Influence of redox conditions on animal distribution and soft-bodied fossil preservation of the Lower Cambrian Chengjiang Biota

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ABSTRACT

The exceptionally preserved Chengjiang Biota (Yunnan, China) is significant for understanding the rapid development of complex animal-rich ecosystems during the evolutionary radiation of the Cambrian. However, the ecological signal provided by the fossils captured in this deposit may not reflect accurately the in-life community, with transport and decay of carcasses being the principal processes responsible for potential modification. The principal fossil-bearing interval (Maotianshan Shale Member, Yu'an Shan Formation) is comprised of claystones of two distinct depositional origins: the “background” beds represent slow hemipelagic deposition into deep waters, while the “event” beds represent distal turbidites or storm-generated beds. Each bed type has a distinct fossil assemblage and preservation mode underscoring the importance of interpreting the palaeoenvironment of each bed type. Here, we interpret palaeo-redox conditions for both the background beds and the event beds by conducting a systematic geochemical study using iron speciation, $\delta^{34}\text{S}_{\text{py}}$, $\delta^{13}\text{C}_{\text{carb}}$, $\delta^{13}\text{C}_{\text{TOC}}$ and molybdenum abundance. These data are from the most complete core recovered from the Chengjiang fossiliferous units and allow us to distinguish redox conditions where the animals lived, and where they were buried and exceptionally preserved. Our results demonstrate that background beds were dominated by dysoxic conditions; here, a diverse sponge community tolerant of low-oxygen conditions lived. In contrast, the shallower shelf and offshore-transitional environments, where event beds were sourced, were almost persistently oxic, and it was here where the diverse Chengjiang Biota flourished. Thus, the Chengjiang sediments record two distinct palaeocommunities within the background and the event beds. The contrasting redox conditions in close spatial proximity likely facilitated the soft-bodied fossil preservation. Our findings provide a valuable case study in the necessity to understand ecological composition and exceptional preservation informed by environmental context.

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48 *Keywords:* Cambrian; Lagerstätten; The Yangtze Platform; Sponges; Ecology

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1. Introduction

That many of the recognized animal phyla appeared in fossil record in an interval represented by just about 20 million years in the Cambrian, is best evidenced by exceptionally well-preserved soft-bodied fossil assemblages, such as the Chengjiang Biota (China) (Hou et al., 2017), Sirius Passet (Greenland) (Conway Morris et al., 1987), Burgess Shale (Canada) (Walcott, 1911) and Emu Bay Shale (Australia) (Glaessner, 1979). Among these Lagerstätten, the Chengjiang Biota is the oldest and richest allowing palaeontologists to investigate one of the earliest known complex metazoan ecosystem (Marshall, 2006; Shu et al., 2014; Hou et al., 2017). Reconstruction of the Chengjiang ecosystem, however, is not a simple matter of determination of fossil species abundance, life-habits and interactions. This is because fossil assemblages may be highly modified representations of life assemblages owing to several processes, foremost of which are transport and decay. Consideration of ecology also requires an understanding of the environmental setting in which this ecosystem emerged; ecological reconstructions on extant systems always include contextual data on the environment. For ancient ecosystems these data must be read from the sediment layers in which the fossils are recovered, and perhaps in marine settings one of the most fundamental in this context is the redox state of the sediment and water column.

The Chengjiang Biota occurs in the Yu'an-shan Formation of eastern Yunnan Province, Southwest China. The formation is comprised of four members, and the main stratigraphic interval of the Chengjiang Biota is located in the Maotianshan Shale Member (Member 3). The interval is marked by hemipelagic “background” beds with intercalated “event”-deposited distal clay turbiditic beds (Zhu et al., 2001; Hu, 2005; Zhao et al., 2009). These beds are easily distinguishable, both in highly-weathered exposed sediments and in subsurface core. The hemipelagic background beds are laminated, whereas the event-deposited distal turbidites are

massive and sometimes normally-graded, indicative of rapid deposition (see also Zhu et al., 2001; Hu 2005; Zhao et al., 2009; Gaines et al., 2012; Hammarlund et al., 2017). This member, through time, records basin filling and an increase in silty turbidite deposition. The youngest member (Member 4, the Upper Siltstone Member) comprises coarser-grained silts and sands representative of shallowing to an upper shoreface to nearshore setting (Zhu et al., 2001).

