Palaeogeography, Palaeoclimatology, Palaeoecology 398 (2014) 86–96

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

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

Composition and tiering of the Cambrian sponge communities

Wen Wu [a], Maoyan Zhu [a,*], Michael Steiner [b]

[a] State Key Laboratory of Palaeobiology and Stratigraphy, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, 210008, China
[b] Institut für Geologische Wissenschaften, Freie Universität Berlin, Malteserstr. 74-100, D-12249 Berlin, Germany

ARTICLE INFO

Article history:
Received 4 February 2013
Received in revised form 15 July 2013
Accepted 1 August 2013
Available online 9 August 2013

Keywords:
Cambrian
Sponges
Chengjiang fauna
Tiering
Palaeoecology

ABSTRACT

Sponges are dominant sessile suspension feeders in the Cambrian metazoan community; thus, sponge tiering and composition in the Cambrian communities will provide important information for elucidating the evolutionary history of the epifaunal community. Based on more than two thousand articulated sponge specimens from the early Cambrian Chengjiang fauna, the present study demonstrates that the Chengjiang sponge community is dominated by demosponges with a well-developed three-level tiering, consisting of 0–5 cm, 5–15 cm and 15–30 cm tiers. The majority of the sponges are restricted to the 0–15 cm tier, suggesting rich nutrients in the bottom seawater of the Cambrian ocean. Tiering in the Cambrian sponge communities is consistent and similar to that of the Ediacaran and Phanerozoic epifaunal communities, but the fourth tier (50–100 cm) in these latter communities is absent in the Cambrian communities. Demosponges dominate the shallow-water sponge communities and occur in all tiers. Hexactinellids are relatively rare and limited in the lower tiers in the shallow-water community, but dominate in the deep-water communities. The composition variation in the Cambrian sponge communities may be controlled by the differences in skeleton architecture between the Demospongiae and Hexactinellida.

1. Introduction

Epifaunal tiering, the subdivision of vertical space within a metazoan community, is a fundamental attribute of the Phanerozoic suspension-feeding communities (Ausich and Bottjer, 1982, 2003). Previous studies indicate that Phanerozoic metazoan tiering may extend back into the late Neoproterozoic, which was dominated by the soft-bodied Ediacaran biota with the tiering heights reaching several decimetres or more (Clapham and Narbonne, 2002). The best epifaunal tiering was developed in the Palaeozoic (post-Ordovician) and the early Mesozoic when skeletal epifaunal communities were stratified into four levels: 0–5 cm, 5–20 cm, 20–50 cm and 50–100 cm above the substrate (Ausich and Bottjer, 1982; Bottjer and Ausich, 1986). According to the tiering history summarized by Ausich and Bottjer (2003), there is a declining trend of the tier height in Cambrian epifaunal communities. It is unclear whether the tiering pattern during the Neoproterozoic–Cambrian transition is (1) the result of an evolutionary decline duo to extinction of the soft-bodied Ediacaran biota and subsequent eruption of skeletonized metazoan communities, or (2) just simply the result of poor preservation (Ausich and Bottjer, 2003).

In the past two decades, discoveries of numerous Cambrian soft-bodied fossil lagerstätten suggest that metazoans experienced an abrupt explosive radiation both in morphospace and ecospace during the Cambrian. Palaeoecological investigations of these Cambrian biotas, such as the Chengjiang and Burgess Shale faunas, indicate that the Cambrian communities are dominated by epifaunal filter-feeding organisms (Conway Morris, 1986, 1993; Dornbos et al., 2005; Caron and Jackson, 2008; Zhao et al., 2010), making it possible to evaluate epifaunal tiering in more detail and thus enhancing our understanding of the Cambrian community structures and food webs (Dunne et al., 2008). For example, a recent quantitative analysis of the feeding strategy in the early Cambrian Chengjiang fauna indicates that the epifaunal suspension feeders comprise 17% of species in the early Cambrian community and that the dominant epifaunal suspension feeders are sponges (Zhao et al., 2010). Thus, the evaluation of the tiering and composition of the early Cambrian sponges is a prerequisite for understanding the tiering and composition of the early Cambrian epifaunal suspension feeding community.

Recent collection of articulated sponges from several early to middle Cambrian deposits has improved our understanding of the sponge tiering and composition in the Cambrian communities. Most of the described Cambrian sponge species are from South China (Carrera and Botting, 2008), including the sponges from the Chengjiang fauna (Chen et al., 1989, 1990, 1996; Hou et al., 1999) and the Sancha, Niutitang, Hetang and Huangbeiling sponge faunas (Steiner et al., 1993; Yuan et al., 2002; Wu et al., 2005; Xiao et al., 2005; Yang et al., 2005b, 2010). As shown by data from the Hetang sponge fauna, most Cambrian sponges occupy the 10 cm tier, but some reach the 20 and 50 cm tiers (Yuan et al., 2002). By comparison with the other Cambrian sponge communities, we attempt to establish what controls the sponge composition in the Cambrian community.

* Corresponding author.
E-mail address: myzhu@nigpas.ac.cn (M. Zhu).

0031-0182/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.palaeo.2013.08.003

2. Stratigraphy, material and methods

The sponge fossils investigated here were collected from the early Cambrian Yu'anshan Formation in Chengjiang, near Kunming, South China. Nearly all specimens originated in the mudstone and silty mudstone of the Yu'anshan Formation's Lithofacies 2 and 3, which represent deposits during the early stages of the regressive phase in a proximal offshore to lower shoreface environment (Zhu et al., 2001). More than two thousand specimens of the sponge fossils are investigated in the present study. All specimens are compressed, their articulated spicules are preserved, and most specimens are embedded in situ by rapid obrution deposition of fine-grain sediments of distal tempestites, showing sharp outlines of the sponge bodies. The sponge fossils comprise at least 18 genera and 25 species according to a systematic study by Wu (2004). The heights of all sponge specimens, including previously published specimens, are measured. The heights of the largest sponges, such as species of the Halichondritidae and Quadrolaminiellidae, may be underestimated because these large sponges are generally incomplete. The maximum height of each sponge species for tiering analysis is adapted on the basis of comparison with the specimens from other Cambrian faunas. All specimens investigated here are housed at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

3. Sponge tiering in the Chengjiang fauna

Based on data of the maximum height of each sponge species from the Chengjiang fauna, a linear pattern of the sponge body size is shown in Fig. 1. Although the boundaries are not clear, a three-level tiering of the sponges can be discerned, i.e. a height of 0–5 cm, 5–15 cm and 15–30 cm above the seafloor. Each tier is characterized by the overlapping of one or several dominant sponge species.

0–5 cm: the tier represents the basal level of the sponges feeding near the seafloor. The sponge species in this level account for about 22.3% of the total species in the Chengjiang fauna. As shown in Fig. 2, the sponge species of the Choiidae (3 and 4 in Fig. 2) and Hamptoniidae (5 in Fig. 2) dominate, accounting for about 86.86% of the total individuals of the sponge specimens at this basal level. *Cystospongia globosa* n. gen. et sp. is also abundant. Together, these sponge fossils constitute 96.2% of the total sponge specimens at this level.

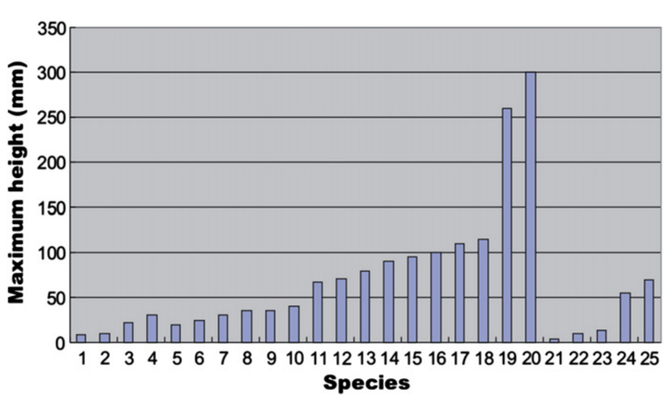

Fig. 1. Maximum size of the Chengjiang sponges. (1–20 = demosponges; 21–25 = hexactinellids): 1, *Choia ridleyi*; 2, *Choiaella radiatia*; 3, *Choiaella* cf. *radiatia*; 4, *Choia carteri*; 5, *Leptomitella conica*; 6, *Allantospongia mica*; 7, *Choia* cf. *utahensis*; 8, *Hamptonia chengjiangensis*; 9, *Ptilispongia maotianshanensis*; 10, *Saetaspongia densa*; 11, *Paraleptomitella globula*; 12, *Ischnospongia dendritica*; 13, *Wapkia grandis*; 14, *Choia hindei*; 15, *Paraleptomitella dictyodroma*; 16, *Quadrolaminiella crassa*; 17, *Leptomitus teretiusculus*; 18, *Leptomitella confusa*; 19, *Halichondrites* cf. *elissa*; 20, *Quadrolaminiella diagonalis*; 21, *Triticispongia diagonata*; 22, *Protospongia* sp.; 23, *Cystospongia globosa*; 24, *Hyalocinica* sp.; 25, *Valospongia* cf. *gigantis*.

