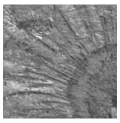
Taphonomy of Cambrian (Stage 3/4) sponges from Yunnan (South China)

ANGELA FORCHIELLI, MICHAEL STEINER, SHIXUE HU & HELMUT KEUPP



Sponges are one of the major faunistic components of the Burgess Shale-type fossil *Lagerstätte* of Chengjiang (Cambrian Stage 3, South China). Although pyritization is often invoked as a key process linked to the early diagenetic preservation in the Chengjiang Fauna, the unweathered specimens analyzed lack evidence of pyrite. Energy dispersive X-ray (EDX) analyses of these specimens show a robust and continuous film of organic carbon. Most of the Chengjiang sponges underwent extensive weathering and diagenetic alteration. The biogenic silica transformed in opal-CT (crystalline type) was dissolved leaving a cavity, successively filled by different minerals, or possibly underwent dissolution under acidic water conditions combined with oxygenation. This resulted in clay and iron oxide replication (framboids or micro-sized crystals) of the sponge spicules. Organic material of the original cellular layer is preserved as depleted organic carbon film. • Key words: taphonomy, sponges, Cambrian, Chengjiang, Yunnan Province.

FORCHIELLI, A., STEINER, M., HU, S.X. & KEUPP, H. 2012. Taphonomy of Cambrian (Stage 3/4) sponges from Yunnan (South China). *Bulletin of Geosciences 87(1)*, 133–142 (7 figures). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received September 12, 2010; accepted in revised form October 10, 2011; published online February 21, 2012; issued February 29, 2012.

Angela Forchielli, Michael Steiner & Helmut Keupp, Freie Universität Berlin, Malteserstraße 74-100 Haus D, 12249 Berlin; afor@zedat.fu-berlin.de, michael.steiner@fu-berlin.de, keupp@zedat.fu-berlin.de • Shixue Hu, Chengdu Institute of Geology and Mineral Resources, 610081 Chengdu, China; hushixue@hotmail.com

Burgess Shale-type preservation is defined as the "exceptional" preservation of non-mineralizing organisms as carbonaceous compressions in marine siliciclastic sediments (Butterfield 1995). The Chengjiang Fauna represents a taxonomically, temporally and spatially specific case of a Burgess Shale-type Fauna (Steiner *et al*. 2005).

In this work we analyzed four Burgess Shale-type fossil associations from several palaeogeographic settings in order to investigate the possible influence of facies on their taphonomic pathways. We compared the classical Chengjiang Fauna of Yunnan Province to fossils from the Guanshan Fauna (*ca* Cambrian Stage 4; Yunnan Province), the Chengjiang-type Fauna from Zunyi (Cambrian Stage 3; Guizhou Province) and the Sancha Fauna from Hunan Province (*ca* Cambrian Stage 3). The Canglangpuan sediments yielding the Guanshan Fauna (north-west of Kunming, Yunnan Province) were deposited as event beds in shallow water environments (Luo *et al*. 2008, Hu *et al*. 2010a). The event cycles may be interpreted as Bouma sequences A and B during the deposition of Wulongqing Formation (Canglangpuan Stage, Cambrian Series 2; Luo *et al*. 2008). Luo *et al*. (2008) demonstrated also that it is possible to obtain exceptional soft-bodied preservation in shallow water environments, under the influence of strong bioturbation and reworking. This hypothesis is supported also by Hu *et al*. (2010) and by our dataset and personal field observations in the Gaoloufang section at Guangwei Village near Kunming. This section shows an exceptionally well preserved Guanshan Fauna: trilobites with antennae preserved, worms (Hu *et al*., this volume), brachiopods with soft part preserved (Hu *et al*. 2010b and personal unpublished data), vetulicolids, lobopodians (Steiner *et al*., this volume) together with strongly bioturbated beds and trace fossils (Weber *et al*., this volume). Similar data are reported also by Liu *et al*. (this volume) for the same fauna, but in another section. The Chengjiang fossil *Lagerstätte* is characterized by couplets of background beds (BGB) and event beds (EB). BGBs are absent in the fossil *Lagerstätte* of the Guanshan (Fig. 1). At Zunyi, green claystones and yellowish siltstone are present. Here the EBs are thinner and rarer than those of the Chengjiang fossil *Lagerstätte*. The Chengjiang-type Fauna of Zunyi, dominated by arthropods (92%) and sponges (6%) is found at the base of green claystones (Steiner *et al*. 2005). The Sancha Fauna was described by Steiner *et al*. (1993) from black shales of the upper Niutitang Formation in the northern Hunan Province. Sponge communities are dominant in this deep water association, in contrast to the arthropod-dominated associations of shallow water (Steiner *et al*. 2005). The association of the Chengjiang Fauna is dominated by arthropods