The abundance and types of fossils were different between the hemipelagic background beds and the event-deposited distal turbidites, which was demonstrated through detailed bed-by-bed fossil collection and sedimentological logging at a quarry (Zhao et al., 2009). In brief, in background beds, poorly-preserved, disarticulated arthropods dominate with poriferans also frequent. By contrast, event beds contain diverse taxa which are numerous and exceptionally well-preserved. Zhao et al. (2009) concluded that distinct faunas in background and event beds were the result of differences in taphonomic processes (e.g. time averaging, oxygen level variation, preferential preservation and burial intensity) operating on essentially the same community. This means that fossils from both the background beds and the event beds could be considered as a single ecosystem with enhanced decay resulting in the poorly-preserved and species-impoverished background beds. Hammarlund et al. (2017) used a multigeochemical redox proxy approach and showed that, during deposition of the fossiliferous interval of the Maotianshan Shale Member, sediments were deposited in chemically inhospitable environmental conditions which would have been inimical to life; thus some degree of transport would have been necessary to account for the rich-fossil diversity of the Chengjiang. However, their study focused on the evolution of redox conditions through the Chengjiang interval, based mainly on data from the background beds. They did not interpret or discuss redox conditions in the event beds. So, in considering the ecosystem of this earliest complex community important questions remain: can we consider all Chengjiang

fossils to have lived together in a community (cf. Zhao et al., 2009), or, are all fossils transported perhaps from a different environment from where they were buried, or, are the fossil assemblages from event beds and background beds representative of different communities, in which case the Chengjiang records two ecosystems?

Here, we use material from an almost complete and unweathered core, through the main interval hosting the Chengjiang Biota. We provide a high-resolution Fe-S-Mo-C profile for background beds and intercalated event beds to reconstruct spatial redox conditions and their variation with time. Our data have important implications for taphonomic and community distribution models of the Chengjiang Biota. We show that an exceptionally preserved biota, here the Chengjiang, is best interpreted within the context of its physical and chemical environment of deposition and fossilization.

2. Geological setting and stratigraphy

2.1. Geological setting

The Yu'an-shan Formation, which hosts the Chengjiang Biota, was deposited in the southwestern edge of the Yangtze Platform during Epoch Two, Age Three of the Cambrian Period. Evidence from sedimentology, palaeobiology and stratigraphic correlation has demonstrated that during the Ediacaran and the earliest Cambrian (Fortunian), the southeastern Yangtze Platform was situated in a deep-water basin in which black shales and cherts with subordinate carbonates were deposited (Wang et al., 2012). In contrast, the northwestern Yangtze Platform, which was mainly seated on a shallow shelf, is characterized by carbonates with variable intercalation of black shales and mudstones (Fig.1A; Wang et al., 2012). During Age 2–3 of the Cambrian Period, black shale/claystone was widely deposited on the Yangtze Platform (Fig.1B; Wang et al., 2015).

2.2. Stratigraphy

The Yu'anshan Formation (Cambrian Series 2, Stage 3) is distributed in the present Eastern Yunnan Province, Southwest China. The formation consists of the lowermost Black Siltstone Member, the lower Black Carbonaceous Shale Member, and the middle Maotianshan Shale Member and the Upper Siltstone Member (Fig. 1C). It overlies the Shiyantou Formation with a phosphorite layer occurring at the boundary between the two formations. The earliest known fossil (*Abadiella*) were found in the Black Carbonaceous Shale Member (Yang et al., 2003; Zhu et al., 2003). The majority of the Chengjiang soft-bodied fossils are recovered from the overlying Maotianshan Shale Member (Yang et al., 2003). The latest U-Pb analyses of detrital zircons by CA-ID-TIMS show that the maximum age of the Chengjiang Biota is $518.03 \pm 0.69/0.71$ Ma (2σ) (Yang et al., 2018).