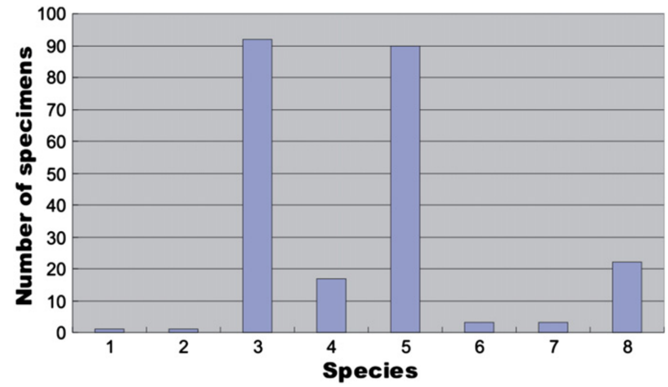

Fig. 2. Abundance of Chengjiang sponges in 0–50 mm tier. 1, *Ptilispongia maotianshanensis*; 2, *Leptomitella conica*; 3, *Choia carteri*, *Choia ridleyi*, *Choia* cf. *utahensis*, *Choiaella radiatia*, *Choiaella* cf. *radiatia*; 4, *Allantospongia mica*; 5, *Hamptonia chengjiangensis*; 6, *Protospongia* sp.; 7, *Triticispongia diagonata*; 8 *Cystospongia globosa*.

Because of living near the bottom, the skeletons of the Choiidae and Hamptoniidae are relatively simple, in general showing radiating patterns of the spicules. The large variation in the width of these sponge bodies may suggest that the sponges in this level adapted a strategy of extending their width to compete for food.

5–15 cm: Most sponge species in the Chengjiang fauna are in this tier, accounting for 60.6% of the total species number. The dominant sponges are two species of leptomitiids, *Paraleptomitella dictyodroma* and *Hyalosinica* sp., consisting of 67.7% of the total sponge specimens in this tier. The skeleton of *P. dictyodroma* is complex.

The spicules of the leptomitiids are bundled, and the big spicules bend to form an arch and cross each other, forming rhomboid frames. As Rigby (1983) pointed out, bundled spicules can reinforce the skeleton better than dispersed spicules. The complex framework of the leptomitiid spicules makes the sponge body stronger so it can stand at a higher level above the seafloor for food competition. It is interesting to note that the specimen numbers of three leptomitiid species increase with the complexity of the spicule framework as shown in Fig. 3. *Leptomitus* with a simple spicule frame is less abundant than *Paraleptomitella dictyodroma*, which has a more complex spicule frame. The data suggest that food competition may be the major force driving the evolution of the three species of the Leptomitiidae through increasing height of the body and complexity of the spicule framework.

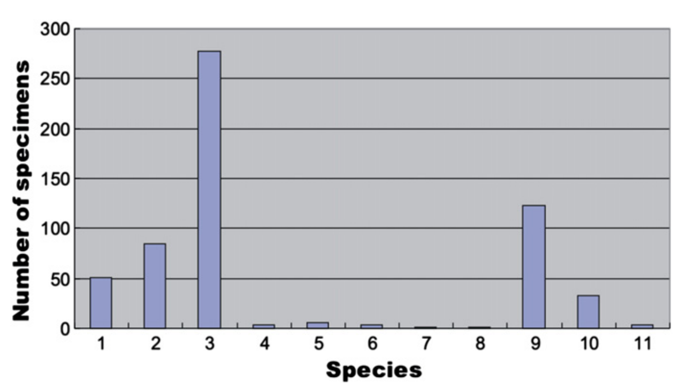

Fig. 3. Abundance of Chengjiang sponges in 50–150 mm tier. 1, *Leptomitus teretiusculus*; 2, *Leptomitella confusa*; 3, *Paraleptomitella dictyodroma*; 4, *Paraleptomitella globula*; 5, *Choia hindei*; 6, *Wapkia grandis*; 7, *Quadrolaminiella crassa*; 8, *Valospongia* cf. *gigantis*; 9, *Hyalocinica* sp.; 10, *Ischnospongia dendritica*; 11, *Saetaspongia densa*.

15–30 cm: Only two species, *Halichondrites* cf. *elissa* and *Quadrolaminiella diagonalis*, are found in this tier and account for 17.1% of the total sponge species. The two largest sponges have similar numbers of specimens in the Chengjiang fauna (97 vs. 71). The skeletons of the two species are more complex than other smaller ones in the lower tiers.

Halichondrites cf. *elissa* incorporates two spicule sizes. The larger prostalia and marginalia seem to be composed of smaller bundled spicules. *Quadrolaminiella diagonalis* is structured by interlaced spicules which form complex reticulations. The complex skeletons of the largest sponges sustain the sponge body with greater height against water current in order to gain a competitive advantage for food competition.

In summary, most of the sponges are within the 0–15 cm tier and account for about 82.9% of the total species in the Chengjiang fauna. A similar concentration of the epifaunal organisms within the 0–20 cm level was also recorded in the Burgess Shale fauna (Yuan et al., 2002). Present data on sessile filter feeders indicate that the Cambrian sponge tiering structure is consistent with that of other tiered epifaunal communities (Clapham and Narbonne, 2002). Therefore, the concentration of the sponges in the lower level suggests a rich nutrition in the water column at 0–15 cm above the seafloor in the Cambrian ocean.

4. Variation of the tiering and composition of the sponges in the Cambrian communities

The sponges in the Chengjiang fauna comprise at least 18 genera and 25 species (Wu, 2004). The well-developed sponge tiering structure in the Chengjiang fauna (Fig. 4) is similar to that in the Cambrian Hetang sponge fauna in the deep-water setting of the Yangtze Platform (Yuan et al., 2002), but sponges with heights up to 50 cm in the deep water do not occur in the Chengjiang fauna, which represents considerably shallower habitats. The reason may be the discrepancy in deposition settings of the two faunas. Shallow water with frequent bottom currents would possibly have prevented the development of the higher tier in the Chengjiang fauna. In comparison with the tiering structure in the Ediacaran communities (8 cm, 22 cm, 35 cm, 90 cm; Clapham and Narbonne, 2002) and the Phanerozoic communities (5 cm, 20 cm, 50 cm and 100 cm; Ausich and Bottjer, 1982; Bottjer and Ausich, 1986), the fourth level is absent in the Chengjiang fauna and other Cambrian biotas; this may be due to extinction of the Ediacaran biota and/or cropping of upper tier organisms by evolving Cambrian macropredators (Clapham and Narbonne, 2002). However, constructional differences between taxa may also have controlled the tiering structure in the Cambrian sponge communities as indicated in the Ediacaran communities (Clapham and Narbonne, 2002).

In order to understand what controlled the tiering structure of the Cambrian sponge communities, we compared the Chengjiang sponge community with other major Cambrian communities including the sponge faunas in the lower Cambrian black shales of South China, middle Cambrian Kaili, Burgess Shale and western Utah faunas (Table 1). The sponge species constitute 12.3% of the total species of the Chengjiang fauna (Zhao et al., 2010). The Chengjiang sponge community is dominated by demosponges, which account for 68% of all sponge species and occur widely in each tiering level in the community (Fig. 1, 1–20; Fig. 4), demonstrating that demosponges are well developed in the early Cambrian shallow water forming the high-level tiering. However, hexactinellids are relatively rare (32%) and limited to the lower level of the Chengjiang community (Fig. 1, 21–25).

