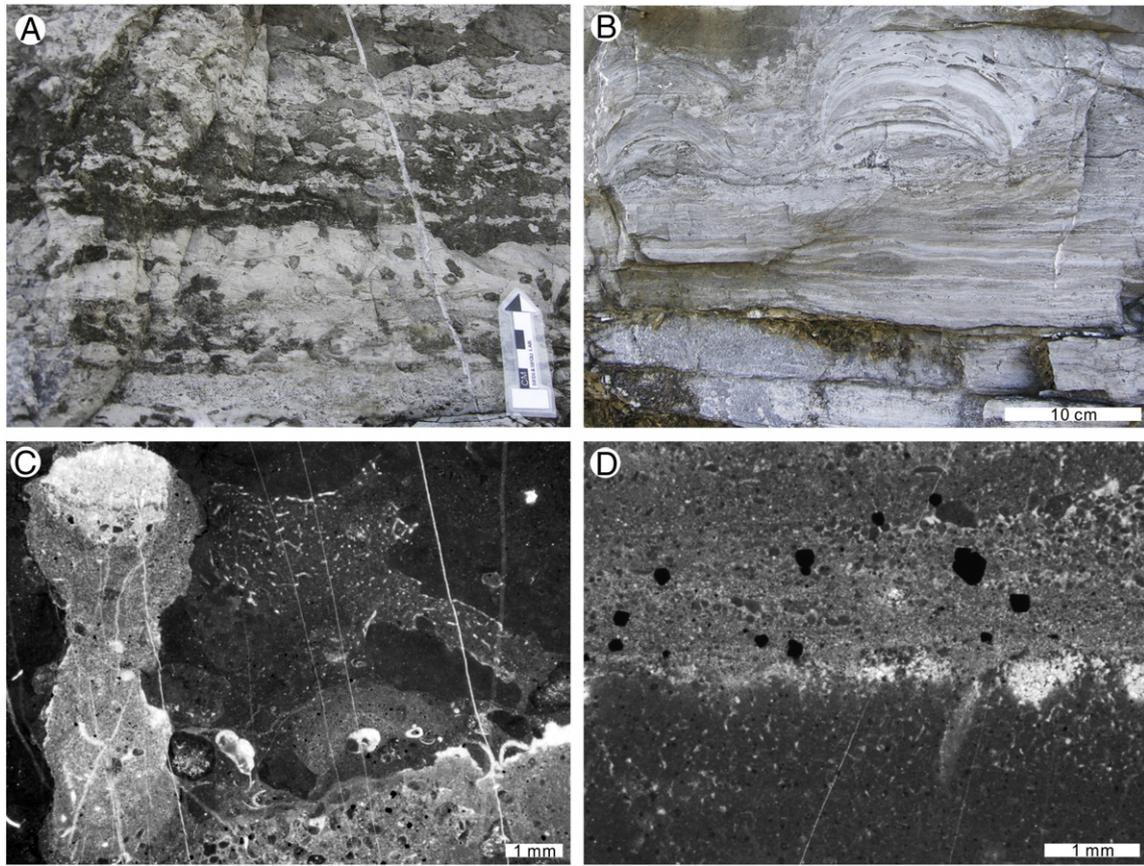
Fig. 6. Sponge remains from the W/Pb and W/Gp facies. (A) Photograph of typical bioturbated wackestone to packstone. Scale is 6 cm in length. (B) Photograph of thinly bedded peloidal wackestone to grainstone with overlying domal stromatolites. (C) Poorly preserved spicule networks (upper centre) in micritic portion of bioturbated wackestone to packstone (W/Pb) facies. (D) Poorly preserved network in the lower micritic area found from peloidal wackestone to grainstone (W/Gp) facies. Photographs and samples for A–D were prepared from the lowermost 25-m interval of the lower limestone member at Zhuzhai (cf. Kwon et al., 2012).