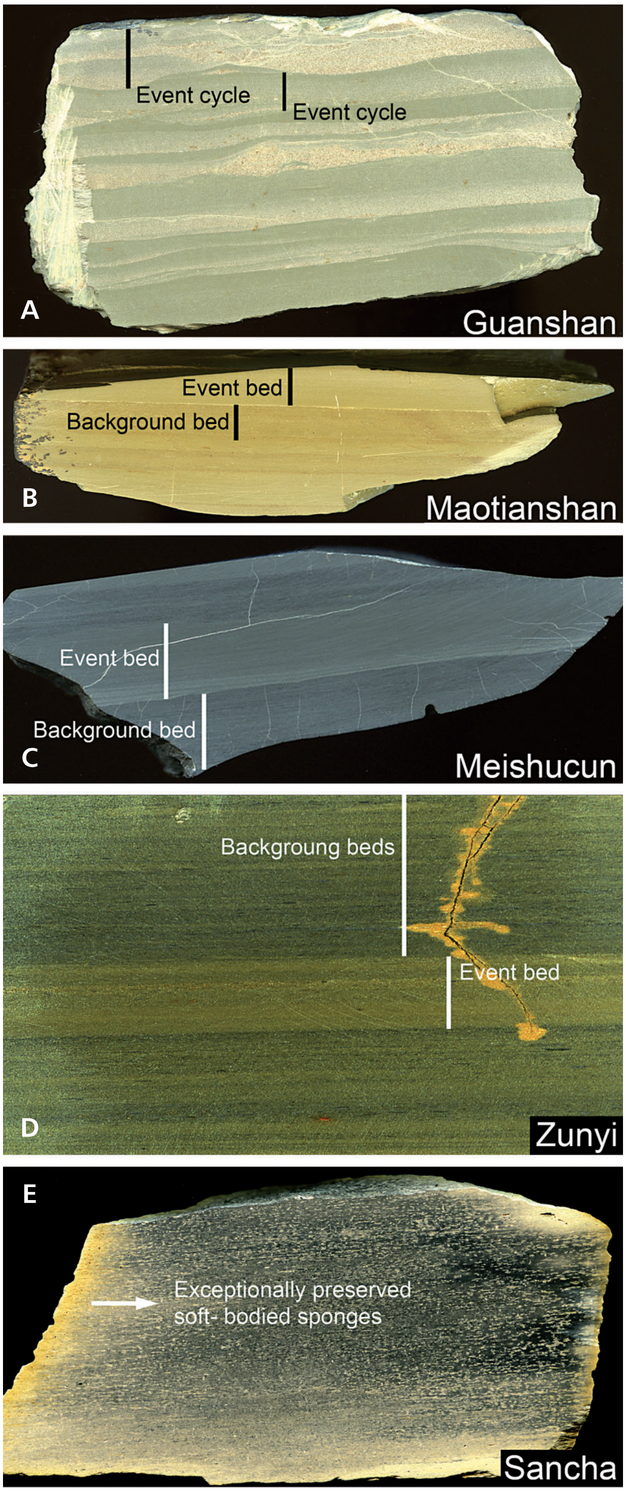


Figure 1. Sedimentology of earliest Cambrian outcrops. Couplets of event beds (EB), background beds (BGB) and event cycle are shown. • A – shallow water deposition of the Guanshan fossil *Lagerstätte*. • B – Maotianshan (Chengjiang County) weathered material from the Chengjiang fossil *Lagerstätte*. • C – Meishucun (Jinning County), unweathered material from the Chengjiang fossil *Lagerstätte*. • D – single thin event bed and massive background beds from the Zunyi fossil *Lagerstätte* (Guizhou Province). • E – deeper water environment of the Sancha fossil *Lagerstätte*.

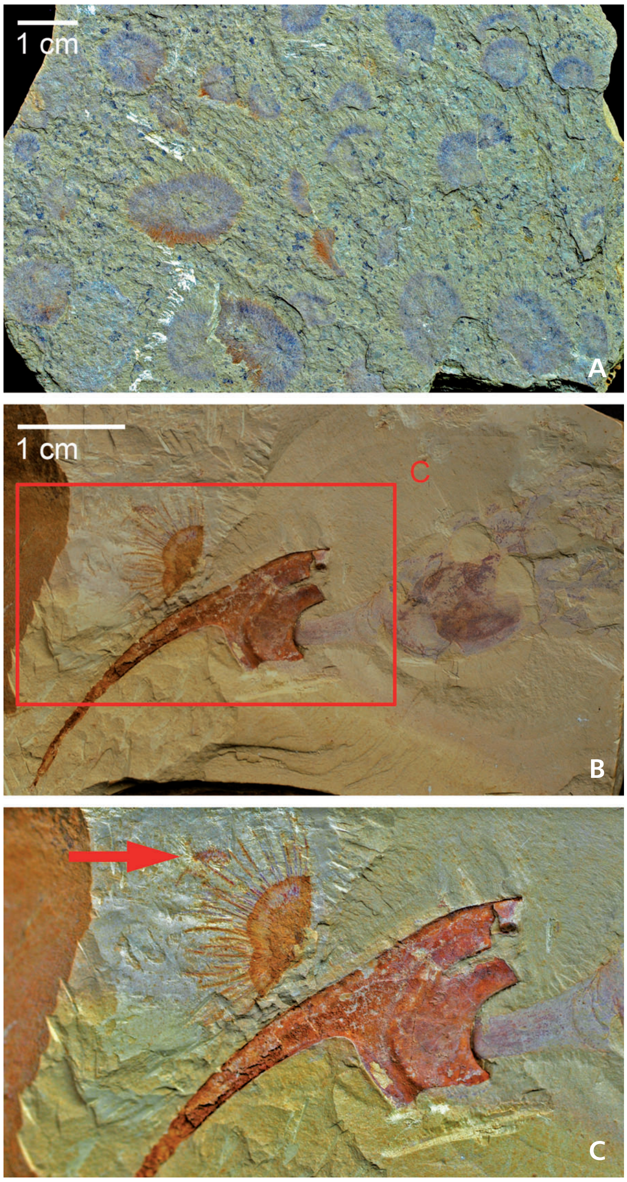


Figure 2. Disparities in sponge preservation. • A – sponge assemblage in background bed. • B – *Choia* sp. preserved in an event bed with soft-bodied preservation of *Phlogites* sp. Frame is enlarged in C. The arrow shows two juveniles attached to the spicule of an adult.

and sponges. In Chengjiang fossil *Lagerstätte* sponges compose more than 8% (individuals) of the Chengjiang Fauna (Hu 2005; table 1 in Zhao *et al.* 2009), with 15 genera and 30 species among demosponges and hexactinellids (Li *et al*. 1998). Here and during previous analysis (Hu 2005), we recognized a significant disparity in sponge preservation in BGBs and EBs (Fig. 2). Sponges are normally preserved in the background beds, associated with organic hash, coprolites ("algae") and disarticulated skeletal material. Sponges are usually missing or extremely rare in EBs (Appendix 2 in Hu 2005). In contrast, sponges are a major faunistical component in BGBs (Hu 2005, Steiner *et al.*