There are abundant sponges in articulate preservation from the lower Cambrian black shale of South China, including the Niutitang sponge fauna in Guizhou (Yang, 2002; Yang et al., 2005a,b, 2010) and Hunan (Steiner et al., 1993; Mehl and Erdtmann, 1994), Hetang and Huangbeiling sponge faunas in southern Anhui (Wu et al., 2005; Xiao et al., 2005). Like the Chengjiang sponge fauna, the Niutitang sponge fauna (A) at Zhongnan, Songlin in northern Guizhou is found in the Niutitang Formation from the shallow water facies; it consists of 13 genera, 55% of which are demosponges (see Table 1). *Leptomitus* dominates the community and accounts for about 20% of all sponge specimens.

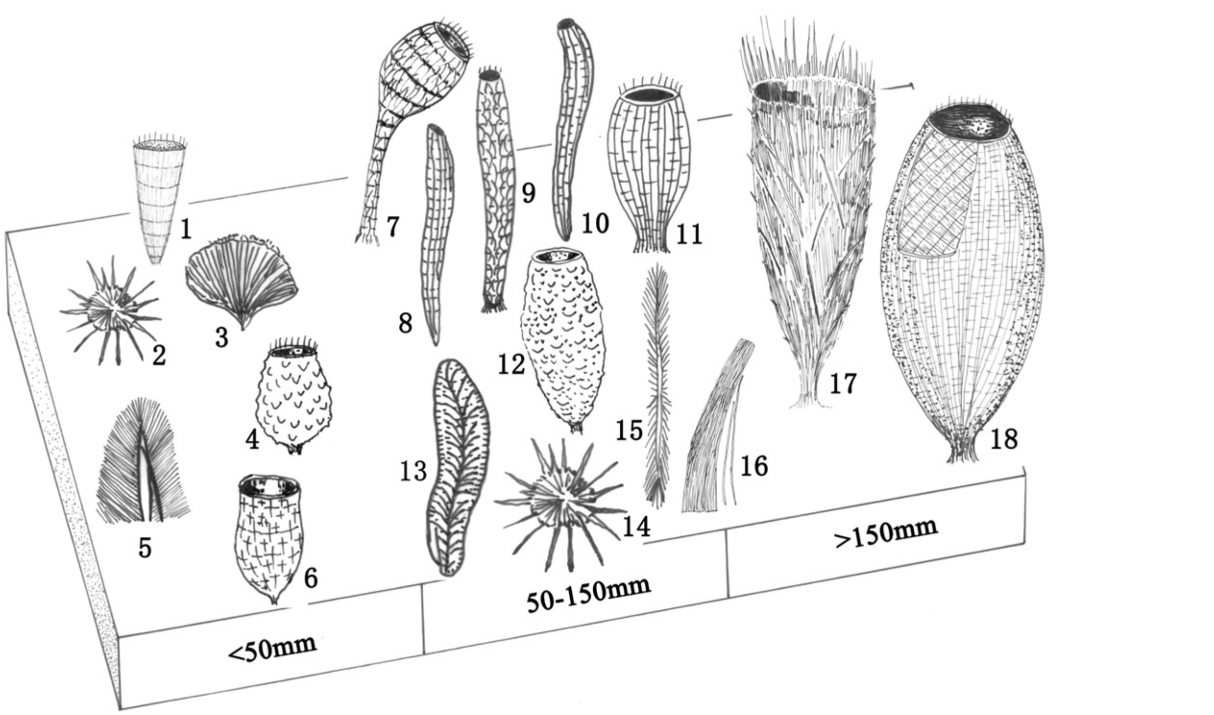

Fig. 4. Diagram showing tiered structure of the sponges in the Chengjiang fauna. 1, *Leptomitella conica*; 2, *Choia ridleyi*, *C. carteri*, *C.* cf. *utahensis*, *Choiaella radiatia*, *C.* cf. *radiatia*; 3, *Hamptonia chengjiangensis*; 4, *Cystospongia globosa*; 5, *Ptilispongia maotianshanensis*; 6, *Protospongia* sp.; 7, *Paraleptomitella globula*; 8, *Leptomitella confusa*; 9, *Paraleptomitella dictyodroma*; 10, *Leptomitus teretiusculus*; 11, *Quadrolaminiella crassa*; 12, *Valospongia* cf. *gigantis*; 13, *Wapkia grandis*; 14, *Choia hindei*; 15, *Ischnospongia dendritica*; 16, *Hyalocinica* sp.; 17, *Halichondrites* cf. *elissa*; 18, *Quadrolaminiella diagonalis*.

Table 1
Comparison of the Cambrian sponge communities.

		Chengjiang Fauna	Niutitang Sponge Fauna (A)	Kaili Fauna	Burgess Shale Fauna	Western Utah	Niutitang Sponge Fauna (B)	Hetang Sponge Fauna
Demospongiae	*Allantospongia*	+						
	Angulosuspongia			+				
	Capsospongia				+			
	Choia	+	+	+	+	+	+	+
	Choiaella	+		+				
	Crumillospongia		+		+			
	Ellspongia		+		+	+		
	Falospongia				+			
	Fieldospongia				+			
	Halichondrites	+	+		+			
	Hamptonia	+	+		+	+		
	Hamptoniella	+						
	Hapalospongia		+		+			
	Hazelia			+	+	+		
	Ischnospongia	+						
	Leptomitella	+	+					
	Leptomitus	+	+	+	+	+	+	
	Moleculospina				+			
	Paraleptomitella	+	+					
	Pirania				+			
	Ptilispongia	+						
	Quadrolaminiella	+						
	Sentinelia				+			
	Takakkawia				+			
	Ulospongiella				+			
	Vauxia			+	+	+		
	Wapkia	+			+			
Hexactinellida	*Cystospongia*	+						
	Diagoniella				+	+	+	+
	Hintzespongia					+	+	
	Hunanospongia						+	
	Hyalocinica	+	+					+
	Gabelia							+
	Kiwetinokia				+	+		
	Lantianospongia							+
	Protoprisma				+			
	Protospongia	+	+	+	+	+	+	+
	Ratcliffespongia					+		
	Saetaspongia	+	+	+			+	
	Sanshapentella						+	+
	Stephenospongia				+			
	Testiispongia					+	+	
	Triticispongia	+	+					+
	Valospongia	+				+		
	Zunyispongia		+					
Calcarea	*Canistrumella*				+			
	Eiffelia				+			
	Eiffelospongia				+			
	Petaloptyon				+			
Incertae sedis	*Solactinella*		+				+	+

However, the Niutitang sponge fauna (B) from the Niutitang Formation in the deeper water facies is dominated by hexactinellids. In the sponge community from the Niutitang Formation at Danzhai, Nangao, Guizhou, 75% of the sponges are hexactinellids, which are characterized by large *Diagoniella* and *Saetaspongia* (Yang et al., 2010). All the described sponges in the sponge community from the Niutitang Formation at Sancha, Zhangjiajie, western Hunan are hexactinellids (Steiner et al., 1993; Mehl and Erdtmann, 1994). Similar hexactinellid-dominated sponge communities are found in the deep-water facies in southern Anhui (Hu et al., 2002; Wu et al., 2005; Xiao et al., 2005).

Well-preserved sponges account for 6% of all species in the middle Cambrian Kaili biota, consisting of 6 genera and 7 species (Yang, 2002; Zhao et al., 2005). Like the Chengjiang fauna, the Kaili sponge fauna is dominated by demosponges, mainly *Leptomitus*.

There are 26 genera and 48 species of the sponge fossils described from the middle Cambrian Burgess Shale fauna of British Columbia, Canada, constituting the second largest group of animals in the fauna (Rigby, 1986; Rigby and Collins, 2004). In addition to demosponges and hexactinellids, Calcarea also appear in the Burgess Shale fauna. Demosponges are again the dominant group and account for 69.2% of the total sponge species in the fauna. Abundant, well-preserved sponges dominated by demosponges are also described from the middle Cambrian Marjum, Spence and Wheeler biotas in Utah, USA (Rigby, 1966, 1969, 1978, 1980, 1983; Rigby and Gutschick, 1976; Rigby and Chruch, 1990; Robison, 1991; Rigby et al., 1997, 2010).

