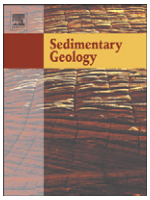
Sedimentary Geology 347 (2017) 1–9

Contents lists available at ScienceDirect

Sedimentary Geology

journal homepage: www.elsevier.com/locate/sedgeo



Crouching shells, hidden sponges: Unusual Late Ordovician cavities containing sponges

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ARTICLE INFO

Article history:
Received 30 August 2016
Received in revised form 2 November 2016
Accepted 4 November 2016
Available online 11 November 2016

Editor: Dr. B. Jones

Keywords:
Intraskeletal crypt
Demosponge
Micritic carbonate
Late Ordovician
South China

ABSTRACT

Marine cavities harbouring cryptic organisms have been ubiquitous throughout the Phanerozoic. However, our knowledge of early cryptic communities is as yet insufficient, and how metazoans began to utilize such habitats remains unknown. In this study, we document demosponge remains within intraskeletal cavities embedded in the micritic succession of a shallow carbonate platform in the Upper Ordovician (Katian) Xiazhen Formation of South China. Molluscs (gastropods, bivalves, and nautiloids) and corals (the solitary rugosan *Tryplasma* and colonial agetolitids) within the succession commonly contain patches of "spicular" demosponge remains (11%; $n = 45/415$), mainly occupying intraskeletal spaces with areas of 1–30 mm^2 in thin-section. Sponge occurrence varies according to sedimentary facies: within lime mudstone facies, sponges commonly occur both inside and outside intraskeletal cavities, suggesting that sponges would have inhabited and become preserved within any available space in this environment. In contrast, when other sessile organisms co-occur in wackestone to packstone facies, there are fewer sponge occurrences both inside and outside cavities, possibly due to competition in open habitats and/or their poorer preservation in such environments. Overall, this result suggests that sponges would have exploited cryptic habitats by normal expansion of the open-surface biota. In addition, compared with coeval reef and hardground crypts, the Xiazhen intraskeletal cryptic biota is monotonous in composition, suggesting "decoupled" occupation of cryptic habitats in different environments.

1. Introduction

Marine cavities in reefs, borings, fissures, the undersides of shells and boulders, and within shells are shaded, semi-protected spaces that provide important marine habitats for many cryptic organisms (Kobluk, 1988b; Glynn and Enochs, 2011). In the geologic record, cryptic organisms are primarily identified by their in-place preservation, and they provide excellent opportunities for palaeoecological analysis (Kobluk, 1988b; Taylor and Wilson, 2003). Since the first appearance of cryptic metazoans in Ediacaran reefs (Wood and Curtis, 2015), cryptic organisms in the geologic record have displayed an overall trend of an increase in diversity and complexity as well as in habitat variety. The main groups of early Palaeozoic cryptic metazoans were sponges, bryozoans, and echinoderms, expanding in the middle to late Palaeozoic to also include tabulate and rugose corals, brachiopods, and foraminifera (Taylor and Wilson, 2003). It is interesting to note that early cryptic metazoans have been reported mainly from reef cavities (Kobluk and James, 1979; Kobluk, 1988a; Zhuravlev and Wood, 1995; Hong et al., 2014; Li et al., in press); it was not until the Late Ordovician that bryozoans and echinoderms invaded crypts associated with hardgrounds (Brett and Liddell, 1978).

In modern shallow-marine environments, discarded shells are frequently utilized by various organisms, including hermit crabs, sipunculid worms, tanaids, fishes, octopuses, amphipods, and polychaetes (e.g., Williams and McDermott, 2004; Glynn and Enochs, 2011). However, fossil records of comparable organisms are scarce (cf. Lukeneder and Harzhauser, 2003; Luci and Cichowolski, 2014), and therefore how metazoans established themselves in these habitats is still an open question (Kobluk, 1988b; Zhuravlev and Wood, 1995; Taylor and Wilson, 2003). In this paper, we document unusual non-reef intraskeletal cavities (sensu Kobluk, 1988b) occupied by sponges from an Upper Ordovician shallow-subtidal micritic limestone succession in South China, in order to provide evidence of how metazoans adapted to such cryptic spaces.

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http://dx.doi.org/10.1016/j.sedgeo.2016.11.003

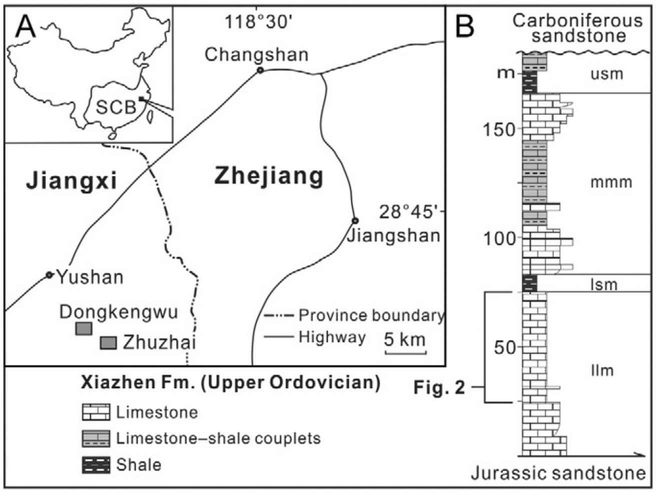

Fig. 1. (A) Location of the study area and two measured sections of the Xiazhen Formation near Dongkengwu and Zhuzhai villages in Yushan County, Jiangxi Province, China. SCB = South China Block. (B) Simplified lithologic log of the Xiazhen Formation. Location map and lithologic log after Park et al. (2015). Abbreviations: llm = lower limestone member; lsm = lower shale member; mmm = middle mixed lithology member; usm = upper shale member.

2. Geologic setting and methods

Upper Ordovician strata with abundant fossils are exposed near the boundary between Jiangxi and Zhejiang provinces, south-eastern China (Zhan et al., 2002; Zhang et al., 2007; Lee et al., 2012) (Fig. 1A). These Upper Ordovician successions are composed of three laterally equivalent lithostratigraphic units: mixed carbonate–clastic tidal flat to lagoon deposits of the Xiazhen Formation, platform-margin carbonates of the Sanjushan Formation, and outer-shelf clastic sediments of the Changwu Formation (Zhan et al., 2002; Li et al., 2004). The Xiazhen and Sanjushan formations have been interpreted as part of the carbonate-platform deposits fringing the north-northwestern Cathaysian Old Land of South China (Li et al., 2004). The recent discovery of the graptolite *Anticostia uniformis* in the upper part of the Xiazhen Formation indicates a Katian age for the formation (Chen et al., 2016).