3. Fossil preservation, samples and methods

3.1. Fossil preservation

The Chengjiang Biota was discovered in 1984 by Hou Xian-Guang and to date over 200 species across 16 phyla have been recognized (Hou et al., 2017). Quantitative taphonomical analyses by Zhao et al. (2009) demonstrated that the background beds and event beds can be characterized by different fossils. In background beds (Fig. 2) disarticulated arthropods are the most abundant specimens (84.3%), followed by poriferans (7.4%) (Zhao et al., 2009). Of the arthropods it is bivalved forms that dominate, for example *Kunmingella douvillei* is the most abundant (61.9% of the total number of specimens in the background beds) with *Isoxys auritus* (6.8%) and *Waptia ovata* (5.9%) also occurring in significant numbers. The background bed assemblage is

impoverished in species and specimens numbers when compared with the event beds (Fig. 2), where *Kunmingella douvillei*, the priapulid *Cricocosmia jinningensis* and the brachiopod *Diandongia pista* are the most abundant species (18–19% each). It is within the event beds where most of the soft-bodied taxa for which the Chengjiang is famous occur and are exceptionally preserved.

3.2. Samples

The drill core is from Jinning County, eastern Yunnan Province (24°42'59"N, 102°31'09"E) (Fig. 1A and B), where 260.7 m core length was recovered; core diameter is 7–9 cm. It includes the Yu'an-shan Formation and underlying Shiyantou Formation. The Yu'an-shan Formation contains four lithostratigraphic members, from oldest to youngest the: Black Siltstone Member (171.9–167.5 m), Black Carbonaceous Shale Member (167.5–162.1 m) and Maotianshan Shale Member (162.1–44.7 m), Upper Siltstone Member (44.7–36.0 m). The main stratigraphic interval of the Chengjiang Biota, which comprises background beds with intercalated event beds or thin siltstone beds (Fig. 1D), are found between 151.4–120.0 m. The Maotianshan Shale Member is the focus of in this paper.

3.3. Methods

Ichnofabric Index is reported by direct bed-by-bed observation of the Jinning core. We use the protocol of Droser and Bottjer (1991) where Ichnofabric Index 1 represents absence of bioturbation and 4–5 represents extensive bioturbation.

For geochemical analyses samples (118 samples, including 38 event bed samples and 43 background bed samples) were collected throughout the Maotianshan Shale Member. Event beds

and intercalated background beds were usually gathered in couplets. Fe, Al, Mo, TOC, $\delta^{13}\text{C}_{\text{TOC}}$ and $\delta^{13}\text{C}_{\text{carb}}$ and $\delta^{18}\text{O}_{\text{carb}}$ were analysed in the State Key Laboratory of Isotope geochemistry, Guangzhou Institute of Geochemistry, Chinese Academy of Sciences. Samples were dried to a constant weight under 60 °C. After ignition under 700 °C, the samples (~ 40 mg) were dissolved with HF + HNO₃ + HClO₄. Finally, samples were completely dissolved in concentrated HNO₃ and then diluted to 2000 times of the sample weight. Fe₂O₃ and Al₂O₃ content were determined on a Varian Vista-PRO ICP-AES. Fitted Background Correction corrected spectral interference. Analytical precision is better than 1 % and accuracy is better than 10 % (Li et al., 2002). For a diluted solution, Rh internal-standard solution (10 ppb) was added according to the weight ratio of 1 : 1. Mo concentration was measured with a PE Elan 6000 ICP-MS. Analytical precision is usually better than 5 % and accuracy is usually better than 10 % (Liu et al., 1996; Li et al., 2002).

3 M HCl was used to remove carbonates in samples. This was performed twice, each time for 24 hours. The residue from samples was then washed with Milli-Q three times in order to eliminate Cl⁻ ions. Finally, residues were dried under 60 °C and weighed to calculate recovery efficiency. These samples were re-ground to 200 mesh. About 50 mg samples were weighed and sealed with tinfoil, then sample total organic carbon (TOC) and isotopic composition of organic carbon ($\delta^{13}\text{C}_{\text{TOC}}$) were analyzed on a Vario PYRO cube elemental analyser (Elementar Ltd) on CN mode coupled with an Isoprime 100 continuous flow Isotope Ratio Mass Spectrometry (IRMS). Three international standards (IAEA-CH3, IAEA-601 and IAEA-CH7) were analyzed at the beginning of a batch sample and one working standard (pure sulfanilamide) was analyzed repeatedly between each 10 samples for correction, monitoring machine drift and analytical precision. Analytical precision for TOC content and $\delta^{13}\text{C}_{\text{TOC}}$ was respectively 3 % (Relative Standard Deviation) and 0.15 ‰ (Standard Deviation).