In conclusion, the Cambrian sponge communities are characterized by demosponges and hexactinellids, although a few Calcarea are also reported in the Cambrian (e.g. Mehl, 1988). However, the sponge composition exhibits distinct variation among the communities (Table 1). Because of the facies in which these sponge fossils are preserved, it is obvious that the water depth may be a primary control on the variation of the sponge composition in these Cambrian communities. These results support the earlier hypothesis (e.g. Mehl-Janussen, 1999) that the demosponges are the dominant sponges in shallow water communities such as the Chengjiang, Kaili and Burgess Shale faunas, whereas hexactinellids dominate the deep-water communities, e.g. the Niutitang (B) in Hunan and Guizhou, and the Hetang sponge fauna. The variation of the demosponges and hexactinellids in different communities may be due to their different skeleton structures. As shown by very common and abundant sponges of the Leptomitiidae, the spicule frameworks of the demosponges are generally a complex network comprising bundled and interlaced spicules. By contrast, the skeletons of the hexactinellids are more regular frames, characterized by hexactins. That is why hexactinellids are rare and limited to the lower tiering level in the shallow water environment with frequent water currents. The very tough organic spongin fibres of Demospongiae probably also play a major role in stabilising their skeletons. By contrast, Hexactinellida have collagen but no spongin in their body (Reiswig, 2002).

Although the sponge composition varies, the sponge tiering is similar in the deep-water and shallow-water communities. The tiering structures in the Cambrian communities challenge the hypothesis that tiering only appears in the shallow-water communities because deep-water organisms tend to be taller to compensate for slower bottom currents and a thicker boundary layer (Bottjer and Ausich, 1986). Similar tiering also exists in the deep-water Ediacaran Mistaken Point community and shallow-water Ediacaran communities (Clapham and Narbonne, 2002).

5. Conclusion

Sponge tiering is well developed in the Cambrian Chengjiang fauna, consisting of three tiers of 0–5 cm, 5–15 cm and 15–30 cm. But the concentration of sponges in the lower tier suggests the presence of rich nutrients in the bottom water of the Cambrian ocean. Tiering in the Cambrian sponge communities is consistent and similar to the Ediacaran and Phanerozoic epifaunal communities, but the fourth tier (50–100 cm) in these latter communities is absent in the Chengjiang fauna and other Cambrian faunas. However, the sponge composition varies in the Cambrian communities. In general, the demosponges dominate the shallow-water communities, and the hexactinellids dominate the deep-water communities; this contrast may be due to the difference in skeleton structures between the demosponges and hexactinellids.

Acknowledgements

We thank J.-Y. Chen for allowing us to investigate most of the sponge specimens collected by him, Dorte Janussen and Andrzej Pisera for their critical comments and suggestions, Anne Beck for English language suggestions, and F. Zhang, L.-J. Qu and W.-Z. Li for preparing graphs. This work is supported by the Chinese Academy of Sciences (KZZD-EW-02), the Ministry of Science and Technology of China (2013CB835006), the National Natural Science Foundation of China and the DFG Forschergruppe 736.

Appendix A. Systematic palaeontology

Phylum Porifera Grant, 1872
Class Demospongiae Sollas, 1885
Subclass Ceractinomorpha Lévi, 1956
Order Halichondrida Gray, 1867
Family uncertain
Genus *Ptilispongia* gen. nov.

Type species. – *Ptilispongia maotianshanensis* gen. et sp. nov.

Diagnosis. – Small-sized, thin-walled, plumose sponge after flattened with about two sizes monaxon (oxeas). The bigger spicule constitutes the axial of the sponge; the smaller one aligns upward and outward on both sides of the axial in a plumose form.

Discussion. – The specimen looks like *Choia* with a radiated skeleton. However, the spicules of the latter radiate from one point. The genus is also similar to *Allantospongia*, but the latter lacks the axial in the middle of the sponge.

Etymology. –'ptil'- [Gr.], plume

***Ptilispongia maotianshanensis* gen. et sp. nov.**
(Fig. 5A–B)

Diagnosis. – As for the genus

Holotype. – Only one specimen is preserved with part and counterpart: holotype MN5-45067a, MN5-45067b housed at NIGPAS.

Description – The specimen looks like a feather with an axial in the middle after being flattened. No obvious osculum in the upper part of the sponge. The height of the sponge is 35 mm, with maximum width of 25 mm. The skeleton is mainly made up of two sizes of spicules. The large type of spicule is 25–30 mm in length and 0.13–0.2 mm maximum in diameter; it lies in the middle part of the sponge as an axial (about 4–6 such spicules). The axial is not a straight line but has a slight arc. These spicules form a lens with 23 mm in length and 0.85 mm in width.

The small spicules are about 10 mm in length and 0.09 mm in diameter and are aligned almost parallel with each other beside the axial. They rarely intrude into the lens. However, they seem to protrude outside and form a faint coronal fringe.

Etymology. – 'Maotianshan' is the fossil site in Chengjiang County

Discussion. – The new species looks like *Solactiniella dendrica* at first glance. Since *S. dendrica* shows more than one axial-like structure, this makes it look like the combination or clusters of the specimens of the new species. However, we found that the body size and the aligned directions of the small spicules of the two species are different.

The species is also similar to *Solactiniella plumata*. However, the latter has more irregular directions of the spicules in the middle part of the sponge.

Locality. – Xiaolantian section, Chengjiang, Yunnan, Yu'anshan Formation.

Genus *Ischnspongia* gen. nov.

Type species. – *Ischnspongia dendritica* gen. et sp. nov.

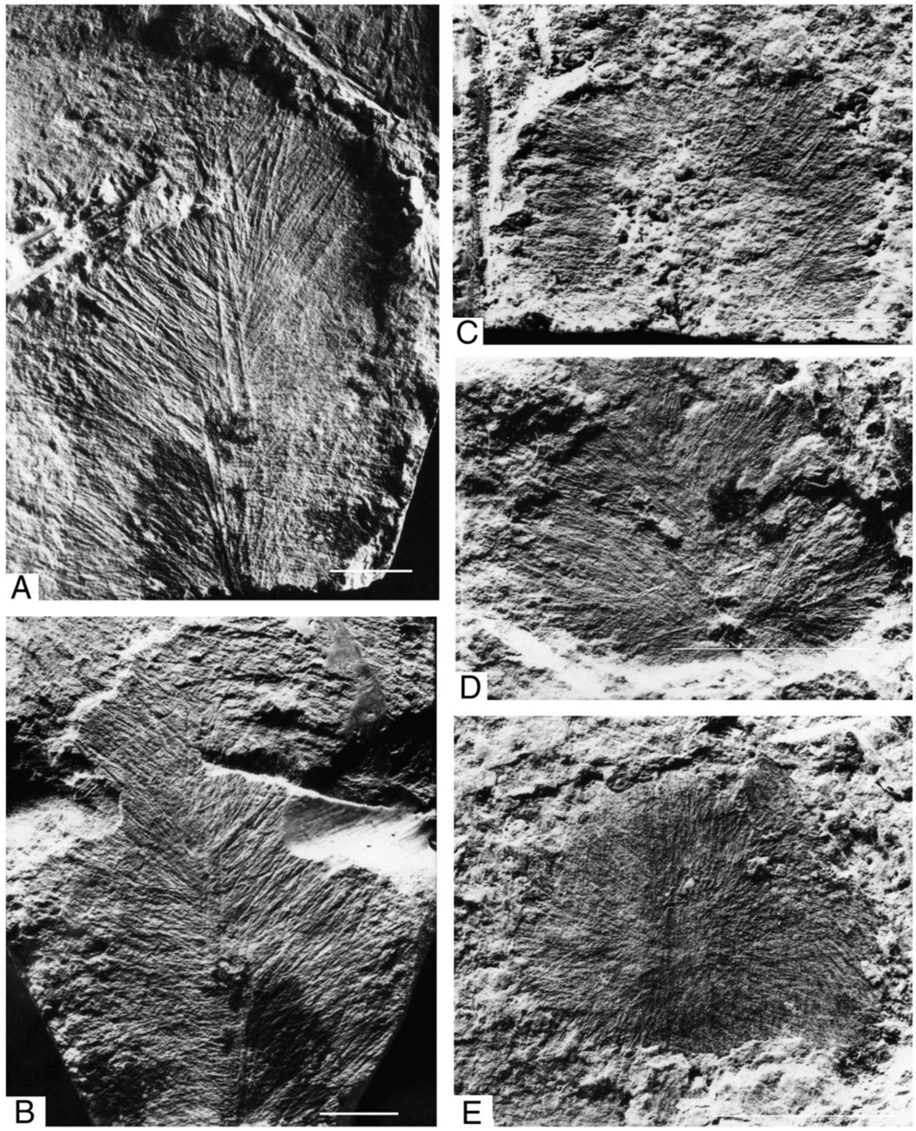

Fig. 5. A. *Ptilispongia maotianshanensis* n. g. et sp., holotype, MN5-45067a. B. *Ptilispongia maotianshanensis* n.g. et sp., MN5-45067b. C. *Hamptonia chengjiangensis* n. sp., 45147. D. *Hamptonia chengjiangensis* n. sp., 42265. E. *Hamptonia chengjiangensis* n. sp., holotype MN6-45004. Scales in 1–3 = 5 mm, 4–5 = 1 cm.