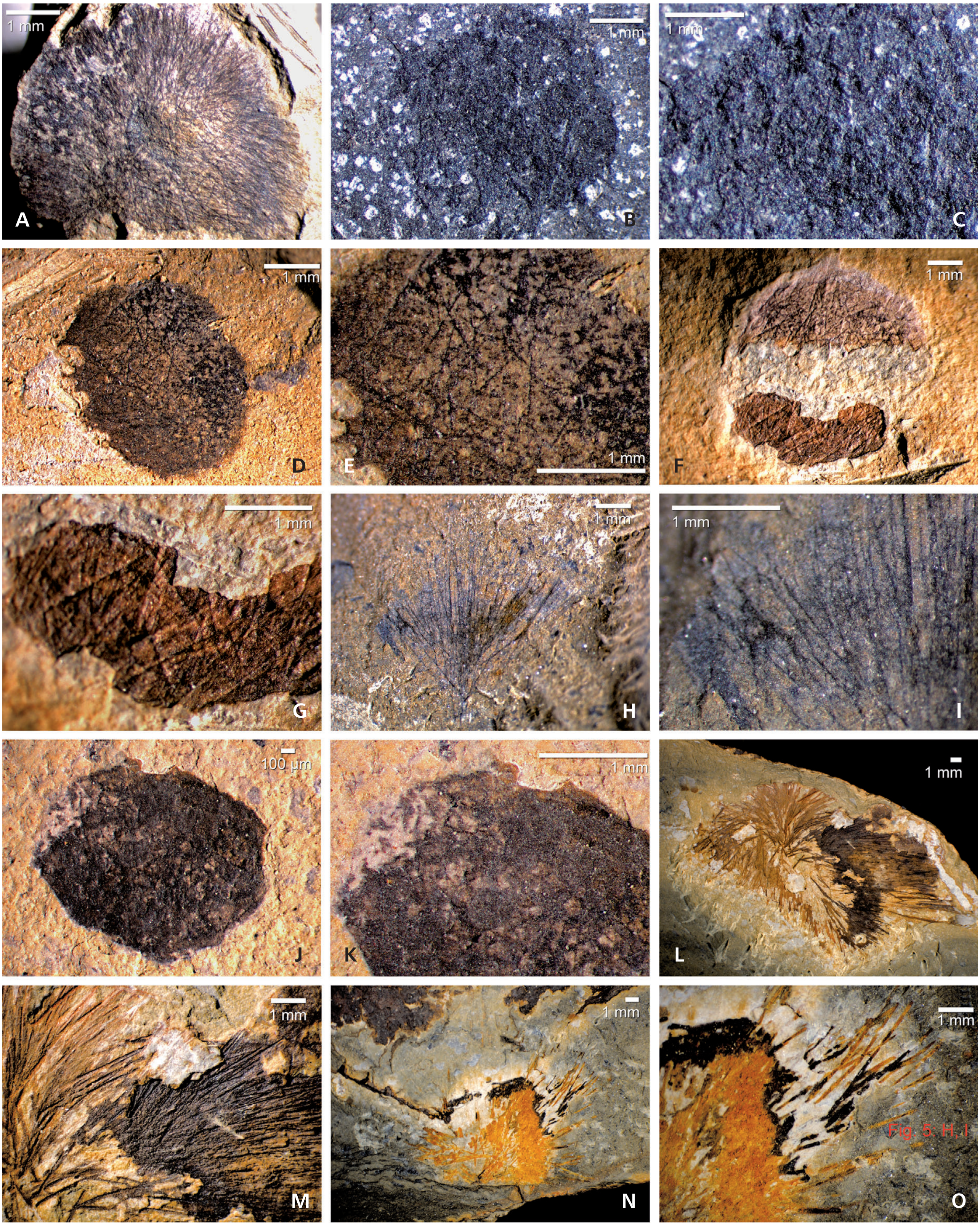


Figure 3. Analyzed material. • A – *Choiaella* sp. (K37 0924). • B, C – *Triticispongia* sp. (MEI 2 0829) from Meishucun, Jinning County. • D, E – *Triticispongia* sp. (Xlt-a-82) from Xiaolantian, Chengjiang County. • F, G – *Triticispongia* sp. (Xlt-a-262) from Xiaolantian, Chengjiang County. • H, I – *Triticispongia* sp. (Y24 017) from Zunyi, Guizhou Province. • J, K – *Triticispongia* sp. (ERC 0841b) from Ercaicun, Haikou County. • L, M – *Choia* cf. *utahensis* Walcott, 1920 (Y24 065B) from Zunyi, Guizhou Province. • N, O – *Choia* cf. *utahensis* Walcott, 1920 (Y24 066) from Zunyi, Guizhou Province.

2005). The few articulated sponges known from event beds belong to the Choiidae (*Choia* sp. Wu 2004, fig. 5.1) and to a questionable demosponge group related to the hazeliidae (Mehl 1999); *Leptomitus* sp. (Hou *et al*. 2004, fig. 8.7) and Wu (2004, fig. 4.4); *Leptomitella* sp. (Wu 2004, fig. 3.7); *Paraleptomitella* sp. (Hou *et al*. 2004, fig. 8.10). Taphonomic bias might be responsible for the different preservation of skeletonized metazoans, such as sponges, in EBs and BGBs. Recently Zhao *et al*. (2009) improved the statistical analysis of faunal components in EBs and BGBs of Chengjiang deposits. These data also support the existence of preservational disparities for sponges in the EBs and BGBs. Sponges only constitute the 0–1% of individuals in the EBs, which contrasts with 7.4% in BGBs (Hu 2005, Zhao *et al*. 2009). This preservational disparity might have been caused by: (1) a parautochthonus origin of the EBs where the fauna was transported from a slightly different environmental setting than the depositional site, which would suggest that the BGBs represent a deeper environment than EBs; (2) the EB fauna having been depleted of sponges indicating that the sponge communities had no time for recovery during more turbiditic intervals; or (3) a taphonomic bias. However, we found no evidence for the last hypothesis in this study. The evaluation of the ecological possibilities is beyond the scope of this study, but we currently favor local transport of sponges during EB deposition that differs in total biomass from the local fauna (represented by sponges in BGBs) as the most plausible cause for the disparity between depositional settings.

The environmental setting and the taphonomic preservation can influence the morphology of fossilized sponges. The bodies of the sponges of Chengjiang fossil *Lagerstätte* occur as various outlines, including spherical, radial, ellipsoidal, conical and sub-column shaped, with elevated variation in morphology and size (Hou & Bergström 2003). More or less complete sponges collected from the Cambrian, Stage 3 of China were described by Chen *et al*. (1989, 1990), Mehl & Reitner (*in* Steiner *et al*. 1993), Mehl & Erdtmann (1994) and Rigby & Hou (1995).

Silica is one of the primary minerals involved in the biomineralization of different taxa as in the modern times, so in the past. Modern siliceous sponges have a skeleton composed of siliceous spicules which are composed of amorphous silica. Each spicule has a central protein (silicatein) filament that triggers silica deposition (Müller *et al*. 2009, Shimizu *et al*. 1998). Such central filaments are also visible in some fossil sponge spicules of the earliest Cambrian Sancha Fauna from Hunan Province (Steiner *et al*. 2005).

This work aims to use material embracing the complete spectrum of weathering grade for the first time on the earliest Cambrian sponges of the South China in order to contribute to the understanding of their taphonomic pathways.

Material and methods

Material was collected from the Yu'anshan and Wulongqing formations of Yunnan Province (South China). Two more specimens, used for comparison were collected approximately 20 km W of Zunyi, northern Guizhou Province (South China). Specimens shown in Fig. 3 are stored at Freie Universität Berlin; specimen figured in Fig. 4 is also temporarily stored at Freie Universität Berlin, whereas specimens in Fig. 2 are stored at Yunnan Geological Survey, Kunming.

Elemental mapping was performed using an energy dispersive X-ray (EDX) Inca analyzer X-max 50 mm^2 coupled to a SEM ZEISS-SUPRA 40VP. Fossils were analyzed uncoated and unpolished using 15 kV voltages. The size of specimens varies from a few mm to 5 cm (Figs 3, 4).

Iron speciation analyses were done according to Poulton's sequential extraction procedure for iron (Poulton *et al*. 2004, 2005).