The Xiazhen Formation at Zhuzhai is thrust faulted over Jurassic sandstone of the Linshan Group (Lee et al., 2012), and is disconformably overlain by the lower Carboniferous Yejiatang Formation (Zhang et al., 2007). The formation is informally divided into four members (Lee et al., 2012) (Fig. 1B). The lower limestone member (Fig. 1B; llm) is the lowermost unit of the formation and is composed of six sedimentary facies: (1) laminated dolomitic mudstone (DMl) with desiccation cracks; (2) domal stromatolite (St); (3) peloidal wackestone to grainstone (W/Gp) composed of sets of graded grainstone to wackestone laminae; (4) bioturbated wackestone to skeletal packstone (W/Pb) with bioherms; (5) bioturbated lime mudstone (LMb); and (6) thin-bedded lime mudstone (LM) facies. The lower third of the lower limestone member is composed primarily of laminae to medium beds of the W/Pb or W/Gp facies at the base of each cycle intercalated with the St and DMl facies, representing deposition under shallow subtidal to intertidal conditions (Kwon et al., 2012). In contrast, the middle to upper part of the lower limestone member is dominated by lime mudstone (LMb and LM facies) with occasional interbeds of the W/Pb and W/Gp facies. This part of the member was formed in quiet, open-marine conditions such as a lagoon (Table 1 of Park et al., 2015). The middle to upper part of the lower limestone member was measured from two outcrop sections and 325 rock samples were collected (Fig. 2). A total of 45 large-format (54 × 76 mm) and 5 standard-format (28 × 48 mm) thin-sections cut perpendicular to the bedding surface containing mollusc shells, coral skeletons, and other organisms were examined. The two-dimensional extent of the cavities and the sediments, cements, and cryptic organisms present within these cavities were measured and calculated from thin-section photomicrographs. As the sizes of cavities and sponges measured in thin-section are random cuts of three-dimensional objects, a certain bias is unavoidable, which we attempted to overcome by measuring a large number of cavities.

3. Results

3.1. Cavity dwellers

Patches of "spicular" networks are present within 11% ($n = 45/415$) of the shells and skeletons investigated (Table 1; Figs. 3 and 4). These spicular networks are composed of curved, bi- or trifurcated spicules filled with calcite spars, 30–50 μm in diameter and up to 500 μm long (Fig. 3B). The outline of each spicule is smooth, without any local enlargement or interlocking relationship with other spicules. These spicules do not cross at right-angles at their intersection points. Typical monaxon, triaxon, tetraxon, and polyaxon spicules, and disarticulated desmas, are not present. Some well-preserved spicule networks display alignment of spicules along the outer boundary, though no discrete canal system or dermal spiculation can be observed (Figs. 3A, 4C and D). The outlines of the spicular networks partly conform to the internal shapes of cavities. Cavity size appears to be related to the preservation of spicular networks: in cavities smaller than 5 mm^2, spicule networks are often less well preserved with partially connected spicules. In contrast, better-preserved spicule networks occur in cavities larger than 20 mm^2 and are either surrounded by micrite or gradationally change into poorly preserved spicule networks, micrite, and peloidal aggregates (e.g., Reitner, 1993; Warnke, 1995; Adachi et al., 2009) (Fig. 3E, F).

Overall, the characteristics of the spicule networks are similar to those of recently reported sponge remains from micritic limestones of the Xiazhen Formation (Park et al., 2015). Although the taxonomy of the spicular networks remains to be resolved, the absence of desmas and zygomes appears to indicate that these remains may not belong to lithistid demosponges. The preservation style of these sponges is similar to those of Early Ordovician "spicular" demosponges (Hong et al., 2014) and Mesozoic cryptic non-rigid demosponges that are interpreted as a byproduct of sponge calcification (Delecat et al., 2001). Similar features from Ordovician, Devonian, and Triassic reefs have recently been suggested to be the "fibrous spongin" networks of keratosan sponges (Luo and Reitner, 2014; Larmagnat and Neuweiler, 2015).

3.2. Cavity providers

The lower limestone member contains various organisms, including gastropods, bivalves, nautiloids, the solitary rugosan *Tryplasma*, the colonial coral *Agetolites*, the stromatoporoid *Clathrodictyon*, bryozoans, brachiopods, ostracods, trilobites, the small-module favositoid coral-like fossil *Amsassia* (Sun et al., 2014), tetradiids, the branching tabulate *Bajgolia* (Young and Xu, 2002), calcimicrobes (*Ortonella*, *Subtifloria* and *Girvanella*-like tubes), and non-lithistid demosponges. Of these, mollusc shells and some coral skeletons often contain sponge remains, while the outer surfaces of some shells and skeletons in the W/Pb facies are encrusted by *Ortonella*, *Clathrodictyon*, juvenile *Tryplasma*, small

Fig. 2. Lithologic logs of the middle to upper part of the lower limestone member at Zhuzhai and Dongkengwu. Occurrences and dimensions of sponges in micritic sediments surrounding cavities (grey bars), intraskeletal cavities (pink bars), sponge remains in crypts (red bars), and cavity providers are marked on the right-hand side. Lithologic logs and sponge occurrence data in the surrounding micritic limestone are after Park et al. (2015). S = shale; M = lime mudstone; W = wackestone; P = packstone; G = grainstone; B = boundstone.