Diagnosis. – As for the species

Etymology. – 'Ischn'- (G.), slim

***Ischnspongia dendritica* gen. et sp. nov.**

(Figs. 6B,7)

Diagnosis. – Small, thin-walled sponge with the skeleton made of diactins. Diactins are arranged outward and upward besides the central axis, which consists of long diactins. The spicules in the middle part of the axis are aligned irregularly.

Material. – There are 35 specimens in all, 13 of which are studied: MW2-42984; MQ1(2)-42040; M2-45116; 45080;M2-45119; M2-45111; 063; 45138; MQA2-43094; MQ1-42121; 42343; 1119; 1120. **Holotype**. – Sample no. MW2-42984, housed at NIGPAS.

Description. – All the specimens are preserved flattened, and most spicules are preserved as mould. The upper part of MW2-42984 is well preserved. But no osculum is observed. The sponge body is preserved flattened with a conical outline. It is 29 mm in height and 15.5 mm in maximum width. The skeleton is made up of 2 to 3 types of spicules. The longer spicules are 11.1–13.5 mm in length and 0.1–0.15 mm in maximum diameter and are parallel to the main axis. Four to seven of such spicules aggregate together and form the axis. There are two axes that can be observed in the specimen. The other type of spicules is shorter, curving outward and upward on both sides of the axis like a plume. These spicules are 1.7–2.2 mm in length and 0.015–0.025 mm in diameter. The holotype (No. MW2-42984) specimen with two axes seems to be individuals flattened together.

Specimen No. 1119 is a completely preserved specimen, 71 mm in height and 8 mm in maximum width. In the middle part of the sponge, there is another kind of spicule which is 2.6–3.5 mm in length and 0.08–0.1 mm in diameter. These spicules are irregularly arranged and cross each other. A long axis extends through the entire sponge body and is made up of 6–8 long spicules, which are 21.6–24 mm long and 0.04–0.08 mm in diameter.

Etymology. – 'dendriticus' tree-like.

Discussion. – The upper part of this species is similar to *Solactiniella plumata* whose spicules radiate from the central part; the specimen represents a conservative skeleton type in the Porifera. Steiner et al. (1993) described dubious stauractins in the type species. However, this is not similar to the specimens of the Chengjiang Fauna.

The middle part of the sponge also resembles *Halichondrites* with two kinds of differently sized spicules. However, the latter is much

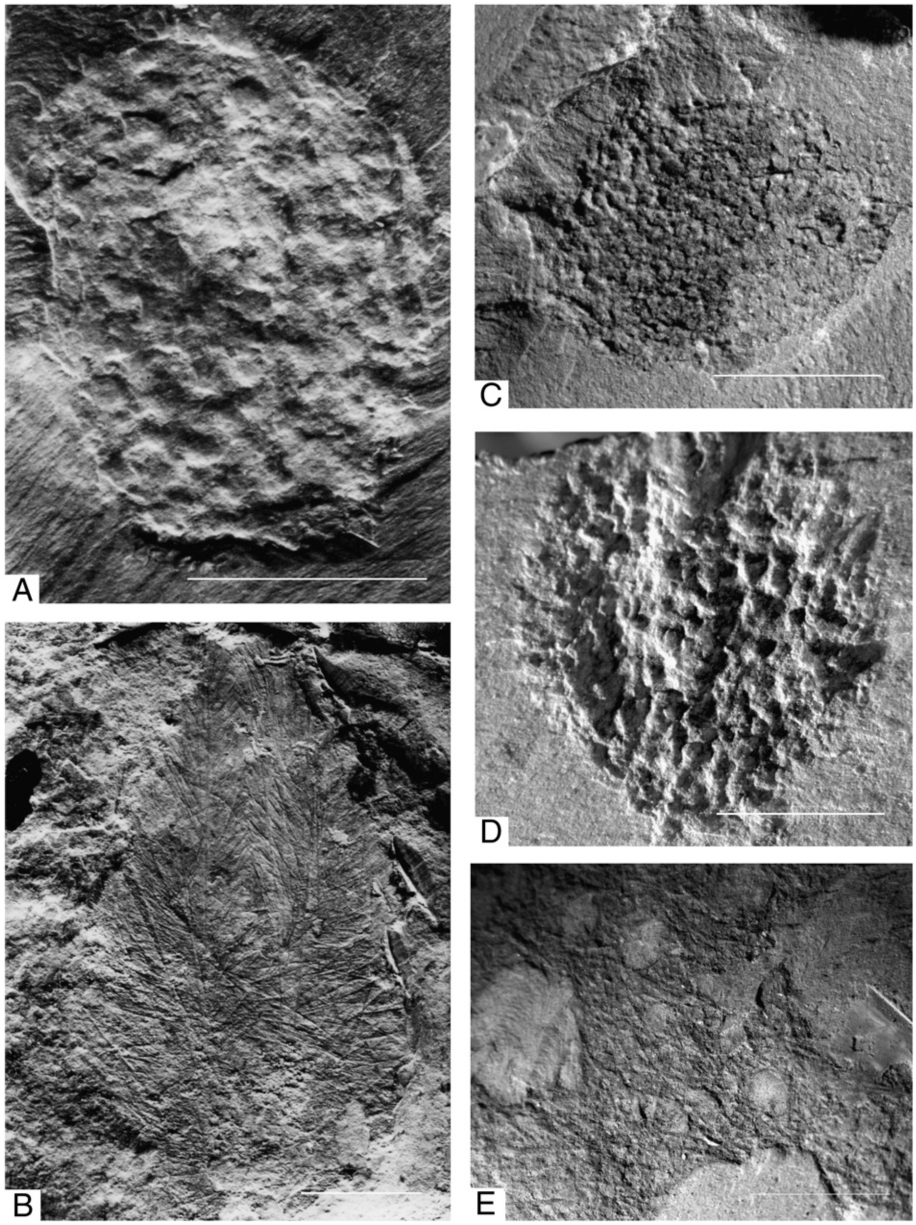

Fig. 6. A. *Cystospongia globosa* n.g. et sp., ME6-11. B. *Ischnspongia dendritica* n.g.et sp., holotype MW2-42984. C. *Cystospongia globosa* n.g.et sp., MW2-42469. D. *Cystospongia globosa* n.g.et sp., MN5-41122. E. Enlargement of *Valospongia* cf. *gigantis* Rigby, 1983, 1136a, showing the spicule and the mound of the wall. Scales in 1–2 = 5 mm, 3–5 = 3 mm.

bigger than the former. In addition, the spicules of the latter do not show any plume-like structure.

Locality. – Yu'anshan Formation, Chengjiang. Early Cambrian

Family Hamponiidae de Laubenfels, 1955

Genus *Hamptonia* Walcott, 1920

***Hamptonia chengjiangensis* sp. nov.**

(Figs. 5C, 5D–E)

Diagnosis. – Small-size mantle sponge with two sizes of spicules (oxeas). The large spicules are 0.1 mm in diameter and occur separately or in bundles. The space between the larger specules (0.4–0.5 mm) is filled with sub-parallel small spicules with maximum length of 0.15 mm. These small spicules align in radiate format in the lower part of the sponge, and cross each other in the upper part of the sponge.

Holotype. – Sample no. MN6-45004, housed at NIGPAS.

Description. – There are six specimens in all: MW2-43111; 45147; 42265; MQA-45078a; MQA-45078b; MN5-1115. All the specimens are flattened and preserved as mould or impression. MN6-45004; MW2-43111; 42265 are better preserved in front with low conical shapes of 15–35 mm in height and 15–26 mm width. The skeleton is made of radiated spicules. The adhesion part of the sponge looks like a stalk and is about 1 mm in width. The spicules radiate from the stalk like an outstretched brush.