Results

No evidence of silicious spicules was found from material from either the Guanshan (Wulongqing Formation, lower part) or the Chengjiang faunas (Yuanshan Formation, Maotianshan Shale Member) neither from Yunnan Province nor from the Chengjiang-type Fauna from Zunyi, Guizou Province. The least weathered specimens from Zunyi, Guizhou Province contained iron and manganese oxides (Fig. 5H, I). Sponge specimens from the Chengjiang Fauna (Fig. 3B, C) showed a robust and continuous carbon film; iron minerals were rare and are present only outside the fossils. Gypsum was present in few samples indicating weathering (Fig. 5A–D). Element mapping analyses carried out on weathered specimens of the Chengjiang Fauna, revealed different results. Fossils were dissolved and replicated by clay minerals and iron oxides in the weathered material (Fig. 5E, F). Back scattered (BSD) images of *Paraleptomitella* sp. from the Guanshan Fauna (Wulongqing Formation) showed globular aggregates replacing the sponge spicules. EDX analyses carried out on different spicules (shown in Fig. 4B) showed different crystal associations. Examination of the negative imprint suggests that these were once framboids (Fig. 6D) that were replaced by a mixture of aluminosilicate, iron hydroxide and iron oxide (Fig. 6A, B, D). Elemental mapping carried out on several areas on this specimen did not expose any siliceous spicules (Fig. 5J–L). The iron oxide and hydroxide globular ag-

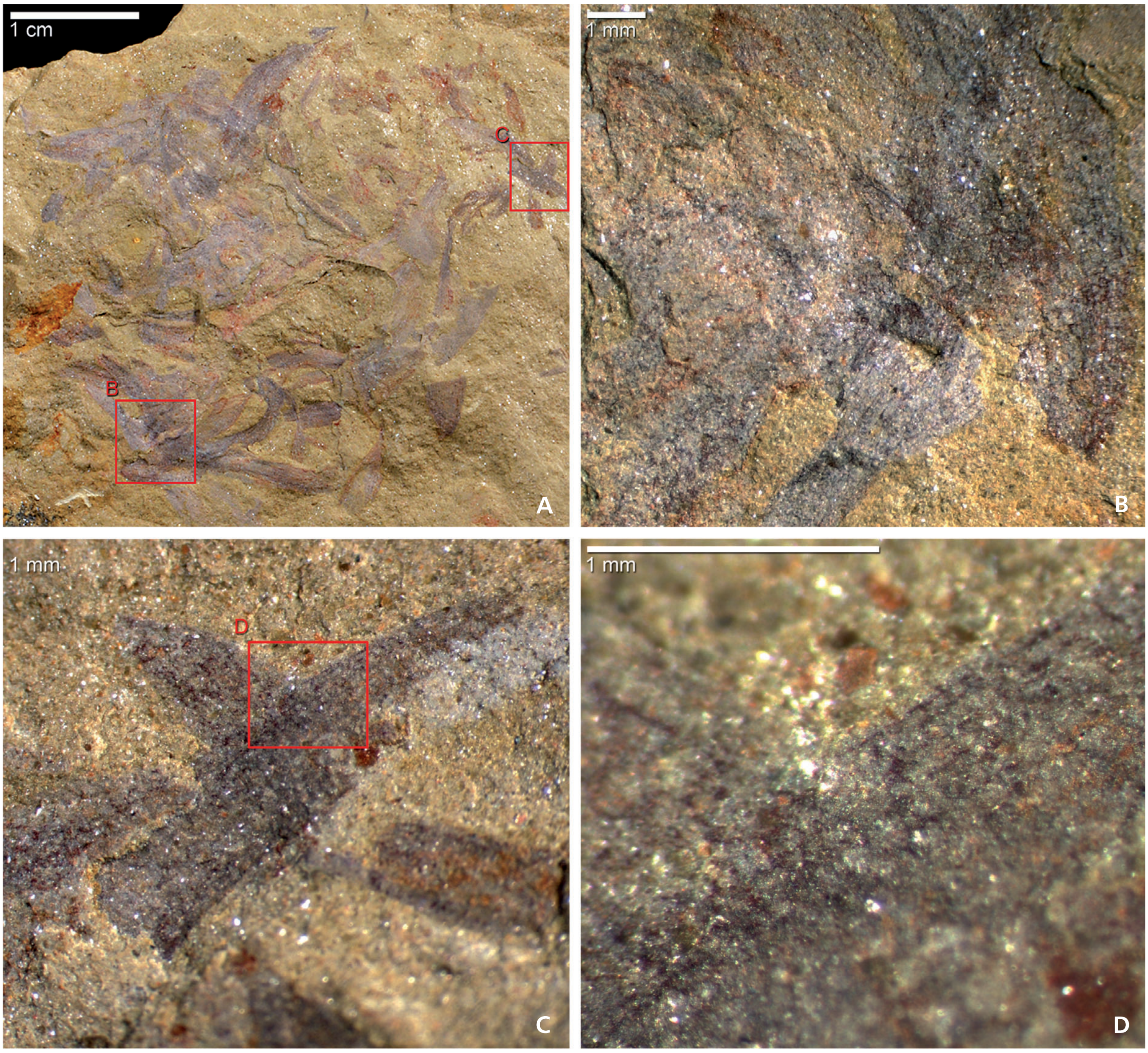


Figure 4. *Paraleptomitella* sp. from the Guanshan Fauna. • A – overview of the specimen, frames are enlarged in B and C. • D – close up of the frame in C.

gregates were rare and ranged in size from 8 μm to 10.5 μm. The iron oxide micro-sized single crystals of specimens from Zunyi in the northern Guizhou Province had similar dimensions. EDX analyses discerned differences in the elemental composition between the weathered (Fig. 7A, ERC 0841b) and unweathered (Fig. 7A, MEI 2 0829) sponges within the Chengjiang Fauna. The huge amount of carbon and the absence of iron indicated Burgess Shale-type preservation. The sulphur peak was related to gypsum. In Zunyi, where sponge spicules were replicated by iron oxides, single crystals and also manganese oxides formed during later weathering. The iron peak was relatively high, although the color of the sediment is suggestive of a lower weathering grade than the weathered Chengjiang material (Fig. 7B). In both sponge analyses from Chengjiang and Zunyi regions (Fig. 7) the silicon peak is related to the embedding clay matrix rather than to remnants of silicate spicules.

Iron speciation analyses performed on Chengjiang fossil *Lagerstätte* sediments from the Yunnan Province showed increasing content of the Fe_{ox} in yellow shale, which we interpret to represent weathered material. In contrast, this value was zero in the dark grey shales, which we interpreted as unweathered material. The opposite was observed in the trend of Fe_{py}. The ratios of reactive/total iron (FeHR/FeT) and pyritic/reactive iron (Fe_{py}/FeHR) were above 0.14 for almost all samples, and below 0.7 for all samples, respectively. Sponges were normally preserved in