The sponges are preserved as spicular networks consisting of curved bifurcated and trifurcated spicules embedded in dark micrite, and are only recognizable under a petrographic microscope. Remains of the sponges were found in all of the lithofacies described, but

Fig. 7. Proportion of sponge skeletal remains in total thin sections (black) and boxplots showing percentage of well-preserved networks compared with the total area of networks per sponge-bearing thin section (grey). Numbers on top of bars indicate number of sponge-bearing thin sections (S) and number of total thin sections (T) in each facies (n = S/T).
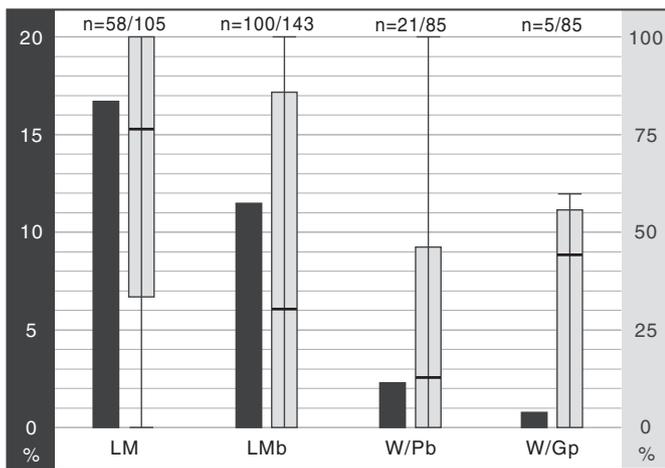
they occur predominantly in the lime mudstone (LM and LMb) facies. We interpret that the Xiazhen non-lithistid demosponges inhabited a wide spectrum of shallow marine environments, but mostly preferred muddy substrates unoccupied by other sessile organisms. Together with some recent reports of comparable non-lithistid demosponges, this study suggests that such sponges were far more widespread in the early Palaeozoic carbonates than previously thought, and demonstrates the necessity for further work to better understand their contribution to the sedimentary records.
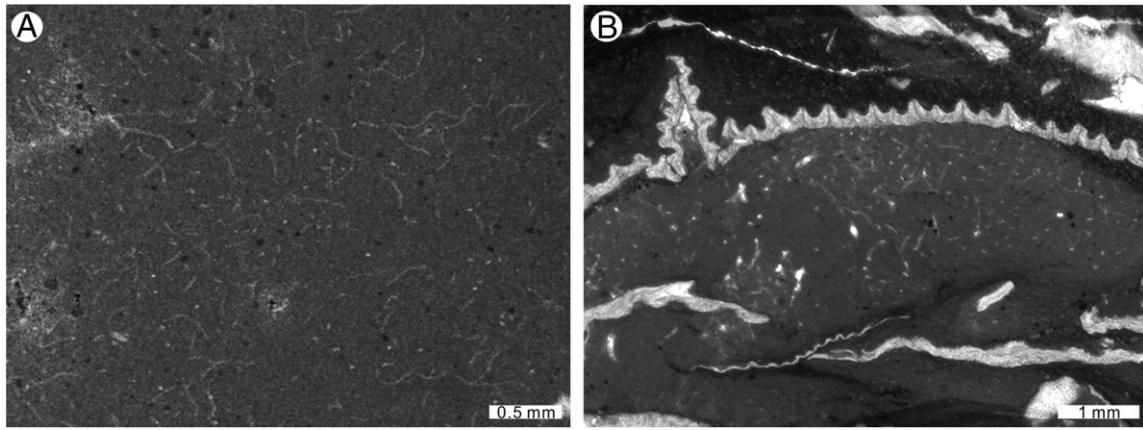
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Supplementary data

Supplementary data associated with this article can be found in the online version, at doi: http://dx.doi.org/10.1016/j.sedgeo.2015.02.002. These data include Google maps of the most important areas described in this article.

Fig. 8. Other spicule network remains similar to the Xiazhen sponges. (A) Spicule network remains in lime mudstone of limestone–shale couplet deposits of the middle Cambrian Gushan Formation (China). (B) A poorly preserved sponge network remains observed in micritic portion of brachiopod-bearing wackestone to packstone of the Middle Ordovician Yeongheung Formation (Korea).

References

Álvaro, J.J., Vennin, E., 1997. Episodic development of Cambrian eocrinoid-sponge meadows in the Iberian Chains (NE Spain). Facies 37, 49–64.

Bourque, P.-A., Boulvain, F., 1993. A model for the origin and petrogenesis of the red stromatactis limestone of Paleozoic carbonate mounds. Journal of Sedimentary Petrology 63, 607–619.