MN6-45004 is well preserved with a round shape and a diameter of 16–21 mm. The skeleton is made up of monaxons whose ends are acuate. However, the complete single spicules are difficult to discern because they are embedded in the dense spicule thatch. These spicules are 1.2–2.1 mm in length, mostly 2 mm, and 0.008–0.01 mm in diameter, with a maximum diameter of 0.015 mm. These spicules are preserved in limonite. Some spicules form tufts which radiate outside and cross each other near the outer part of the sponge. But no coronal fringe formed. The tufts are 4.8–6 mm in length and 0.05–0.2 mm in width with spaces of about 0.4–0.5 mm. There are about 4–6 spicules in one tuft. These spicules are spliced with each other. So the skeleton is three-dimensional.

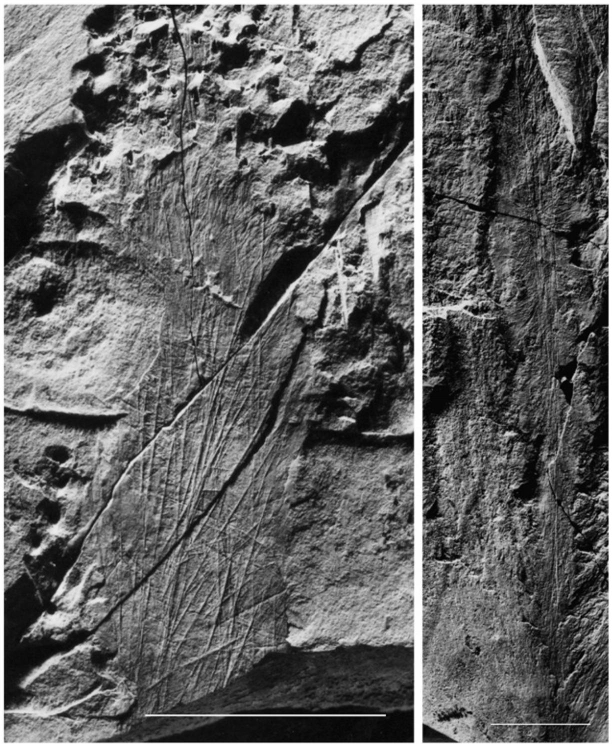

Fig. 7. *Ischnspongia dendritica* n.g. et sp. 1. M2-45116. 2. 1119a. Scales in 1 = 2 cm, 2 = 1 cm.

The middle part of some sponges is covered, possibly by the adhesive stalk.

Etymology. – 'Chengjiang' is the locality name, the specimens are collected from Chengjiang.

Discussion. – The species is similar to *Hamptonia bowerbanki* not only in spicule type, but also in the format of the skeleton. However, the specimen from the Chengjiang Fauna is small in size. The diameters of its spicules are bigger than in the type species. Moreover, the other data of the characters also indicate smaller dimensions than in the type species.

This species also resembles representatives of *Choia*, which both have two type spicules radiating from the centre. However, the latter has an obvious coronal fringe, so it is easy to distinguish them.

This new species is also similar to species of *Hazelia*. But their spicule tufts are different. The latter has a crossed tuft not only in the middle part of the sponge but also in its outer part. However, the former has a crossed tuft only in the outer part of the sponge.

Compared with *Choiaella*, the specimen has two sizes of spicules and an obvious tuft. However, the latter has spicules of only one size, and the possible "tuft" is only an artefact of preservation due to flattening.

The difference between *Hamptonia* and *Allantospongia* is that the latter has a coronal fringe. In addition, the body of *Allantospongia* shows three distinct parts that do not exist in the former.

Locality. – Xiaolantian section, Chengjiang, Yunnan, Yu'anshan Formation.

Class Hexactinellida Schmidt, 1870

Order Lyssacinosida Zittel, 1877

Family uncertain

Genus *Cystospongia* gen. nov.

Type species. – *Cystospongia globose* gen. et sp. nov.

Diagnosis. – Small, rounded and thin-walled sponge with round and low conical mounds on the surface. The spicules align irregularly around the mounds. There are some stauractins or triaxons between the mounds. The osculum is made up of monaxons, which align in parallel and form the coronal fringe.

Discussion. – Chen et al. (1996) included similar sponge individuals in the Demospongiae under the genus name of *Crumillospongia* due to the similar rounded or elliptical mounds. However, *Crumillospongia* is made up of monaxons, and there are no stauractins or triaxons in the space between the mounds. We found the faint impression of the staurectins in the Chengjiang specimens. Similar triaxons are also found in the specimens from Guizhou Province (Yang and Zhao, 2000). Accordingly, it seems that the sponge should be assigned to the Family Hydnodictyidae. However, Hydnodictyidae are cone-shaped and occurred in the Ordovician. Moreover, this sample was rounded after flattening. So the new genus is temporarily assigned here to the Order Lyssacinoskida.

Etymology. – 'cysto' [Gr.], vesicle-like.

***Cystospongia globosa* gen. et sp. nov.**

(Figs. 6A, 6C–D, 8A–F).

Diagnosis. – Small, rounded and thin-walled sponge with rounded basement and rounded low conical mounds on the surface. The diameter of these mounds is 0.8–1.2 mm. The monaxons running in irregular directions constitute the skeleton of the sponge. Staurectins or triaxons appear between the spaces of the mounds. The osculum is made up of monaxons, which align in parallel and form the coronal fringe. No obvious attachment.

Holotype. – Sample no. MN5-1127, housed at NIGPAS.

Material. – There are 22 specimens in all: MN5-1123; MW2-1124; MW2-1125; MQA-1126; MN5-1127; MQA1-1128; MN6-1129; MN5-1130; 1131; MN5-1132; MN6-1133; MQ1-41037; MN5-41122; MW2-42470; ME6-41157; MQ1-41126; MQA1-41104; MW2-42469; MN5-1134; ME6-11; ME6-41952; MN5-1135.

Description. – All the specimens are rounded after flattening, with diameters of 6–14 mm, mostly about 10 mm and preserved in half-relief. The osculum is preserved only in MN5-1123 and MN5-1127. The osculum of MN5-1123 is nearly rounded, with a diameter of 2.5 to 2.9 mm, so it can be assumed that the specimen is flattened from the upper direction with a little deflection, and the osculum of the specimen is rounded. The osculum is supported by monaxons, which align parallel to the axial of the sponge and, brush-like, form the coronal fringe. These spicules are 0.5–0.8 mm in length and 0.02 mm in diameter.

MW2-1124a and MW2-1124b are well preserved with diameter of 11.5–13.5 mm. They are part and counterpart. The mounds on the sponge surface, which are the typical character of this genus, are 0.8–1.2 mm in diameter and 0.1–0.2 mm in height. The dark-coloured space between the mounds contains some monaxons with diameters of 0.05–0.08 mm. There are also some faint impressions of staurancts between the spaces of the mounds.

Etymology. – 'globose' means the sponge may be a ball-like sponge after restoration.

Discussion. – *Cystospongia globosa* is similar to *Parvulonoda* (Rigby and Hou, 1995). However, there are no definite spicules in the latter genus. Moreover, its body is conical with hook-like nodes. This species is also similar to *Sentinelia draco*. However, there are some parietal gaps scattered over the surface, and its skeleton consists of monaxons.

The new species is similar to *Crumillospongia* as well; both have rounded or elliptical mounds. However, the skeleton of *Crumillospongia* is made up of monaxons. Moreover, *Crumillospongia frondosa* is larger than the present species and has two kinds of mounds. Yang (2002) also described triaxons in the specimens from Guizhou.

Locality. – Xiaolantian section, Chengjiang, Yunnan, Yu'anshan Formation.