$\delta^{13}\text{C}_{\text{carb}}$ and $\delta^{18}\text{O}_{\text{carb}}$ analysis was performed using a GV Isoprime II stable isotope ratio mass spectrometry coupled with an online carbonate preparation device (MultiPrep). About 2 mg of each sample was put into an individual reaction vessel and reacted with 102 % H_3PO_4 with a specific gravity of 1.92 g/cm^3 at 90 °C in the MultiPrep system. The released CO_2 was collected and purified, and finally transferred to the mass spectrometry for measurement through an online Dual Inlet system. Isotope data were normalized against the Vienna Pee Dee Belemnite (V-PDB) using the NBS-19 standard ($\delta^{13}\text{C}_{\text{carb}} = 1.95 \text{ ‰}$, $\delta^{18}\text{O}_{\text{carb}} = -2.20 \text{ ‰}$). Multiple measurements (n = 80) on a Chinese national carbonate standard GBW04405 yielded a standard deviation of 0.03 ‰ for $\delta^{13}\text{C}_{\text{carb}}$ and 0.06 ‰ for $\delta^{18}\text{O}_{\text{carb}}$.

Total carbon content (TC), total sulfur content (TS), iron speciation and sulfur isotopic composition of pyrites were determined in the State Key Laboratory of Biogeology and Environmental Biology, China University of Geosciences (Wuhan). In detail, TC and TS were measured by an Analytikjena Multi EA 4000 (made in Germany). Under 1350 °C, samples reacted with oxygen and produce CO_2 and SO_2 . Both were determined to calculate TC and TS. The analytical precision is $\pm 0.20 \text{ ‰}$. Sulfur in pyrites was extracted through the Cr reduction method and formed H_2S reacting with silver nitrate solution to precipitate Ag_2S (Canfield et al., 1986). Ag_2S precipitates were dried and collected with a recovery of better than 92 % based on a parallel pyrite standard in each run. Sulfur content of Ag_2S was used to calculate Fe in pyrites (Fe_{py}) content according to stoichiometric ratio of pyrites for Fe : S of 1 : 2. Highly reactive iron species (Fe_{HR}), including Fe in carbonates (Fe_{carb}), oxides (Fe_{ox}) and magnetite (Fe_{mag}) were extracted sequentially based on procedures described in Poulton and Canfield (2005). They were measured for iron content with a TAS-990 AAS. The analytical precision is better than 10 % based on duplicate analyses of laboratory standards. Ag_2S was ground evenly and then was measured for sulfur

isotopic composition of pyrite ($\delta^{34}\text{S}_{\text{py}}$) on a Thermo Scientific DELTA V PLUS isotope Ratio MS. The results (Table 1) show that Fe_{carb} %, Fe_{ox} %, and Fe_{mag} % for two internal lab standards CUG-2 and CUG-3 are consistent with reported values (Li et al., 2015). For samples in the Jinning core, three pairs of duplicates are identical with each other for Fe_{carb} %, Fe_{ox} %, and Fe_{mag} % while two pairs of duplicates are identical with each other for Fe_{py} and $\delta^{34}\text{S}_{\text{py}}$ (Table 1).

4. Results and discussion

We interpret, similar to Zhu et al. (2001), that the Maotianshan Shale Member is comprised of a stack of sediments representing slow accumulation from the water column, in an offshore deep-water setting (background beds) with pulsed input of rapidly depositing sediments (event beds), that were initially accumulating on a transitional-offshore or even shallow shelf environment. Our detailed logging of the core provides a perspective on the evolution of the depositional environment through the principal fossil-bearing units. Here the cumulative thickness of background beds per meter (the thickness range for individual background beds is 153 cm to 0.1 cm) become thinner upwards. The occurrence of hummocky cross-stratification at ~120 m (Fig. 3) indicates the transition from offshore to an offshore transitional environment – essentially water depth became shallower. Burrows (typically <1 cm in length, Fig. 4) occur frequently from ~120 m and above (Fig. 5A), suggesting a transformation to an environment suitable for infauna and vagrant benthos. From ~100 m upwards the background beds and event beds are difficult to distinguish from each other both texturally and geochemically. We interpret this to indicate basin infilling such that there was no longer sufficient water depth contrast to support a sedimentological difference between the background and event beds.