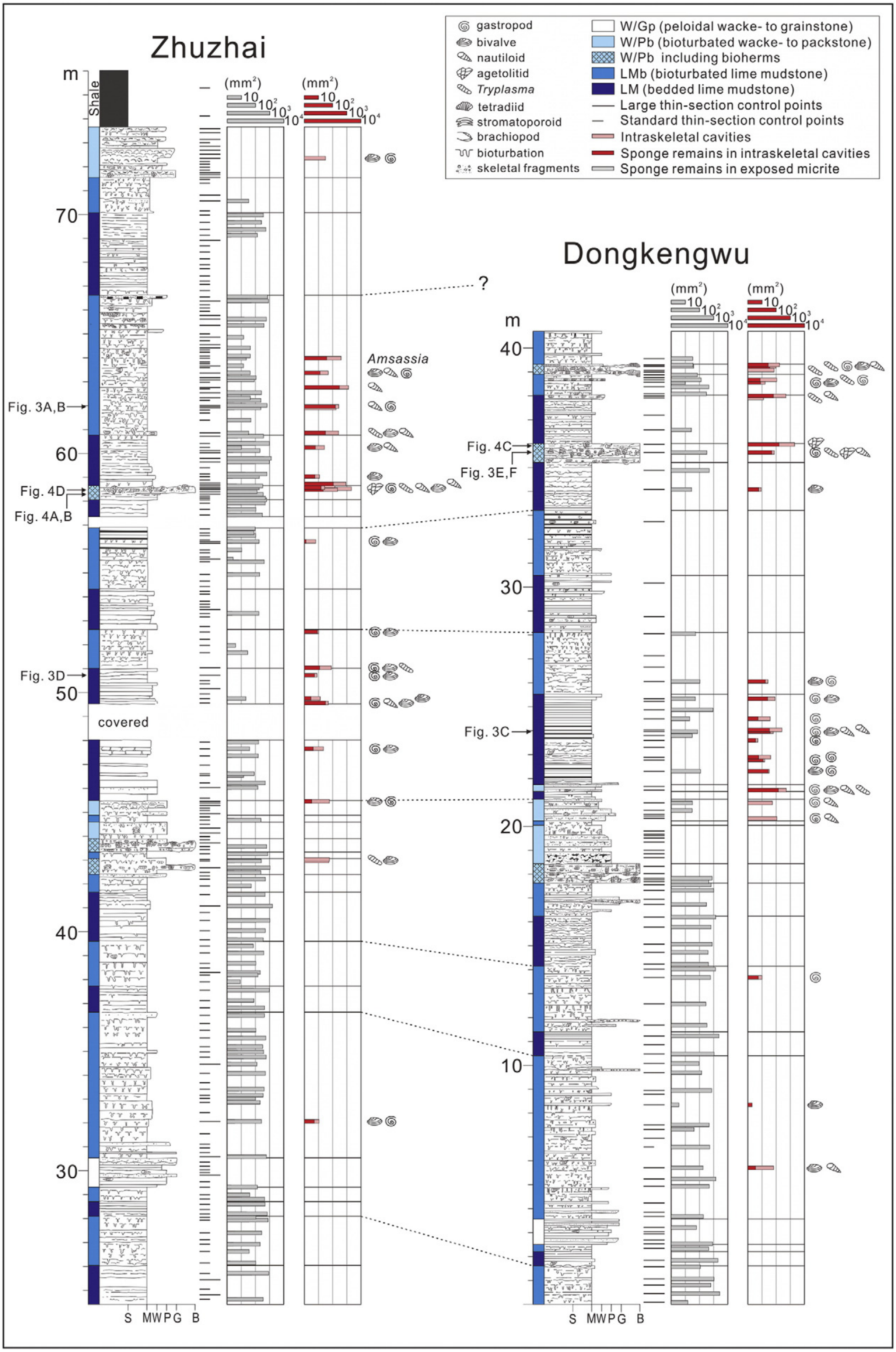
Zhuzhai
Dongkengwu
m
Shale
70
60
50
40
30
covered
Fig. 3A,B
Fig. 4D
Fig. 4A,B
Fig. 3D
(mm²)
10
10²
10³
10⁴
Amsassia
?
40
30
20
10
Fig. 4C
Fig. 3E,F
Fig. 3C
S MWPG B
gastropod
bivalve
nautiloid
agetolitid
Tryplasma
tetradiid
stromatoporoid
brachiopod
bioturbation
skeletal fragments
W/Gp (peloidal wacke- to grainstone)
W/Pb (bioturbated wacke- to packstone)
W/Pb including bioherms
LMb (bioturbated lime mudstone)
LM (bedded lime mudstone)
Large thin-section control points
Standard thin-section control points
Intraskeletal cavities
Sponge remains in intraskeletal cavities
Sponge remains in exposed micrite

Table 1
Distribution of intraskeletal cavities and sponges by facies. Parentheses denote the number of intertabularial spaces within coral skeletons.

Cavity type		LM[a]			LMb[b]			W/Pb[c]			Total		
		Number of shells/skeletons	Sponge-bearing cavities		Number of shells/skeletons	Sponge-bearing cavities		Number of shells/skeletons	Sponge-bearing cavities		Number of shells/skeletons	Sponge-bearing cavities	
Mollusc	Bivalve	48	8	17%	34	5	15%	70	2	3%	152	15	10%
	Gastropod	42	3	7%	17	2	12%	79	4	5%	138	9	7%
	Nautiloid	7	3	43%	10	5	50%	36	4	11%	53	12	23%
	Subtotal	97	14	14%	61	12	20%	185	10	5%	343	36	10%
Coral	*Tryplasma*	–	–		1	1	100%	54	3	6%	55	4	7%
					[8]	[1]	13%	[165]	[3]	2%	[173]	[4]	2%
	Agetolites	–	–		–	–		3	3	100%	3	3	100%
								[1979]	[301]	15%	[1979]	[301]	15%
	Subtotal	–	–		1	1	100%	57	6	11%	58	7	12%
					[8]	[1]	13%	[2144]	[304]	14%	[2152]	[305]	14%
Other		–	–		1	1	100%	13	1	8%	14	2	14%
Total		97	14	14%	63	14	22%	255	17	7%	415	45	11%

[a] LM = lime mudstone facies.
[b] LMb = bioturbated lime mudstone facies.
[c] W/Pb = bioturbated wacke- to packstone facies.

agetolitids, and rare cryptostome bryozoans. Both molluscs and corals are common in the W/Pb facies, whereas mollusc shells predominate in the LM and LMb facies. The total of 415 shells and skeletons investigated comprise 83% ($n = 343$) mollusc shells, 14% ($n = 58$) corals, and 3% ($n = 14$) other taxa. Of 255 cavities of the W/Pb facies, 73% ($n = 185$) are in intact to partially fragmented mollusc shells; the rest are in coral skeletons ($n = 57$) and shells of uncertain affinity ($n = 13$). Cavities in the LMb and LM facies ($n = 160$) occur almost entirely in mollusc shells ($n = 158$), with rare rugose coral ($n = 1$) and *Amsassia* ($n = 1$) cavities in the LMb facies (Table 1).

3.3. Sponge occurrences in intraskeletal cavities

Some of the intraskeletal cavities in the mollusc shells and coral skeletons of the shallow-subtidal micritic carbonates of the Xiazhen Formation are occupied by non-lithistid demosponges (11%; $n = 45/415$). The spicular networks within intraskeletal cavities vary in size from 0.2 to 304 mm^2. The overall distribution of sponges (80% mollusc, 16% coral, and 4% others) is close to the proportion of cavity types (83% mollusc, 14% coral, and 3% others).