Order Reticulosa Reid, 1958

Family Hydnodictyidae Rigby, 1971

Genus Valospongia Rigby, 1983

Valospongia* cf. *gigantis Rigby, 1983

(Figs. 6E, 9)

Diagnosis. – Large, keg-shaped, thin-walled sponge with numerous low, round mounds of two general sizes over the entire surface. Skeleton net hexactin-based, but with irregular orientation as in Hydnodictyidae,

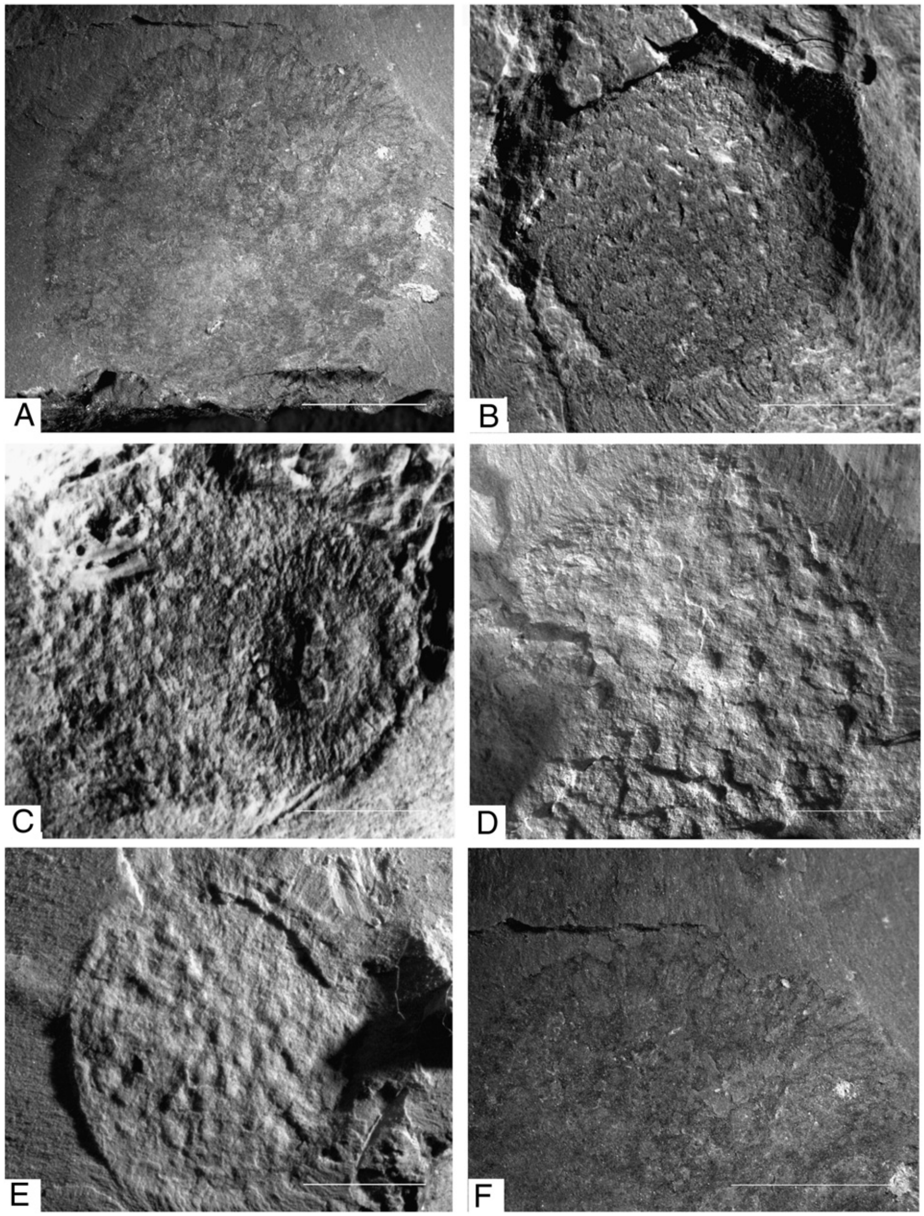

Fig. 8. *Cystospongia globosa* n.g. et sp. A. holotype MN5-1127. B. MQA1-1128. C. MN5-1123. D. MN5-1125. E. MW2-1124a. F. Enlargement of the specimen MN5-1127 showing the osculum. Scales in 1–2 = 3 mm, 3 = 2 mm, 4 = 3 mm, 5 = 5 mm, 6 = 3 mm.

with various sizes of spicules whose rays range from 0.3 mm up to several centimetres long, all with basal rays only a few tenths of a millimetre in diameter, even in the large spicules. Main spicule rays are in the interior part of the wall and do not arch over mounds. Mound skeleton with smaller, diagonally oriented spicules.

Material. – There is only one specimen, part and counterpart: No. 1136a and 1136b.

Description. – The specimens are weathered and the sponge is flattened. The spicules are faint and preserved as mould or impression. However, some monaxons and triaxons can be recognized.

The sponge body is column-shaped with a preserved height of 70 mm and maximum width of 41 mm. The counterpart is 77.4 mm in height and 47 mm in width. No osculum and basal part can be observed, nor any obvious marginalia. On the surface of the sponge, there are many rounded or elliptical low mounds with two different sizes. These mounds extend along the axial of the sponge. The peripheries of the mounds are smooth and have distinct margin. The big mounds are 4–5 mm in diameter and aligned irregularly. The distance between the mounds is 2–3 mm. The small mounds occur between the spaces of the big mounds with diameters of 0.8–1.8 mm. The space of the small mounds is 1–3 mm. These mounds cannot be regarded as parietal gaps on the surface of the sponge because of the spicule impressions in the mounds.

The skeleton is composed of two kinds of spicules. The first type has large spicules (possibly triaxons); however, the centres of these spicules cannot be seen. They are 2.2–3.0 mm in length and 0.1–0.15 mm in diameter at the basal part of the ray. These spicules are preserved as mould. The spicules cross each other in horizontal and longitudinal directions, forming rectangles. The rays of the spicules seem to change direction at the edge of the mound and are arranged in tangential direction. The second type of spicules is the stauractins (?), which are distributed between the mounds. Their rays are 0.3–0.6 mm long, and the diameter of the basal part of the rays is 0.03–0.05 mm. They are arranged diagonally to the axis of the sponge.

Discussion. – The specimens are similar to the type species in the characters of the skeleton and mound. However, the specimens are smaller than the type species, which is 173 mm in height with better preserved skeleton and osculum. The specimen of Chengjiang fossil

Fig. 9. *Valospongia* cf. *gigantis* Rigby, 1983, 1136a. Scale = 1 cm.

lagerstätte is not fully preserved, and the skeleton in the mounds is not clear. Therefore, it is assigned to the species with some doubts.

Valospongia is also easily confused with *Ratcliffespongia* Rigby (1969). However, there are clear elliptical parietal gaps on surface of the sponge and no distinct mounds in the latter, while the former has rounded mounds.

Valospongia, *Hintzespongia* and *Teganium* are all based on triaxons, not on monaxons. However, there is no low mound on the surface of *Teganium*. The skeleton of *H. bilamina* has two layers.

Locality. – Xiaolantian section, Chengjiang, Yunnan, Yu'anshan Formation.

References

Ausich, W.I., Bottjer, D.J., 1982. Tiering in suspension-feeding communities on soft substrate throughout the Phanerozoic. Science 216, 173–174.

Ausich, W.I., Bottjer, D.J., 2003. Sessile invertebrates. In: Briggs, D.E.G., Crowther, P.R. (Eds.), Palaeobiology II. Blackwell, Oxford, pp. 384–386.

Bottjer, D.J., Ausich, W.I., 1986. Phanerozoic development of tiering in soft substrate suspension-feeding communities. Paleobiology 12, 400–420.

Caron, J.B., Jackson, D.A., 2008. Paleoecology of the Greater Phyllopod Bed community, Burgess Shale. Palaeogeography, Palaeoclimatology, Palaeoecology 258, 222–256.

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

Chen, J., Hou, X., Lu, H., 1989. Lower Cambrian leptomitids (Demospongea), Chengjiang, Yunnan. Acta Palaeontologica Sinica 28 (1), 17–30 (In Chinese with English abstract).

Chen, J., Hou, X., Li, G., 1990. New Lower Cambrian demosponges—*Quadrolaminiella* gen. nov. from Chengjiang, Yunnan. Acta Palaeontologica Sinica 29 (4), 402–414 (In Chinese with English abstract).

Chen, J., Zhou, G., Zhu, M., Yeh, G., 1996. The Chengjiang Biota: A Unique Window of the Cambrian Explosion. National Museum of Natural History, Taichung, China (222 pp.).

Clapham, M.E., Narbonne, G.M., 2002. Ediacaran epifaunal tiering. Geology 30 (7), 627–630.

Conway Morris, S., 1986. The community structure of the Middle Cambrian Phyllopod Bed (Burgess Shale). Palaeontology 29, 423–468.

Conway Morris, S., 1993. The fossil record and the early evolution of the Metazoa. Nature 361 (6409), 219–225.

Dornbos, S.Q., Bottjer, D.J., Chen, J., 2005. Paleoecology of benthic metazoans in the Early Cambrian Maotianshan Shale Biota and the Middle Cambrian Burgess Shale Biota: evidence for the Cambrian substrate revolution. Palaeogeography, Palaeoclimatology, Palaeoecology 220, 47–67.