4.1. Redox conditions of event beds and background beds using Fe-S-Mo-C proxies

All samples from the Jinning core were found to have $\text{Fe}_T > 3\%$ (Supplementary Table DR1), indicating that Fe speciation can be utilized to indicate water redox conditions (Clarkson et al., 2014). Studies of modern and Phanerozoic marine sediments have demonstrated that $\text{Fe}_{\text{HR}}/\text{Fe}_T \leq 0.22$ and $\text{Fe}_{\text{HR}}/\text{Fe}_T \geq 0.38$ indicate oxic and anoxic conditions, respectively (Poulton and Canfield, 2011). Under anoxic conditions, sediments with $\text{Fe}_{\text{py}}/\text{Fe}_{\text{HR}} > 0.7\text{--}0.8$ and $\text{Fe}_{\text{py}}/\text{Fe}_{\text{HR}} < 0.7\text{--}0.8$ are regarded to have been deposited under euxinic conditions and ferruginous conditions, respectively. The transition metal molybdenum is a valuable, multipurpose palaeoredox tool and its abundance in sediment is used to indicate water column redox state. Broadly, Mo abundance in sediments deposited under an oxic water column will be close to the average for continental crust (1.1 ppm). Under euxinic water column conditions, the speciation and reactivity of Mo change such that it is converted from molybdate to a series of particle-reactive species of thiomolybdate (Helz et al., 1996). These ions are rapidly scavenged by organic matter and other reduced substrates resulting in Mo being retained within sediment; the burial rate of Mo in sulfidic environments is two or three orders of magnitude higher than in oxic environments (Bertine and Turekian, 1973; Scott et al., 2008).

The lower-most units of the Maotianshan Shale Member, an interval between 162–151 m, comprises background beds which are occasionally interbedded with thin event beds or siltstone beds (Fig. 5A). The interval shows a $\text{Fe}_{\text{HR}}/\text{Fe}_T$ decrease from 0.46 to 0.33 upwards and $\text{Fe}_{\text{py}}/\text{Fe}_{\text{HR}}$ decreases from 0.81 to 0.59 for background beds. In the same interval Mo concentrations for background beds drop from 24 to 7.3 ppm (Fig. 5B). Mo concentration tends to be close to the average value (1.1 ppm) of upper continental crust under dysoxic–oxic conditions (Algeo and Maynard, 2004), under anoxic conditions, and especially under sulfidic waters and sediments Mo

would be significantly elevated (Helz et al., 1996; Tribovillard et al., 2006). Thus, this combination of Fe-Mo data indicates that the bottom waters were progressively transformed from euxinic to ferruginous through the interval of 161–152 m, and finally even to ferruginous–suboxic.

In the interval of peak fossil occurrence, between 151–120 m of the Maotianshan Shale Member (Fig. 5A), event beds have $\text{Fe}_{\text{HR}}/\text{Fe}_{\text{T}}$ of 0.15–0.33 with an average value of 0.23 ± 0.12 (2σ , $n = 16$), except one anomalously high value (0.47) at 146.27 m. Most event beds have $\text{Fe}_{\text{HR}}/\text{Fe}_{\text{T}}$ close to or lower than 0.22, the boundary between possibly anoxic and oxic (Poulton and Canfield, 2011). The iron speciation data suggest a dominantly oxic bottom-water condition for the deposition of event beds between 152–120 m of the Maotianshan Shale Member, which indicates the condition before being transported to the deep-water environment. That rapidly deposited event beds record their originally oxic redox signal is perhaps surprising. However, data have suggested that long distance transport cannot significantly alter enrichment of Fe_{HR} (Lyons and Severmann, 2006). In addition, studies have shown that rapidly redeposited muds retained their originally low $\text{Fe}_{\text{HR}}/\text{Fe}_{\text{T}}$ redox signal even in euxinic bottom water environments (Canfield et al., 1996; Lyons and Severmann, 2006). Thus, we consider that iron speciation data of event beds did not alter significantly and that these values record original redox conditions of bottom waters prior to transportation.