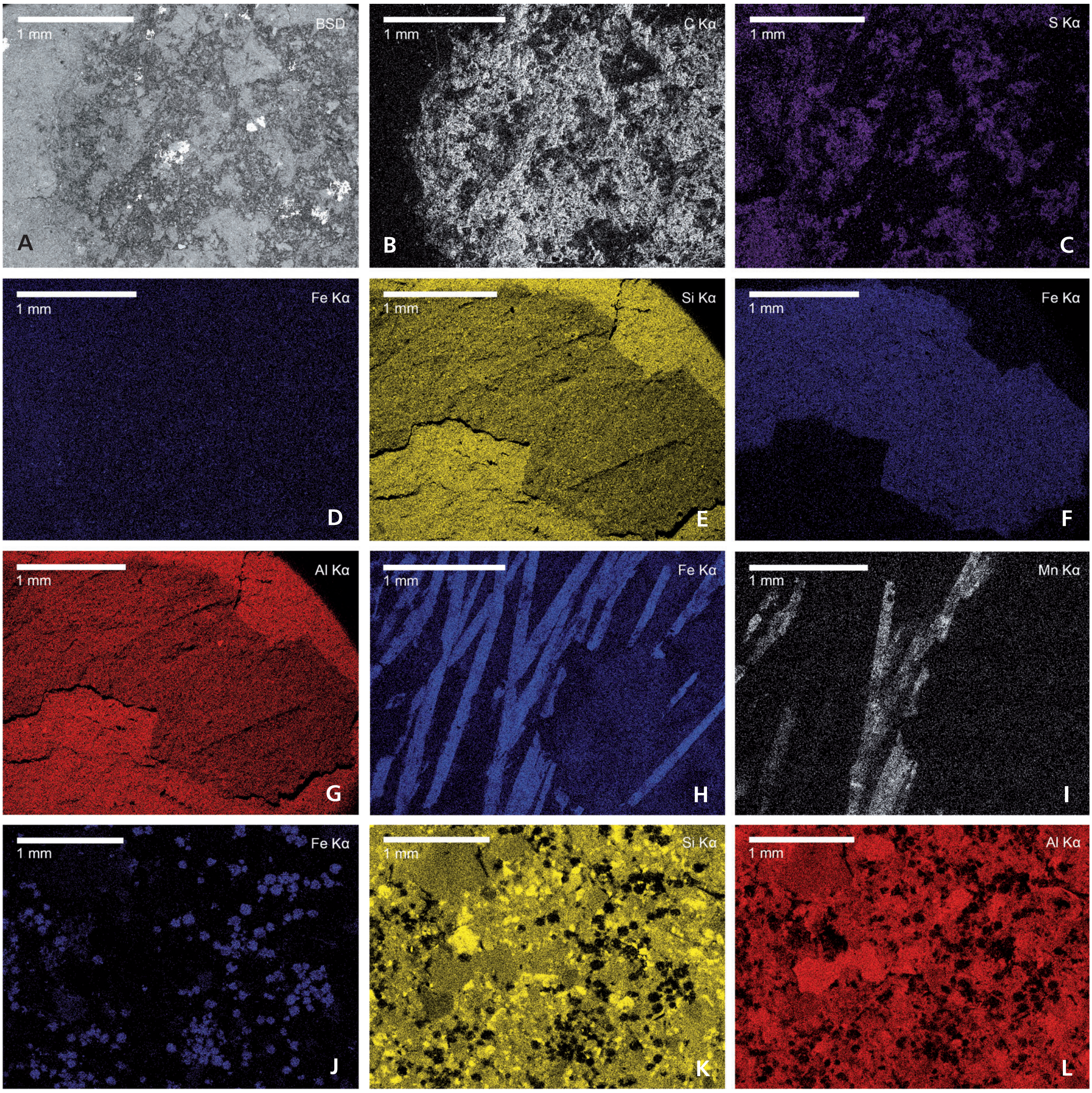


Figure 5. Elemental mapping analyses. • A–D – elemental mapping carried out on specimens B, C in Fig. 3. • E–G – elemental mapping of Fig. 3G. • H, I – elemental mapping of frame in Fig. 3O. • J–L – elemental mapping carried out on an enlarged area in Fig. 4C.

BGBs. Total organic carbon (TOC) values of unweathered samples in the Meishucun area for BGBs and EBs were 0.20% and 0.21%, respectively, while values of the weathered samples from the Ercaicun area were 0.13% for the BGBs and less than 0.10% for EBs. The sulphur (S) was 0.352% for the BGBs and 0.346% for EBs. Fe was 5.04% for BGBs and 4.74% for EBs. Analyses carried out on EBs of the Guanshan fossil *Lagerstätte* had TOC values below 0.10 %. Iron and sulphur percentages were 5.16% and below 0.01%, respectively.

Discussion

The results presented here are based on observations of sponges from different outcrops. Elemental mapping analyses were performed on specimens with a broad spectrum of weathering grades among the Chengjiang and Guanshan faunas and a few from the Zunyi (Figs 3, 4). The material comes from different palaeogeographic settings. The Guanshan and Chengjiang faunas from Yunnan and the Chengjiang-type Fauna from Guizhou represent nearshore shallow