3.3.1. Molluscs

Three major types of molluscs are identified from the study interval: bivalves, gastropods, and nautiloids. Molluscs provide the largest number of cavities ($n = 343/415$; 83%) in the studied interval. The cavities range in size from 0.04 to 1322.7 mm^2, dominated by the 0.2–4 mm^2 fraction, though the occurrence of cryptic sponge remains is skewed toward larger mollusc cavities of 1–30 mm^2 in size (Fig. 5D).

Articulated bivalves make up slightly more than one-third of the studied cavities (37%; $n = 152/415$). Their size measured in thin-section ranges from ~0.1 to 27.9 mm^2, dominated by the 0.6–4 mm^2 fraction (Fig. 5A), and there are no discernible size differences in bivalves by facies. A total of 10% ($n = 15$) of bivalves with cavities measuring 1–23 mm^2 contain sponge remains of 0.9–17.2 mm^2 in size (Fig. 3D). Sponges occur mainly within bivalves of size 1–6 mm^2. Though more bivalves occur in the W/Pb ($n = 70$) facies than in the LM ($n = 48$) and LMb ($n = 34$) facies, there are more bivalves with sponge remains in the LM ($n = 8/48$; 17%) and LMb ($n = 5/34$; 15%) facies than in the W/Pb ($n = 2/70$; 3%) facies (Table 1).

Gastropods provide one-third of the studied intraskeletal cavities (33%; $n = 138/415$). Cavity size ranges from 0.04 to 60.5 mm^2, dominantly 0.2–0.4 mm^2 (Fig. 5B). Gastropods in the W/Pb facies are generally larger than those in the LM and LMb facies. Compared with bivalves, a smaller fraction (7%; $n = 9/138$) of gastropods contain sponge remains of 3.3–21.6 mm^2 in size (Fig. 3C, E). The occurrence of sponge remains is conspicuously skewed toward larger (>3.3 mm^2) gastropods (Fig. 5B). A larger number of gastropods occur in the W/Pb ($n = 79$) than in the LM ($n = 42$) and LMb ($n = 17$) facies (Table 1), whereas the percentage of gastropods with sponges is higher in the LMb ($n = 2/17$; 12%) than in the LM ($n = 3/42$; 7%) and W/Pb ($n = 4/79$; 5%) facies (Table 1).

Nautiloids make up a subordinate group of the studied cavities (13%; $n = 53/415$) and are the largest molluscs in the lower limestone member. In outcrop, these nautiloids are up to 4 cm in diameter and 30 cm long, and in thin sections their sizes vary greatly from 0.5 to 1322.7 mm^2, with two peaks in size at 10–15 mm^2 and 2.5–4 mm^2 (Fig. 5C). Most of the larger (>200 mm^2) nautiloids occur in the LMb facies ($n = 4/6$). One-fourth ($n = 12/53$; 23%) of nautiloids (11.7–1322.7 mm^2) contain sponge remains of 6–304 mm^2 in size (Fig. 5C). Similar to bivalves and gastropods, more nautiloids occur in the W/Pb ($n = 36$) than in the LMb ($n = 10$) and LM ($n = 7$) facies (Table 1), whereas the proportion of nautiloids with sponges is higher in the LMb ($n = 5/10$; 50%) and LM ($n = 3/7$; 43%) facies than in the W/Pb ($n = 4/36$; 11%) facies.

3.3.2. Corals

The solitary rugosan *Tryplasma*, which is a maximum of 8 cm in length and 1 cm in diameter, is the most common coral in the W/Pb facies. *Tryplasma* contains numerous internal chambers (intertabularial spaces) partitioned by horizontal tabulae, each of which is treated as a discrete cavity in this study. A total of 173 intertabularial spaces of 0.04–27.3 mm^2 in size with a peak at 1–6 mm^2 were examined from 54 and 1 *Tryplasma* specimens in the W/Pb and LMb facies, respectively (Fig. 5E; Table 1). Only a few intertabularial cavities (2%; $n = 4/173$) of 4.8–24 mm^2 in size contain sponge remains (Fig. 4A, B); the remaining cavities are mostly filled with cement.

Three large (>20 cm across), dome-shaped agetolitid corals from three different beds of the W/Pb facies contain sponge remains within their intertabularial spaces (Fig. 4C, D). These intertabularial spaces are 0.02–25.9 mm^2 in size, dominated by the 1–3 mm^2 fraction. A total of 15% ($n = 301/1979$) of intertabularial cavities enclose sponge remains of 0.2–15.4 mm^2 in size, the majority of which occur in cavities of 1–6 mm^2 in size (Fig. 5F).

3.3.3. Other organisms

Amsassia rarely occurs in the LMb facies, where a single *Amsassia* specimen contains sponge remains (Table 1). An unidentified skeleton in the W/Pb facies contains sponge remain ($n = 1/13$) (Table 1). Other organisms in the W/Pb facies possess cavities of sizes <0.03 mm^2 (ostracod), <0.04 mm^2 (bryozoan), <1 mm^2 (tetradiid), and <1 mm^2 (*Bajgolia*). In addition, rare disarticulated brachiopods up to 5 cm long could potentially provide space for sponges underneath the valves