Bova, J.A., Read, J.F., 1987. Incipiently drowned facies within a cyclic peritidal ramp sequence, Early Ordovician Chequltepec interval, Virginia Appalachians. Geological Society of America Bulletin 98, 714–727.

Brachert, T.C., 1991. Environmental control on fossilization of siliceous sponge assemblages: a proposal. In: Reitner, J., Keupp, H. (Eds.), Fossil and Recent Sponges. Springer-Verlag, Berlin, pp. 543–553.

Brasier, M., Green, O., Shields, G., 1997. Ediacarian sponge spicule clusters from south-western Mongolia and the origins of the Cambrian fauna. Geology 25, 303–306.

Brunton, F.R., Dixon, O.A., 1994. Siliceous sponge-microbe biotic associations and their re-currence through the Phanerozoic as reef mound constructors. Palaios 9, 370–387.

Carrera, M.G., Botting, J.P., 2008. Evolutionary history of Cambrian spiculate sponges: implications for the Cambrian evolutionary fauna. Palaios 23, 124–138.

Carrera, M.G., Rigby, M.G., 1999. Biogeography of Ordovician sponges. Journal of Paleon-tology 73, 26–37.

Carrera, M.G., Rigby, M.G., 2004. Sponges. In: Webby, B.D., Paris, F., Droser, M.L., Percival, I.G. (Eds.), The Great Ordovician Biodiversification Event. Columbia University Press, New York, pp. 102–111.

Clausen, S., Álvaro, J.J., 2006. Skeletonized microfossils from the Lower–Middle Cambrian transition of the Cantabrian Mountains, northern Spain. Acta Palaeontologica Polonica 51, 223–238.

Conway, K.W., Barrie, J.V., Austin, W.C., Luternauer, J.L., 1991. Holocene sponge bioherms on the western Canadian continental shelf. Continental Shelf Research 11, 771–790.

Deusch, M., Friebe, A., Krautter, M., 1991. The spongiolithic facies in the Upper Jurassic of Spain. In: Reitner, J., Keupp, H. (Eds.), Fossil and Recent Sponges. Springer-Verlag, Berlin, pp. 498–505.

Droser, M.L., Bottjer, D.J., 1986. A semiquantitative field classification of ichnofabric. Journal of Sedimentary Petrology 56, 558–559.

Droser, M.L., Bottjer, D.J., 1993. Trends and patterns of Phanerozoic ichnofabrics. Annual Review of Earth and Planetary Sciences 21, 205–225.

Elrick, M., Snider, A.C., 2002. Deep-water stratigraphic cyclicity and carbonate mud mound development in the Middle Cambrian Marjum Formation, House Range, Utah, USA. Sedimentology 49, 1021–1047.

Erwin, D.H., Laflamme, M., Tweedt, S.M., Sperling, E.A., Pisani, D., Peterson, K.J., 2011. The Cambrian conundrum: early divergence and later ecological success in the early history of animals. Science 334, 1091–1097.

Finks, R.M., Rigby, J.K., 2004. Paleozoic demosponges. In: Kaesler, R.L. (Ed.), Treatise on Invertebrate Paleontology, Part E (Revised), *Porifera* vol. 3. The Geological Society of America, Boulder, Colorado, and the University of Kansas, Lawrence, pp. 9–173.

Franseen, E.K., 2006. Mississippian (Osagean) shallow-water, mid-latitude siliceous sponge spicule and heterozoan carbonate facies: an example from Kansas with impli-cations for regional controls and distribution of potential reservoir. Current Research in Earth Sciences: Kansas Geological Survey, Bulletin 252, pp. 1–23.

Gammon, P.R., James, N.P., 2001. Palaeogeographical influence on Late Eocene biosiliceous sponge-rich sedimentation, southern Western Australia. Sedimentology 48, 559–584.

Gehling, J.G., Rigby, J.K., 1996. Long expected sponges from the Neoproterozoic Ediacara fauna of South Australia. Journal of Paleontology 70, 185–195.

Hong, J., Cho, S.-H., Choh, S.-J., Woo, J., Lee, D.-J., 2012. Middle Cambrian siliceous sponge-calcimicrobe buildups (Daegi Formation, Korea): metazoan buildup constituents in the aftermath of the Early Cambrian extinction event. Sedimentary Geology 253–254, 47–57.