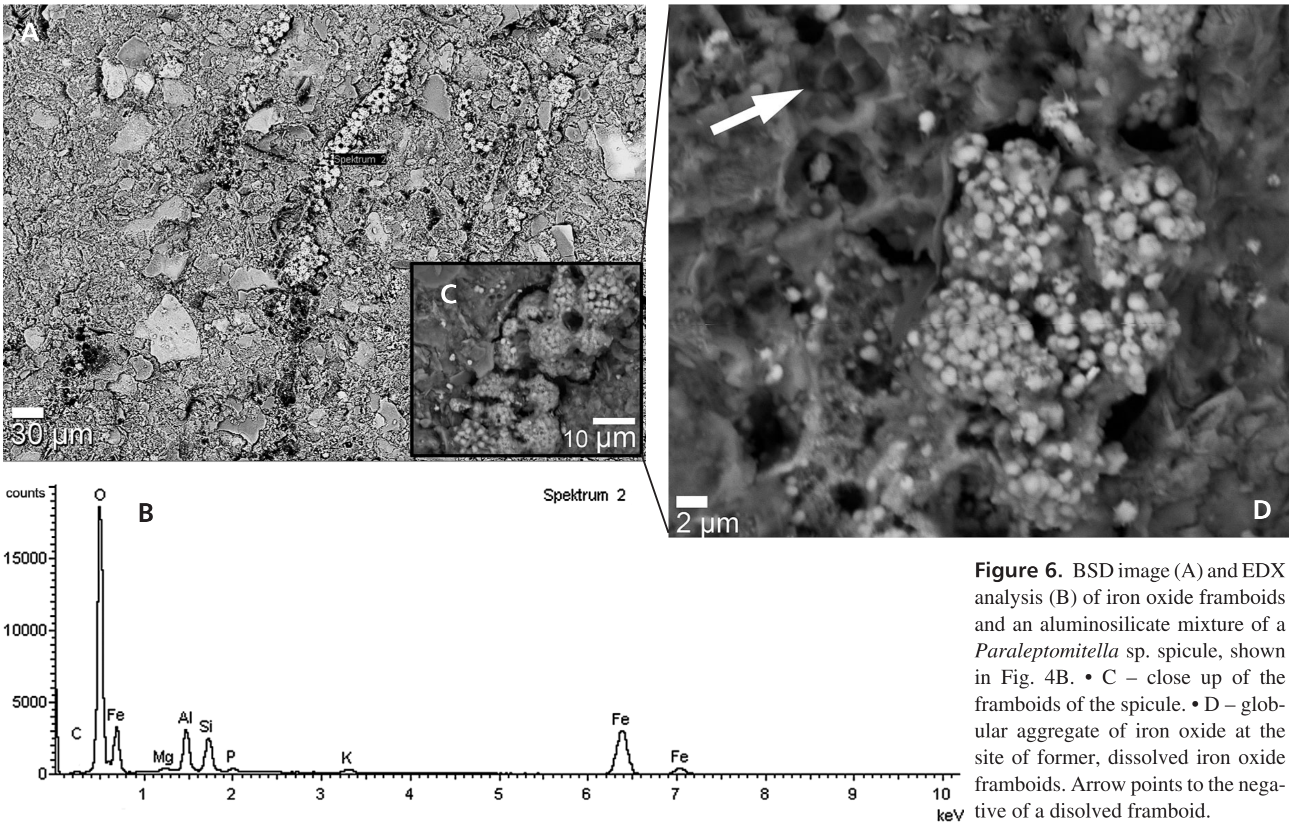


Figure 6. BSD image (A) and EDX analysis (B) of iron oxide framboids and an aluminosilicate mixture of a *Paraleptomitella* sp. spicule, shown in Fig. 4B. • C – close up of the framboids of the spicule. • D – globular aggregate of iron oxide at the site of former, dissolved iron oxide framboids. Arrow points to the negative of a disolved framboid.

water and slope facies (Hu 2005, Hu *et al*. 2010b, Steiner *et al*. 2005), while the Sancha Fauna from Hunan area represents a deeper shelf-basin facies of the Yangtze Platform (Steiner *et al*. 2005, fig. 10). These differences in settings can be linked to different taphonomic models. Among all the sponges collected in the Yunnan and Guizhou 10 specimens (the most suitable for taphonomic studies) were analyzed in detail. Results were compared with those of the Hunan Province from a previous study (Steiner *et al*. 2005).

The sponges from the Chengjiang and Guanshan faunas show no evidence of siliceous or pyritized spicules like those from the Early Cambrian Hetang Formation in Anhui (Chen *et al*. 2004, Yuan *et al*. 2002) or the Jinsha, Guizhou Province (Yang *et al*. 2005). Jinsha belongs to the Zunyi-Zhijin stratigraphic sub-district (Yang *et al*. 2005); our samples from Zunyi (Y24 series numbers) show elevated values of iron oxides and partially manganese oxides, but no evidence of SiO_2 was revealed by EDX for the sponge spicules. The Guanshan and Chengjiang sponges, as for all other groups of these faunas in Yunnan Province, underwent extensive weathering. Most of the analyzed individuals show only clay minerals with little replacement of spicules by iron oxide minerals. Here, for the first time, we report element mapping of unweathered sponge specimens from Meishucun (Jinning County) showing a robust and continuous carbon film. Organic preservation was also reported by Zhu *et al*. (2005) for black-colored spines attached to a frontal-grasping appendage of *Anomalocaris* from a classic locality yielding fossils of the Chengjiang Biota in the Chengjiang County. Our dataset in contrast with previous works (*e.g.* Gaines *et al*. 2008 and reference therein) show diffuse presence of organic preservation not only in unweathered material (most of our data) but also in several weathered specimens, whereas pyrite was not found in unweathered material. There is no evidence of early pyritization of sponge spicules in our specimens from the Chengjiang and Guanshan faunas. Our results did indeed indicate the preservation of the organic matter, evident in those specimens which did not undergo strong weathering. Early pyrite formation is often considered as a key process linked to the early diagenetic preservation of the Chengjiang-type Fauna (Gabbott *et al*. 2004). Framboids and micro-sized crystals are the two most common morphologies of early diagenetic pyrite. Framboids precipitate from porewater supersaturated with respect to pyrite and iron monosulphides; euhedral crystals precipitate from porewater oversaturated with respect to pyrite, but undersaturated with respect to iron monosulphides (Raiswell 1982, Passier *et al*. 1997, Sweeney & Kaplan 1973, Taylor *et al*. 2000). Sponge spicules are composed of amorphous silica (Müller *et al*. 2009), which is transformed during early diagenesis in opal-CT (Steiner *et al.*

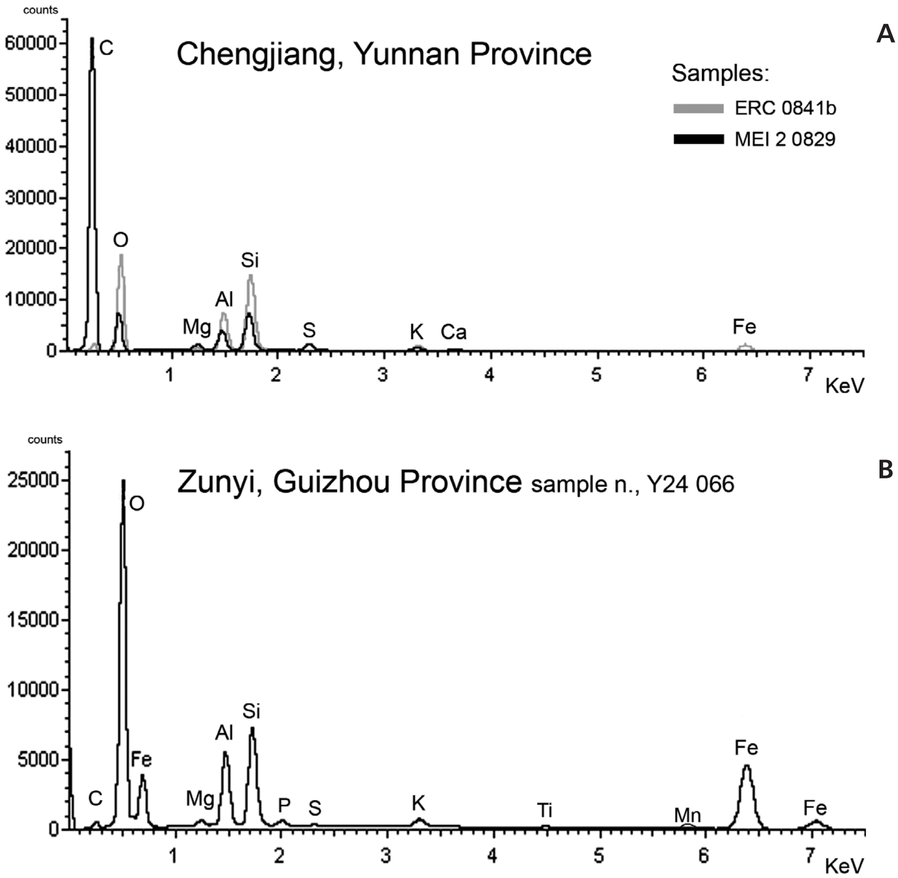


Figure 7. EDX analyses of sponges from Chengjiang and Zunyi.