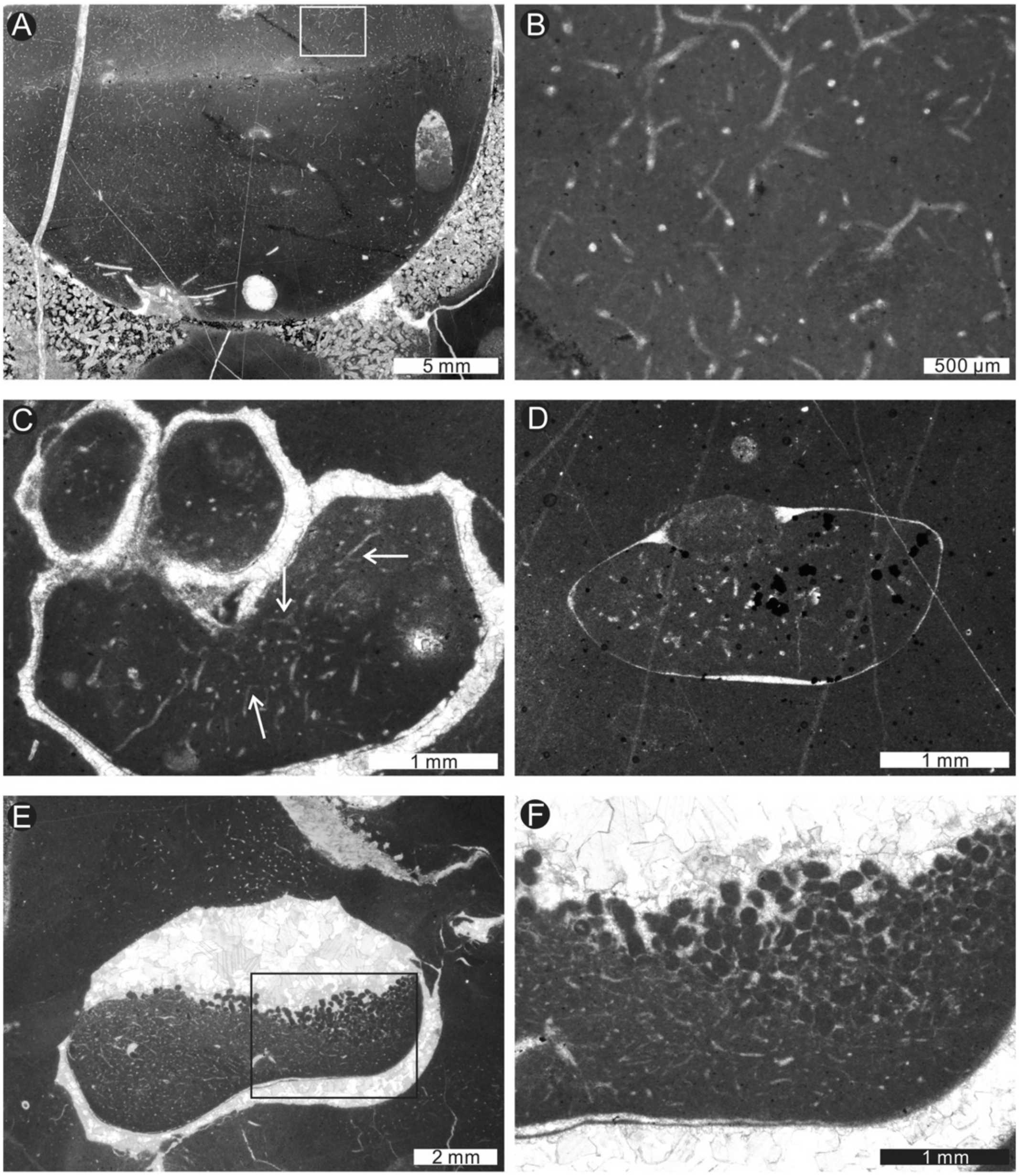

Fig. 3. Photomicrographs of sponge remains in mollusc shells. (A) Orthoconic nautiloid shell cut perpendicular to the long axis (103 mm^2 in size), filled with spicular networks surrounded by dark micrite and some burrows. (B) Enlargement of the area outlined by the white rectangle in (A), showing spicular networks consisting of smooth, slightly curved spicules without desmas with articulation (zygomes). (C) Oblique cut through a gastropod (4.1 mm^2 in size) partly filled with poorly preserved spicular networks composed of bifurcating curved spicules (arrows). (D) Bivalve (3.1 mm^2 in size) enclosing poorly preserved spicular networks. (E) Gastropod (31 mm^2 in size) in which spicular networks occur both inside and outside (upper centre and two lower corners) the shell. (F) Enlargement of the area indicated by the black rectangle in (E), showing the gradational change from a spicular network to a peloidal texture.

(i.e., shelter cavity); however, no sponge remains are found between nor underneath the valves.

3.4. Sponge occurrence by sedimentary facies

The three sedimentary facies of the lower limestone member contain cavities of different numbers and sizes: the LM facies ($n = 97$, 0.05–243.1 mm^2); the LMb facies ($n = 63$ including 8 intertabularial spaces of 1 coral, 0.1–1322.7 mm^2); and the W/Pb facies ($n = 255$ including 2144 intertabularial spaces of 57 corals, 0.02–300.0 mm^2). Sponge remains of 0.2–134.4 mm^2 in size occur in 17 cavities of the W/Pb facies, with lower numbers in the LM ($n = 14$, sponge size: 1.5–37.9 mm^2) and LMb ($n = 14$, sponge size: 0.9–304.0 mm^2) facies (Table 1). The areal percentage of cryptic sponges compared with the total thin-section area is highest in the W/Pb facies (2.1%), followed by the LMb (2.0%) and LM (0.5%) facies (Table 2). The results for the areal coverage of sponges compared with total cavity area demonstrate that sponges occupy a larger proportion of cavities in the W/Pb (23%) than in the LMb (19%) and LM (19%) facies. Excluding the bias resulting from the rarity of cavities larger than 200 mm^2 ($n = 7$; nautiloids and an *Amsassia*) and agetolitid corals ($n = 3$; >20 cm across), the LM facies contains the highest areal percentages of cryptic sponges (0.4%), followed by the LMb (0.2%) and W/Pb (0.2%) facies.

3.5. Interpretation

Sponge spicule networks in Xiazhen cavities are interpreted to be in situ preservation of sponge remains, and are not likely to be transported and preserved within skeletal cavities because of following reasons.