Hong, J., Choh, S.-J., Lee, D.-J., 2014. Tales from the crypts: early adaptation of cryptobiontic sessile metazoans. Palaios 29, 95–100.

Hong, J., Choh, S.-J., Lee, D.-J., 2015. Untangling intricate microbial-sponge frameworks: the contributions of sponges to Early Ordovician reefs. Sedimentary Geology 318, 75–84.

Keller, M., Buggisch, W., Lehnert, O., 1998. The stratigraphical record of the Argentine Precordillera and its plate-tectonic background. In: Pankhurst, R.J., Rapela, C.W. (Eds.), The Proto-Andean Margin of Gondwana. Geological Society of London, Special Publications 142, pp. 32–56.

Klappa, C.F., James, N.P., 1980. Small lithistid sponge bioherms, early Middle Ordovician Table Head Group, western Newfoundland. Bulletin of Canadian Petroleum Geology 28, 425–451.

Krautter, M., Conway, K.W., Barrie, J.V., Neuweiler, M., 2001. Discovery of a "Living Dinosaur": globally unique modern hexactinellid sponge reefs off British Columbia, Canada. Facies 44, 265–282.

Kwon, S.-W., Park, J., Choh, S.-J., Lee, D.-C., Lee, D.-J., 2012. Tetradiid-siliceous sponge patch reefs from the Xiazhen Formation (late Katian), southeast China: a new Late Ordovician reef association. Sedimentary Geology 267–268, 15–24.

Lavoie, D., 1995. A Late Ordovician high-energy temperate-water carbonate ramp, southern Quebec, Canada: implications for Late Ordovician oceanography. Sedimentology 42, 95–116.

Lee, D.-C., 2013. Late Ordovician trilobites from the Xiazhen Formation in Zhuzhai, Jiangxi Province, China. Acta Palaeontologica Polonica 58, 855–882.

Lee, D.-C., Park, J., Woo, J., Kwon, Y.K., Lee, J.-G., Guan, L., Sun, N., Lee, S.-B., Liang, K., Liu, L., Rhee, C.-W., Choh, S.-J., Kim, B.-S., Lee, D.-J., 2012. Revised stratigraphy of the Xiazhen Formation (Upper Ordovician) at Zhuzhai, South China, based on palaeontological and lithological data. Alcheringa 36, 387–404.

Lee, J.-H., Chen, J., Choh, S.-J., Lee, D.-J., Han, Z., Chough, S.K., 2014. Furongian (late Cambrian) sponge-microbial maze-like reefs in the North China Platform. Palaios 29, 27–37.

Li, Y., Kershaw, S., Mu, X., 2004. Ordovician reef systems and settings in South China before the Late Ordovician mass extinction. Palaeogeography, Palaeoclimatology, Palaeoecology 205, 235–254.

Love, G.D., Grosjean, E., Stalvies, C., Fike, D.A., Grotzinger, J.P., Bradley, A.S., Kelly, A.E., Bhatia, M., Meredith, W., Snape, C.E., Bowring, S.A., Condon, D.J., Summouns, R.E., 2009. Fossil steroids record the appearance of *Demospongiae* during the Cryogenian period. Nature 457, 718–721.

Luo, C., Reitner, J., 2014. First report of fossil "keratose" demosponges in Phanerozoic car-bonates: preservation and 3-D reconstruction. Naturwissenschaften 101, 467–477.

Muir, L.A., Botting, J.P., Carrera, M.G., Beresi, M., 2013. Cambrian, Ordovician and Silurian non-stromatoporoid *Porifera*. In: Harper, D.A.T., Servais, T. (Eds.), Early Paleozoic Biogeography and Palaeogeography. Geological Society of London, Memoires 38, pp. 81–95.

Neuweiler, F., Daoust, I., Bourque, P.-A., Burdige, D.J., 2007. Degradative calcification of a modern siliceous sponge from the Great Bahama Bank, the Bahamas: a guide for in-terpretation of ancient sponge-bearing limestones. Journal of Sedimentary Research 77, 552–563.

Olóriz, F., Reolid, M., Rodríguez-Tovar, F.J., 2003. A Late Jurassic carbonate ramp colonized by sponges and benthic microbial communities (External Prebetic, Southern Spain). Palaios 18, 528–545.