Dunne, J.A., Williams, R.J., Martinez, N.D., 2008. Compilation and network analyses of Cambrian food webs. PLoS Biology 6 (4), E102. http://dx.doi.org/10.1371/Journal.Pbio.0060102.

Gray, J.E., 1867. Notes on the arrangement of sponges, with the description of some new genera. Proceedings of the Scientific Meetings of the Zoological Society of London 1867, 492–558.

Hou, X., Bergström, J., Wang, H., Feng, X.H., Chen, A., 1999. The Chengjiang Fauna: exceptionally well-preserved animals from 530 million years ago. Yunnan Science and Technology Press, Kunming. China (170 pp.).

Hu, J., Chen, Z., Xue, Y., Wang, J., Wang, J., Yuan, X., 2002. Sponge spicules in Early Cambrian Hetang Formation, Xiuning, Southern Anhui. Acta Micropalaeontologica Sinica 19 (1), 53–62 (In Chinese with English abstract).

Mehl, D., 1988. Porifera and chancelloriidae from the Middle Cambrian Georgina Basin, Australia. Palaeontology 41 (6), 1153–1182.

Mehl, D., Erdtmann, B.D., 1994. *Sanshapentella dapingi* n. gen., n. sp. — a new hexactinellid sponge from the Early Cambrian (Tommotian) of China. Berliner Geowiss. Abh E 13, 315–319.

Mehl-Janussen, D., 1999. Die frühe evolution der Porifera.- Münchner Geowiss. Abh. Reihe A 37, 1–72.

Reid, R.E.H., 1958. A monograph of the Upper Cretaceous Hexactinellida of Great Britain and Northern Ireland. Part I. Monographs, 111. Palaeontographical Society, pp. i–xlvi.

Reiswig, H.M., 2002. Class Hexactinellida Schmidt, 1870. In: Hooper, J.N.A., an Soest, R.W.M.V. (Eds.), A Guide to the Classification of Sponges. Kluwer Academic/Plenum Publishers, New York, pp. 1201–1202.

Rigby, J.K., 1966. *Protospongia hicksi* Hinde from the Middle Cambrian of western Utah. Journal of Paleontology 40 (3), 549–554.

Rigby, J.K., 1969. A new Middle Cambrian hexactinellid sponge from western Utah. Journal of Paleontology 43 (1), 125–128.

Rigby, J.K., 1971. Sponges of the Ordovician Cat Head Member, Lake Winnipeg, Manitoba. In: McGregor, D.C., Cramer, F.H., Flower, Rousseau H., Rigby, J.K. (Eds.), Contributions to Canadian Paleontology, Fossils of the Ordovician Red River Formation (Cat Head Member), Manitoba. Geological Survey of Canada Bulletin, 202, pp. 35–78. 6 pl.

Rigby, J.K., 1978. Porifera of the Middle Cambrian Wheeler Shale from the Wheeler Amphitheater, House Range, in Western Utah. Journal of Paleontology 58, 1005–1012.

Rigby, J.K., 1980. The new Middle Cambrian sponge *Vauxia magna* from the Spence Shale of northern Utah and taxonomic position of the Vauxildae. Journal of Paleontology 54 (1), 234–240.

Rigby, J.K., 1983. Sponges of the Middle Cambrian Marjum Limestone from the House Range and Drum Mountains of western Millard Country, Utah. Journal of Paleontology 57 (2), 240–270.

Rigby, J.K., 1986. Sponges of the Burgess Shale (Middle Cambrian), British Columbia. Paleontographica Canadiana 2, 1–105.

Rigby, J.K., Chruch, S.B., 1990. A new Middle Cambrian hexactinellid, *Ratcliffespongia wheeleri*, from western Utah, and skeletal structure of *Ratcliffespongia*. Journal of Paleontology 64, 331–334.

Rigby, J.K., Hou, X.-G., 1995. Lower Cambrian demosponges and hexactinellid sponges from Yunnan, China. Journal of Paleontology 69, 1009–1019.

Rigby, J.K., Collins, D., 2004. Sponges of the Middle Cambrian Burgess Shale and Stephen Formations, British Columbia. ROM contributions in Science 1, 1–155.

Rigby, J.K., Gutschick, R.C., 1976. Two new Lower Paleozoic hexactinellid sponges from Utah and Oklahoma. Journal of Paleontology 50 (1), 79–85.

Rigby, J.K., Gunther, L.G., Gunther, F., 1997. The first occurrence of the Burgess Shale demosponge *Hazelia palmata* Walcott, 1920, in the Cambrian of Utah. Journal of Paleontology 71 (6), 994–997.

Rigby, J.K., Church, S.B., Anderson, N.K., 2010. Middle Cambrian sponges from the Drum Mountains and House Range in western Utah. Journal of Paleontology 84 (1), 66–78.

Robison, R.A., 1991. Middle Cambrian biotic diversity: examples from four Utah Lagerstätten. In: Simonetta, A.M., Conway Morris, S. (Eds.), The Early Evolution of Metazoa and Significance of Problematic Taxa. Cambridge University Press, pp. 77–98.

Steiner, M., Mehl, D., Reitner, J., Erdtmann, B.D., 1993. Oldest entirely preserved sponges and other fossils from the lowermost Cambrian and a new facies reconstruction of the Yangtze Platform (China). Berliner Geowiss. Abh. (E)9, 293–329.

Wu, W., 2004. Fossil sponges from the early Cambrian Chengjiang Fauna, Yunnan, China. Doctoral Dissertation Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing, China (190 pp., In Chinese with English abstract).

Wu, W., Yang, A., Janussen, D., Steiner, M., Zhu, M., 2005. Hexactinellide sponges from the Early Cambrian black shale of South Anhui, China. Journal of Palaeontology 79 (6), 1043–1051.

Xiao, S., Hu, J., Yuan, X., Parsley, R.L., Cao, R., 2005. Articulated sponges from the lower Cambrian Hetang Formation in southern Anhui, South China: their age and implications for the early evolution of sponges. Palaeogeography, Palaeoclimatology, Palaeoecology 220, 89–117.

Yang, X., 2002. Cambrian Sponge (attach: Chancelloriids) of Guizhou. Master Thesis Guizhou Industrial University, Guiyang, China (92 pp.).

Yang, X., Zhao, Y., 2000. Sponges of the Lower Cambrian Niutitang Formation Biota in Zunyi, Guizhou, China. Journal of Guizhou University of Technology (Natural Science Edition) 29 (6), 30–36.

Yang, X., Zhao, Y., Zhu, M., 2005a. New sponges from the Lower Cambrian of Guizhou. Acta Palaeontologica Sinica 44 (3), 454–463 (In Chinese with English abstract).

Yang, X., Zhu, M., Zhao, Y., Wang, Y., 2005b. Cambrian sponge assemblages from Guizhou. Acta Micropalaeontologica Sinica 22, 295–303 (In Chinese with English abstract).

Yang, X., Zhao, Y., Zhu, M., Cui, T., Yang, R., 2010. Sponges from the Early Cambrian Niutitang Formation of Danzhai, Guizhou and their environmental background. Acta Palaeontologica Sinica 49, 348–359 (In Chinese with English abstract).

Yuan, X., Xiao, S., Parsley, R.L., Zhou, C., Chen, Z., Hu, J., 2002. Towering sponges in an Early Cambrian Lagerstätte: disparity between nonbilaterian and bilaterian epifaunal tierers at the Neoproterozoic–Cambrian Transition. Geology 30 (4), 363–366.

Zhao, Y., Zhu, M., Babcock, L.E., Yuan, J., Parsley, R.L., Peng, J., Yang, X., Wang, Y., 2005. Kaili Biota: a taphonomic window on diversification of metazoans from the basal Middle Cambrian: Guizhou, China. Acta Geologica Sinica 79, 751–765 (In Chinese with English abstract).

Zhao, F., Zhu, M., Hu, S., 2010. Community structure and composition of the Cambrian Chengjiang Biota. Science in China (Earth Sciences) 53, 1784–1799.

Zhu, M., Zhang, J., Li, G., 2001. Sedimentary environments of the Early Cambrian Chengjiang Biota: sedimentology of the Yu'anshan Formation in Chengjiang County, eastern Yunnan. Acta Palaeontologica Sinica 40, 80–105 (Sup., In Chinese with English abstract).

Zittel, K.A., 1877. Studien über fossile Spongien. I: Hexactinellidae. Abhandlungen der Mathematisch-Physikalischen Classe der Königlich-Bayerischen Akademie der Wissenschaften. München 13 (1), 1–63.