2005, fig. 6). The substitution of the spicules by pyrite crystals is unlikely to have been performed during early diagenesis. There is no evidence of pyrite associated with the soft-tissue of sponges in the deep water conditions of the Sancha fossil *Lagerstätte*, even though deep water anoxic to dysoxic conditions have been suggested (Steiner *et al*. 2001). Furthermore, there is little evidence of pyrite in the unweathered material of Chengjiang fossil *Lagerstätte*. These iron oxide framboids are interpreted as replacement of later diagenetic pyrite precipitates into voids of sediment, such as dissolved sponge spicules.

During diagenesis, sulphate is reduced to sulphide (operated by bacteria in anoxic water). The sulphide can precipitate in the presence of reduced iron as iron sulphide (FeS), found in the form of pyrite (FeS_2). The values of reactive iron/total iron (FeHR/ FeT) are mostly above 0.38, and all are above the 0.14 threshold for ancient rocks (Poulton *et al*. 2004), which is indicative of an anoxic environment in the Chengjiang fossil *Lagerstätte*. At the same time, the ratio of pyritic iron/reactive iron (Fe_{py}/FeHR), with values below 0.8–0.9 (Poulton *et al*. 2004) shows no presence of stratified sulphidic bottom water. These data are consistent with that of Hammarlund (2007) who noted that pyrite content is low in Chengjiang, even if the FeHR/FeT ratio indicates anoxia. Pyrite formation was limited by the lack of sulphide ions, not by iron.

There are two main taphonomic pathways involved in the sponge preservation of the Chengjiang-type fossil *Lagerstätten*. The Sancha fossil deposits (Hunan Province) show evidence of recrystalization of the amorphous silica of the spicules into crystalline type silica. EDX analyses of the sponge spicules indicate composition of Si and O. In the Guanshan sponges, the biogenic silica of the spicules was first recrystallized as opal-CT, later dissolved, and was replicated by pyrite framboids, which were later pseudomorphically replaced by iron oxides and hydroxides during late stage weathering. Some of these framboids underwent subsequent weathering and changed in micro-crystal morphology and chemistry. This suggests a late diagenetic origin of the framboids, although when related to organic matter, this morphology is often found in early diagenetic precipitation (Taylor *et al*. 2000). Chengjiang sponges underwent extensive weathering. The opal-CT was dissolved leaving a cavity, successively filled by different minerals; alternatively, it possibly underwent dissolution under acidic conditions combined with oxygenation. This resulted in clay and iron oxide replication of the sponge spicules.

Conclusions

There is a disparity in sponge preservation between BGBs and EBs that is not related to taphonomic bias, but can be explained with a short-distance transportation of fauna during EBs deposition.

The Chengjiang sponges (Cambrian Stage 3) have a similar taphonomic pathway as the slightly younger Guanshan sponges (Canglangpuan Stage), whereas the Guanshan material underwent further subsequent weathering stages. There is a substantial difference between weathered material and unweathered material in the Chengjiang fossil *Lagerstätte*. The unweathered material suggests Burgess Shale-type preservation for the Chengjiang sponges. In the Sancha fossil *Lagerstätte*, sponge spicules are preserved as opal-CT. Iron oxide and hydroxide framboids, and globular crystal aggregates in the sponge spicules of Guanshan material, suggest a possible late diagenetic replacement of the sponge spicules by several minerals during different weathering stages.

Acknowledgements

The authors thank J.O. Evers (FU Berlin) for assistance in photo and graphic work. We very much acknowledge L. Och and G.A. Shields for iron speciation analyses. The authors are also grateful to R. Vodrážka and an anonymous reviewer for useful suggestions that improved the manuscript. This study was financially supported by DFG (Grant No. Ke 322/34-1) and National Natural Science Foundation of China (Grant No. 40772020) and is part of the Sino-German project Forschergruppe 736 ("The Precambrian-Cambrian Ecosphere (R)evolution: Insights from Chinese microcontinent".

References

Butterfield, N.J. 1995. Secular distribution of Burgess Shale-type preservation. *Lethaia 28*, 1–13. DOI 10.1111/j.1502-3931.1995.tb01587.x

Chen, J.Y., Hou, X.G. & Lu, H.Z. 1989. Lower Cambrian leptomitids (Demospongea), Chengjiang, Yunnan. *Acta Paleontologica Sinica 28*, 17–31.

Chen, J.Y., Hou, X.G. & Li, G.X. 1990. New Lower Cambrian demosponges *Quadrolaminella* gen. nov. from Chengjiang, Yunnan. *Acta Paleontologica Sinica 29*, 402–413.

Chen, Z., Hu, J., Zhou, C., Xiao, S. & Yuan, X. 2004. Sponge fossil assemblage from the Early Cambrian Hetang Formation in Southern Anhui. *Chinese Science Bulletin 49(15)*, 1625–1628.

Gabbott, S.E., Hou, X.G., Norry, M.J. & Siveter, D.J. 2004. Preservation of Early Cambrian animals of the Chengjiang biota. *Geology 32*, 901–904. DOI 10.1130/G20640.1

Gaines, R.R., Briggs, D.E.G. & Zhao, Y.L. 2008. Burgess Shale-type deposits share a common mode of fossilization. *Geology 36*, 755–758. DOI 10.1130/G24961A.1

Hammarlund, E. 2007. *The ocean chemistry at Cambrian deposits with exceptional preservation & the influence of sulphate on soft-tissue decay*. 64 pp. Master thesis, Odense, Denmark, University of Southern Denmark.

Hou, X.G. & Bergström, J. 2003. The Chengjiang fauna – the oldest preserved animal community. *Paleontological Research 7(1)*, 55–70. DOI 10.2517/prpsj.7.55

Hou, X.G., Aldridge, R.J., Bergström, J., Siveter, David J., Siveter, Derek J. & Feng, X.H. 2004. *The Cambrian fossils of Chengjiang, China: The flowering of early animal life.* 248 pp. Blackwell Publishing, Malden & Oxford. DOI 10.1002/9780470999950

Hu, S.X. 2005. Taphonomy and palaeoecology of the Early Cambrian Chengjiang Biota from Eastern Yunnan, China. *Berliner Paläobiologische Abhandlungen 7*, 1–197.