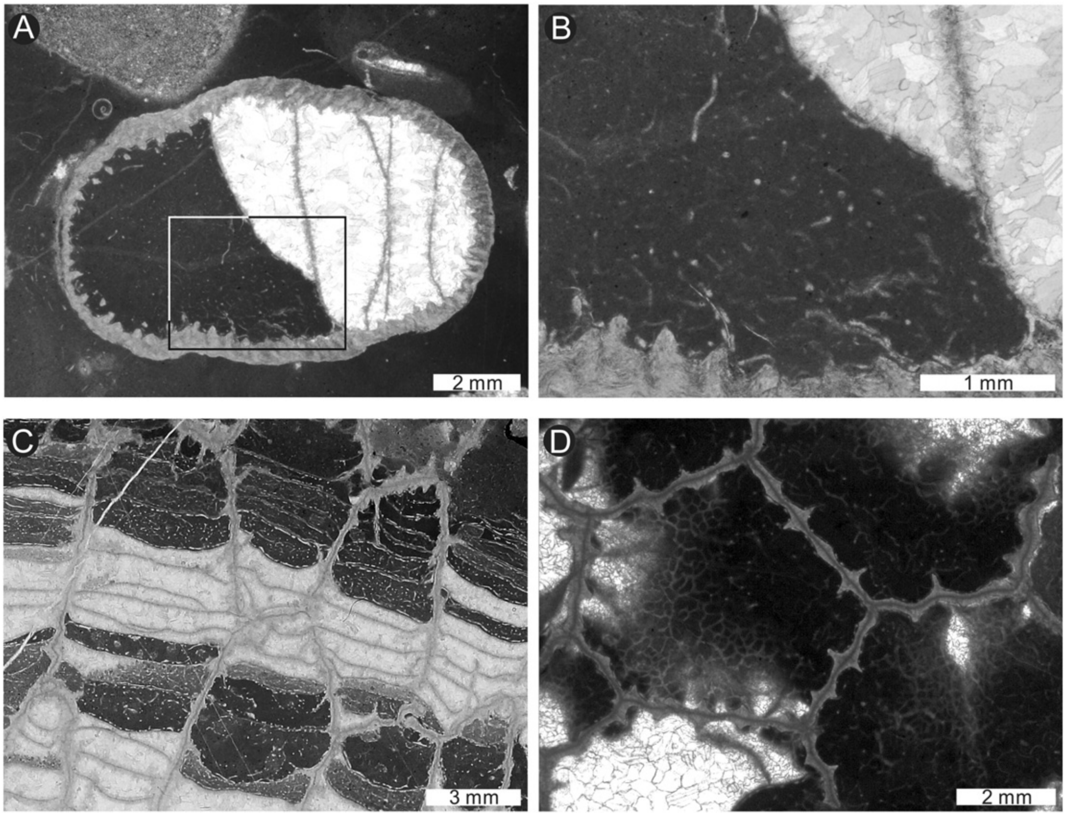

Fig. 4. Photomicrographs of sponge remains in coral skeletons. (A) Solitary rugosan *Tryplasma* cut obliquely to the growth direction. A sponge is present in an intertabularial space that is 18 mm^2 in size. (B) Enlargement of the area indicated by the black rectangle in (A), showing poorly preserved spicular networks. (C) Agetolitid coral cut parallel to the growth direction. Sponge remains are unevenly distributed in some intertabularial spaces. (D) Agetolitid coral cut perpendicular to the growth direction, in which sponges partially occupy some of the intertabularial spaces.

Sponge remains are often well-preserved within skeletal cavities and their outlines follow the internal shapes of the cavities (Fig. 4A, B, D). If they are washed into cavities from outside, they would be preserved as scattered spicules or lump of spicule networks (cf. Poźaryska and Voigt, 1995). Some sponge remains are larger than openings of skeletal cavities (e.g., intertabularial space of agetolitid corals), suggesting their growth within cavities (Fig. 4C, D). In addition, many sponge-bearing cavities occur within LM and LMb facies, which were deposited in low-energy environment lacking transportation of sediment (Table 1). These collectively suggest that at least some of the sponges, and possibly most of them, grew and preserved within the studied cavities.

It is estimated that the non-reef, shallow-marine intraskeletal cavities inside mollusc shells and some coral skeletons investigated in this study would have been exposed on the seafloor for less than a few years prior to burial (e.g., Parsons-Hubbard et al., 1999). Sponges would have infiltrated any available cavity spaces within molluscs and corals, as indicated by the distribution of sponges regardless of cavity type. Therefore, the occurrence of sponges within intraskeletal crypts shows the ability of sponges to invade and utilize short-lived cavities of any shape on the seafloor. In the modern ocean, sponge larvae of a wide range of sizes (50 μm to 5 mm) actively swim or passively float through the water or creep on the seafloor for a few hours to several weeks, until the larvae settle and attach to a substrate. Subsequently, the larvae turn into juvenile sponges over a short period of time (Maldonado and Bergquist, 2006). It is speculated that the Xiazhen sponges would also have dispersed throughout the shallow-marine environment during their larval stages and settled on various substrates including intraskeletal crypts, thus enabling their widespread distribution.

The preferential occurrence of sponges within cavities of 1–30 mm^2 in size (Fig. 5) suggests that most of the sponge larval settlement, growth, and subsequent preservation occurred in these cavities. Similar occurrences of sponges enclosed within intraskeletal cavities in reefs of Cambrian to Triassic age are found in bivalves (~10 mm^2), brachiopods (~25 mm^2), gastropods (~120 mm^2), calathids (~180 mm^2), and lithistid sponges (10–790 mm^2) (Hong et al., 2014; Lee et al., 2014, 2016a, 2016b; Luo and Reitner, 2014; Luo, 2015). Of these occurrences, all are found in cavities larger than 10 mm^2, except for those occurring within bivalves of bivalve-sponge-microbe reefs (> ~1 mm^2) (Lee et al., 2016b). One of the key findings of the current study is the preservation of cryptic sponges within cavities as small as 0.2 mm^2 and their widespread occurrence in cavities larger than 1 mm^2. This finding, coupled with the absence of sponge remains in the skeletons of tetradiids, *Bajgolia*, bryozoans, and ostracods, in which the cavities have a size range of 0.03–1 mm^2, indicates that a cavity size of 1 mm^2 is near the lower limit for the preservation of sponge remains in the geologic record.

It is noteworthy that sponge remains similar to those in intraskeletal cavities are also present in the Xiazhen Formation micritic limestones outside of the cavities (Park et al., 2015). These sponge remains constitute a significant part of the micritic carbonates, constituting 16.7% and 11.5% of the LM and LMb facies, respectively, though they comprise only 2.3% of the W/Pb facies (Table 2). These occurrences have been interpreted as sponges thriving better and being more likely to be preserved in a calm environment without other metazoans (LM facies) than in a slightly higher-energy environment with other metazoans (W/Pb facies) (Park et al., 2015). Similarly, the areal percentages of sponges within cavities decrease from the LM to the LMb and the W/Pb facies (0.4%, 0.2%, and 0.2%, respectively). These results suggest that sponge larvae did not preferentially settle in either open or semi-