Osleger, D., Read, J.F., 1991. Relation of eustasy to stacking patterns of meter-scale carbon-ate cycles, Late Cambrian, U.S.A. Journal of Sedimentary Petrology 61, 1225–1252.

Pisera, A., 1991. Upper Jurassic sponge megafacies in Spain: preliminary report. In: Reitner, J., Keupp, H. (Eds.), Fossil and Recent Sponges. Springer-Verlag, Berlin, pp. 486–497.

Pisera, A., 1997. Upper Jurassic siliceous sponges from the Swabian Alb: taxonomy and paleoecology. Palaeontologia Polonica 57, 3–216.

Pisera, A., 2006. Palaeontology of sponges — a review. Canadian Journal of Zoology 84, 242–262.

Pisera, A., Lévi, C., 2002. 'Lithistid' *Demospongiae*. In: Hooper, J.N.A., Van Soest, R.W.M. (Eds.), Systema *Porifera*: A Guide to the Classification of Sponges vol. 1. Kluwer Academic/Plenum Publishers, New York, pp. 299–300.

Reid, R.E.H., 2003. Class *Demospongea*: general morphology and classification. In: Kaesler, R.L. (Ed.), Treatise on Invertebrate Paleontology, Part E (Revised), *Porifera* vol. 2. The Geological Society of America, Boulder, Colorado, and the University of Kansas, Lawrence, pp. 15–62.

Reitner, J., 1993. Modern cryptic microbialite/metazoan facies from Lizard Island (Great Barrier Reef, Australia) formation and concepts. Facies 29, 3–40.

Reitner, J., Neuweiler, F., 1995. Mud mounds: a polygenetic spectrum of fine-grained carbonate buildups. Facies 32, 1–70.

Reitner, J., Wörheide, G., 2002. Non-lithistid fossil *Demospongiae* — origins of their palaeobiodiversity and highlights in history of preservation. In: Hooper, J.N.A., Van Soest, R.W.M. (Eds.), Systema *Porifera*: A Guide to the Classification of Sponges. Kluwer Academic/Plenum Publishers, New York, pp. 52–68.

Reolid, M., 2007. Taphonomy of the Oxfordian–lowermost Kimmeridgian siliceous sponges of the Prebetic Zone (Southern Iberia). Journal of Taphonomy 5, 71–90.

Rosales, I., Mehl, D., Fernández-Mendiola, P.A., Carcía-Mondéjar, J., 1995. An unusual poriferan community in the Albian of Islares (north Spain): Palaeoenvironmental and tectonic implications. Palaeogeography, Palaeoclimatology, Palaeoecology 119, 47–61.

Semeniuk, V., 1973. Nearshore to offshore facies and depositional history of the Ordovician Daylesford Limestone, New South Wales. Journal of the Geological Society of Australia 20, 449–464.

Trammer, J., 1982. Lower to Middle Oxfordian sponges of the Polish Jura. Acta Geologica Polonica 32, 1–39.

Trammer, J., 1991. Ecologic history of the Oxfordian sponge assemblage in the Polish Jura Chain. In: Reitner, J., Keupp, H. (Eds.), Fossil and Recent Sponges. Springer-Verlag, Berlin, pp. 506–515.

Warnke, K., 1995. Calcification processes of siliceous sponges in Viséan limestones (Counties Sligo and Leitrim, northwestern Ireland). Facies 33, 215–228.

Wendt, J., Wu, X., Reinhardt, J.W., 1989. Deep-water hexactinellid sponge mounds from the Upper Triassic of northern Sichuan (China). Palaeogeography, Palaeoclimatology, Palaeoecology 76, 17–29.

Zhan, R.-B., Rong, J.-Y., Jin, J., Cocks, L.R.M., 2002. Late Ordovician brachiopod communities of southeast China. Canadian Journal of Earth Sciences 39, 445–468.

Zhang, Y., Chen, X., Yu, G., Dan, G., Liu, X., 2007. Ordovician and Silurian Rocks of Northwest Zhejiang and Northeast Jiangxi Provinces, SE China. University of Science and Technology of China Press, Hefei.

Zimmerle, W., 1991. Stratigraphic distribution, lithological paragenesis, depositional environments and diagenesis of fossil siliceous sponges in Europe. In: Reitner, J., Keupp, H. (Eds.), Fossil and Recent Sponges. Springer-Verlag, Berlin, pp. 554–577.