Hu, S.X., Steiner, M., Zhu, M.Y., Luo, H.L., Forchielli, A., Keupp, H., Zhao, F.C. & Liu, Q. 2012. A new priapulid assemblage from the early Cambrian Guanshan fossil *Lagerstätte* of SW China. *Bulletin of Geosciences 87(1)*, 93–106. DOI 10.3140/bull.geosci.1238

Hu, S.X., Zhang, Z.H., Holmer, L.E. & Skovsted, C.B. 2010b. Soft-part preservation in a linguliform brachiopod from the lower Cambrian Wulongqing Formation (Guanshan Fauna) of Yunnan, southern China. *Acta Palaeontologica Polonica 55(3)*, 495–505. DOI 10.4202/app.2009.1106

Hu, S.X., Zhu, M.Y., Steiner, M., Luo, H.L., Zhao, F.C. & Liu, Q. 2010a. Biodiversity and taphonomy of the early Cambrian Guanshan biota, eastern Yunnan. *Science China, Earth Sciences 53(12)*, 1765–1773. DOI 10.1007/s11430-010-4086-9

Li, C.W., Chen, J.Y. & Hua, T.E. 1998. Precambrian sponges with cellular structures. *Science 279(5352)*, 879–882. DOI 10.1126/science.279.5352.879

Liu, J., Ou, Q., Han, J., Zhang, Z.F., He, T.J., Yao, X.Y., Fu, D.J. & Shu, D. 2012. New occurence of the Cambrian (Stage 4, Series 2) Guanshan Biota in Huize, Yunnan, South China. *Bulletin of Geosciences 87(1)*, 125–132. DOI 10.3140/bull.geosci.1229

Luo, H., Li, Y., Hu, S.X., Fu, X., Hou, S., Liu, X., Chen, L., Li, F., Pang, J. & Liu, Q. 2008. *Early Cambrian Malong Fauna and Guanshan Fauna from Eastern Yunnan, China.* 134 pp. Yunnan Science and Technology Press, Kunming, China.

Mehl, D. 1999. Die frühe Evolution der Porifera. Phylogenie und Evolutionsökologie der Poriferen im Paläzoikum mit Schwerpunkt der desmentragenden Demospongiae ("Lithistide"). *Münchener Geowissenschaftliche Abhandlungen 37*, 1–72.

Mehl, D. & Erdtmann, B.-D. 1994. *Sanshapentella dapingi* n. gen. n. sp. A new hexactinellid sponge from the Early Cambrian (Tommotian) of China. *Berliner Geowissenshaftliche Abhandlungen 13*, 315–319.

Mehl, D. & Reitner, J. 1993. Porifera Grant 1836, 293–329. *In* Steiner, M., Mehl, D., Reitner, J. & Erdtmann, B.-D. *Oldest entirely preserved sponges and other fossils from the lowermost Cambrian and a new facies reconstruction of the Yangtze platform (China). Berliner Geowissenshaftliche Abhandlungen, series E, 9*.

Müller, W.E.G., Wang, X., Burghard, Z., Bill, J., Krasko, A., Boreiko, A., Schloßmacher, U., Schröder, H.C. & Wiens, M. 2009. Bio-sintering processes in hexactinellid sponges: Fusion of bio-silica in giant basal spicules from *Monorhaphis chuni*. *Journal of Structural Biology 168*, 548–561. DOI 10.1016/j.jsb.2009.08.003

Passier, H.F., Middelburg, J.J., de Lange, G.J. & Bottcher, M.E. 1997. Pyrite contents, microtextures, and sulfur isotopes in relation to formation of the youngest eastern Mediterranean sapropel. *Geology 25*, 519–522. DOI 10.1130/0091-7613(1997)025<0519:PCMASI>2.3.CO;2

Poulton, S.W. & Canfield, D.E. 2005. Development of a sequential extraction procedure for iron: Implications for iron partitioning in continentally derived particulates. *Chemical Geology 214*, 209–221. DOI 10.1016/j.chemgeo.2004.09.003

Poulton, S.W., Fralick, P.W. & Canfield, D.E. 2004. The transition to a sulphidic ocean ~1.84 billion years ago. *Nature 431*, 173–177. DOI 10.1038/nature02912

Raiswell, R. 1982. Pyrite texture, isotopic composition and the availability of iron. *American Journal of Science 82*, 1244–1263. DOI 10.2475/ajs.282.8.1244

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

Shimizu, K., Cha, J., Stucky, G.D. & Morse, D.E. 1998. Silicatein α: cathepsin L-like protein in sponge biosilica. *Proceeding of the National Academy of Sciences 95*, 6234–6238. DOI 10.1073/pnas.95.11.6234

Steiner, M., Hu, S., Liu, J. & Keupp, H. 2012. A new species of *Hallucigenia* from the Cambrian Stage 4 Wulongqing Formation of Yunnan (South China) and the structure of sclerites in lobopodians. *Bulletin of Geosciences 87(1)*, 107–124. DOI 10.3140/bull.geosci.1280

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 Geowissenshaftliche Abhandlungen, Serie E 9*, 293–329.

Steiner, M., Wallis, E., Erdtmann, B.-D., Zhao, Y. & Yang, R. 2001. Submarine-hydrothermal exalative ore layers in black shales from South China and associated fossils – insight into a Lower Cambrian facies and bio-evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology 169*, 165–191.

Steiner, M., Zhu, M., Zhao, Y. & Erdtmann, B.-D. 2005. Lower Cambrian Burgess shale-type fossil associations of South China. *Palaeogeography, Palaeoclimatology, Palaeoecology 220*, 129–152.

Sweeney, R.E. & Kaplan, I.R. 1973. Pyrite framboid formation: laboratory synthesis and marine sediments. *Economic Geology 68*, 618–634.

Taylor, K.G. & Macquaker, J.H.S. 2000. Early diagenetic pyrite morphology in a mudstone-dominated succession: the Lower Jurassic Cleveland Ironstone Formation, eastern England. *Sedimentary Geology 131*, 77–86.

Weber, B., Hu, S.X. & Steiner, M. 2012. A diverse ichnofauna from the Cambrian Stage 4 Wulongqing Formation near Kunming (Yunnan Province, South China). *Bulletin of Geosciences 87(1)*, 71–92. DOI 10.3140/bull.geosci.1239

Wu, W. 2004. *Fossil sponges from the Early Cambrian Chengjiang Fauna, Yunnan, China.* 181 pp. Ph.D. thesis, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences, Nanjing.

Yang, X., Zhao, Y., Wang, Y. & Wang, P. 2005. Discovery of sponge body fossils from the late Meishucunian (Cambrian) at Jinsha, Guizhou, south China. *Progress in Natural Science 15(8)*, 708–712.

Yuan, X., Xiao, S., Parsley, R., Zhan, 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*, 363–366.

Zhao, F.C., Caron, J.B., Hu, S.X. & Zhu, M.Y. 2009. Quantitative analysis of taphofacies and paleocommunities in the Early Cambrian Chengjiang Lagerstätte. *Palaios 24*, 826–839. DOI 10.2110/palo.2009.p09-004r

Zhu, M.Y, Babcock, L.E. & Steiner, M. 2005. Fossilization modes in the Chengjiang Lagerstätte (Cambrian of China): testing the roles of organic preservation and diagenetic alteration in exceptional preservation. *Palaeogeography, Palaeoclimatology, Palaeoecology 220*, 31–46. DOI 10.1016/j.palaeo.2003.03.001