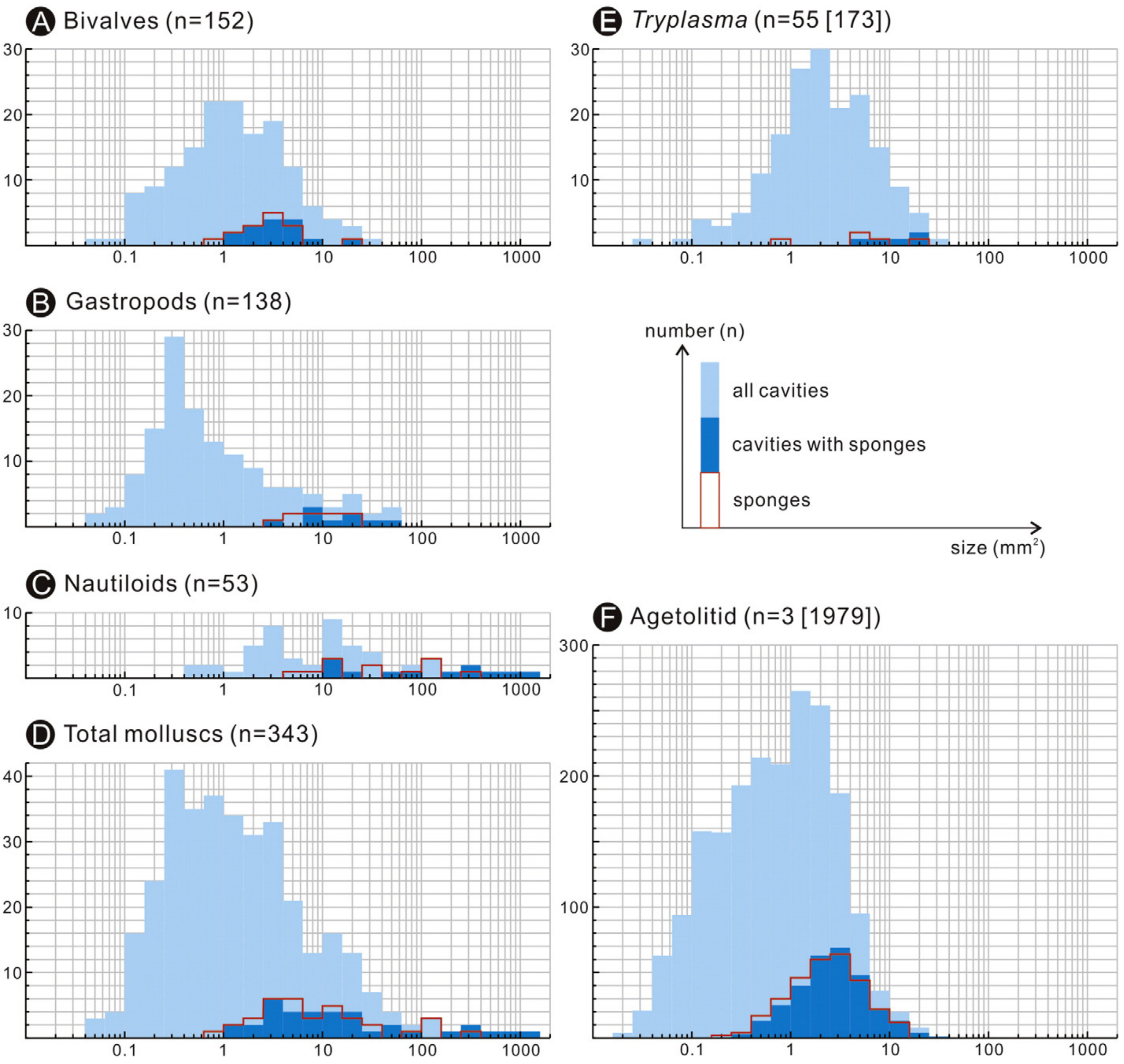

Fig. 5. Distribution of cavities, sponge-bearing cavities, and sponges by size according to cavity type. Intraskeletal cavities in bivalves (A), gastropods (B), nautiloids (C), and total molluscs (D). Intertabularial spaces of *Tryplasma* (E) and agetolitid corals (F). The number of cavity-providing individuals is indicated by n; the number in parentheses is the total number of cavities.

closed habitats, indicating that these sponges were generalists rather than specialists, and their presence and/or preservation would have been affected by the surrounding sedimentary environment as well as the presence of other organisms. The sponges could have easily dispersed within the environment, and would have been avid pioneers of the simple intraskeletal cavities littered around the seafloor.

4. Discussion

4.1. Early history of cryptic metazoans and the importance of small crypts

Cloudina and *Namacalathus*, which occur in framework and crevice cavities of Ediacaran reefs, constitute the earliest record of cryptic metazoans (Wood and Curtis, 2015). In subsequent early Cambrian microbialite–archaeocyath reefs, "surprisingly diverse" (Zhuravlev and Wood, 1995, p. 443) cryptic organisms such as archaeocyaths, cribricyaths, calcified microbes, putative primitive cnidarians, arthropods, brachiopods, echinoderms, and sponges (preserved as scattered spicules) are found within reef cavities (Kobluk and James, 1979; Kobluk, 1981b, 1985; Zhuravlev and Wood, 1995). These early cryptic metazoans waned by the end of the early Cambrian due to the demise of archaeocyaths and the ensuing decline of reef-framework cavities throughout the rest of the Cambrian, and were largely replaced by calcimicrobes (James, 1981; Hong et al., 2012; Kruse and Reitner, 2014; Adachi et al., 2015), except for rare examples of cryptic sponges inside the spongocoels of Cambrian Series 3 lithistid sponge–microbial reefs (Lee et al., 2016a) and of Furongian bivalve shells incorporated within sponge–microbial reefs (Lee et al., 2014).

As the sessile metazoan groups of bryozoans, corals, and stromatoporoids began to appear in the Ordovician, larger reef cavities became available for cryptic communities (Kobluk, 1988a, 1988b).

Table 2
Proportion of sponge remains by facies. *Estimates of sponges outside cavities are after Park et al. (2015).

Facies	Cavity type	Cumulative area of thin section (mm^2)	Cumulative area of cavity (mm^2)	Cryptic sponge remains (mm^2)	Cryptic sponge remains (%)	Sponges outside cavities (%)*
LM[a]		22,369.0	540.6	102.9	0.5	16.7
	bivalve		107.4	24.3	0.1	
	gastropod		92.6	31.2	0.1	
	nautiloid		340.6	47.4	0.2	
	Tryplasma		–	–	–	
	Agetolites		–	–	–	
	other		–	–	–	
LMb[b]		33,417.0	3611.4	676.6	2.0	11.5
	bivalve		117.3	31.1	0.1	
	gastropod		33.4	14.1	0.04	
	nautiloid		3005.3	610.0	1.8	
	Tryplasma		53.6	4.9	0.01	
	Agetolites		–	–	–	
	other		401.8	16.5	0.1	
W/Pb[c]		56,531.0	5289.0	1209.2	2.1	2.3
	bivalve		172.9	4.6	0.01	
	gastropod		403.8	55.2	0.1	
	nautiloid		1076.4	159.3	0.3	
	Tryplasma		600.3	33.6	0.1	
	Agetolites		2991.8	949.0	1.7	
	other		43.8	7.5	0.01	

[a] LM = lime mudstone facies.
[b] LMb = bioturbated lime mudstone facies.
[c] W/Pb = bioturbated wacke- to packstone facies.

Early Ordovician reef crypts were still monotonous and were occupied mainly by calcimicrobes (James, 1981; Pratt and James, 1982), except for some bryozoans (Adachi et al., 2012), sponges (Hong et al., 2014), and possibly stromatoporoids (Li et al. in press). Cryptic metazoans of the Middle to Late Ordovician consist of encrusting bryozoans and sponges preserved as scattered spicules (Kobluk, 1980, 1981a, 1988a) or spicule networks similar to this study (Lee et al., 2016b), vagile metazoans such as burrowers in reef cavity sediments (Kobluk, 1981a, 1981b), as well as bryozoans and pelmatozoans in the undersides of Late Ordovician hardgrounds (Brett and Liddell, 1978). However, aside from the undersides of hardgrounds, there has been as yet no example of non-reef cavity dwellers from lower Palaeozoic deposits.

The current study demonstrates the common (11%; $n = 45/415$) occurrence of sponges within non-reef intraskeletal cavities from the Upper Ordovician succession of South China. To our knowledge, no other study has focused on such small cavities, which has possibly hindered understanding of the geologic record of cryptic organisms. It has been suggested that delicate cryptic organisms occupying large cavities such as those within modern reefs would not have well been preserved in the fossil record because of other crypt-dwelling organisms, bioerosional activity, and the degradation of soft tissues (Rasmussen and Brett, 1985; Kobluk and van Soest, 1989). On the other hand, small cryptic cavities similar to those of the Xiazhen intraskeletal crypts have been predicted to preserve records of cryptic communities due to their rapid burial (Rasmussen and Brett, 1985). The present study confirms this previous prediction and furthermore suggests that future studies on small cavities within lower Palaeozoic successions worldwide as well as those in rocks of other geologic ages will improve our understanding of the evolution of cryptic ecosystems.

4.2. Invasion of early cryptic organisms into crypts

The fundamental issues of why and how certain metazoans were pioneers into cryptic space remain to be resolved (Palmer, 1982; Brett, 1988; Kobluk, 1988b; Zhuravlev and Wood, 1995; Taylor and Wilson, 2003). Several hypotheses for the invasion mode of early cryptic organisms have been proposed based on research on early Cambrian reefs (Kobluk and James, 1979), including the normal expansion of open-space benthic organisms into crypts during radiation by exploitation of niches; the forced expansion of less-well-performing, open-space benthos into crypts as refuges; and the origination of new benthic organisms within cavities and their radiation to open surfaces. The advent of scleractinian corals in the Middle Jurassic might have triggered cryptic invasions of brachiopods and coralline sponges via the formation of larger framework cavities, suggesting an opportunistic invasion mode (Jackson et al., 1971). In early Cambrian reefs, Zhuravlev and Wood (1995) documented the simultaneous emergence of several archaeocyath species on both open and cryptic surfaces, together with the selective appearance of many new species only in crypts. The occurrence of Ediacaran *Cloudina* and *Namacalathus* within reefal crypts formed by other individuals of *Cloudina* and *Namacalathus* (Wood and Curtis, 2015) could be evidence for the normal expansion of benthic organisms into crypts. On the other hand, Li et al. (in press) suggested that stromatoporoids would have initially diversified from reefal cavities based on the occurrence of the labechiid stromatoporoid *Cystostroma* in Early Ordovician lithistid sponge–*Calathium* reefs.

It is noteworthy that among the organisms capable of living in the Late Ordovician crypts (e.g., Brett and Liddell, 1978; Kobluk, 1980, 1981a, 1988a) that commonly occur in the open-surface, shallow-marine environments of the Xiazhen Formation, sponges are the only metazoans to have exploited these short-lived intraskeletal cavities. The Xiazhen intraskeletal crypts scattered on the micritic seafloor with demosponges are monotonous in composition compared with other Middle to Late Ordovician reefs (Kobluk, 1980, 1981a) and hardgrounds (Brett and Liddell, 1978), instead resembling the earlier primitive cryptic systems of the middle Cambrian to Early Ordovician reef crypts (James, 1981; Pratt and James, 1982; Adachi et al., 2012, 2015; Hong et al., 2012, 2014; Kruse and Reitner, 2014; Lee et al., 2014, 2016a). The non-preferential occurrence of sponges both outside and inside the Xiazhen cavities suggests that the adaptation of cryptic sponges into non-reef intraskeletal cavities would have been due to normal colonization in a wide range of shallow-marine environments, whereas other crypt-dwelling organisms of the early Palaeozoic could not at that time have occupied these “short-lived” cavities.

5. Conclusions

Sponge-bearing intraskeletal cavities are reported from the micritic carbonate succession of the Upper Ordovician Xiazhen Formation of South China. Mollusc shells and coral skeletons commonly contain patches of spicular networks of demosponges (11%; $n = 45/415$), which are very similar to sponges that lived on micritic substrates outside of the crypts. It is interpreted that sponges were capable of invading short-lived intraskeletal crypts, possibly by sending out numerous sponge larvae that sought to become established on suitable substrates. The current findings suggest that vacant intraskeletal spaces in the Late Ordovician carbonate platform were occupied by sponges through normal colonization processes. As intraskeletal cavities similar to those in this study commonly occur within carbonate successions of the early Palaeozoic, further studies elsewhere may reveal a wider distribution of cryptic organisms during that time interval. In addition, the low diversity of the Xiazhen non-reef cryptic ecosystem is comparable to that of reefal crypts of the Precambrian and the middle Cambrian to Early Ordovician, and quite different from other Middle to Late Ordovician reef and hardground cavities that show a higher diversity, thereby suggesting that the evolutionary pathways of cryptic ecosystems were intermittent and independent in different sedimentary environments.

Acknowledgements

We thank two anonymous reviewers and editor Brian Jones for constructive suggestions. This study was supported by grants from the

National Research Foundation of Korea to JHL (2016R1C1B1012104), SJC (2015R1A2A2A01007063), DCL (R1A400720100011026), and DJL (2013R1A2A2A01067612), and the research grant of the Chungbuk National University in 2015 to DCL. We also thank J. Jeon, H.-J. Cho, H. Park, N.K. Kim, and M. Lee of Andong National University for assistance in the field and with thin-section preparation.

Supplementary data

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.sedgeo.2016.11.003. These data include the Google maps of the most important areas described in this article.

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