In contrast to event beds, intercalated background beds between 151–120 m commonly have higher $\text{Fe}_{\text{HR}}/\text{Fe}_{\text{T}}$ values between 0.26–0.39 with the average value of 0.32 ± 0.07 (2σ , $n = 17$), and almost all of them fall between 0.22 and 0.38—a range indicating possibly anoxic depositional conditions (Poulton and Canfield, 2011), but this is equivocal based on iron speciation data alone. However, other evidence suggests a dysoxic–dominated bottom waters. For example, compared to intercalated event beds, background beds have notably lower $\delta^{13}\text{C}_{\text{TOC}}$ values but almost

indistinguishable $\delta^{13}\text{C}_{\text{carb}}$ values. If oxidation of organic matter was significantly apparent lower $\delta^{13}\text{C}_{\text{carb}}$ values would have resulted; this is opposite to the observed results. Accordingly, the difference of $\delta^{13}\text{C}_{\text{TOC}}$ values between background beds and event beds is independent of oxidation of organic matter. Lower $\delta^{13}\text{C}_{\text{TOC}}$ values of background beds were consistent with the contribution of chemotrophic biomass to sedimentary organic matter, which usually occurs in dysoxic to anoxic waters (Hayes et al., 1999; Pimenov and Neretin, 2006). In addition, background beds have lower $\delta^{34}\text{S}_{\text{py}}$, suggesting sulfate availability was relatively not restricted. Under oxic bottom waters, pyrites are formed in sediments where sulfate availability are restricted by pore-water diffusion. In contrast, partial pyrites can form in dysoxic–anoxic bottom waters which commonly have more abundant sulfate supply, resulting in lower $\delta^{34}\text{S}_{\text{py}}$ for dysoxic–anoxic sediments in the same basin (Raiswell et al., 1997; Sageman et al., 2014). Thus, carbon–sulfur isotope evidence supports the deposition of background beds under dysoxic–anoxic bottom waters. In addition, background beds commonly have very low Mo concentrations (~1 ppm), close to values from upper continental crust, further suggesting that dysoxic conditions dominated (Algeo and Maynard, 2004). $\delta^{13}\text{C}_{\text{TOC}}$ values for background beds increase progressively upward through the core, indicating that the dysoxic–dominated condition was gradually attenuated.

The interval between 120–100 m records the initial occurrence of abundant bioturbation in background beds and decreasing fossil occurrence in the Maotianshan Shale Member (Fig. 5A). In this interval background beds display similar, even indistinguishable Mo concentrations and $\text{Fe}_{\text{HR}}/\text{Fe}_{\text{T}}$ values to intercalated event beds (Fig. 5B). Thus, geochemistry and bioturbation both provide strong evidence that deposition of these background beds occurred under an oxic water column.

4.2. *Spatial redox environments of the Chengjiang Biota*

Our results demonstrate that during deposition of the main stratigraphic interval of the Chengjiang Biota, the deep-water environment in which background beds were deposited, was mainly dysoxic, which is in agreement with that of Hammarlund et al. (2017). Furthermore, our data from the event beds (which were not discussed in detail in Hammarlund et al. (2017)), indicate that the shallow-water environment, from which these sediments were transported, was predominantly oxic. The dysoxic-dominated condition for deep-waters was gradually attenuated with time. Due to regression during deposition of the Maotianshan Shale Member, the basin would have become progressively shallower, which could cause the observed redox transformation of the bottom waters. The deep water dysoxic-dominated condition eventually became oxic when the deep-water environment was transformed to the offshore transitional environment, indicating that the redox interface is at the storm-wave base.

4.3. *Redox influence on animal distribution and soft-bodied fossil preservation*

Our data contrast with previous interpretations that the background beds were oxygenated (Zhu et al., 2001; Zhao et al., 2009) and agree with those of Hammarlund et al. (2017) indicating extremely low-oxygen prevailed during deposition of these beds. As such most animals were prohibited from living in the depositional environment of the background beds and a low fossil abundance results. However, several taxa do occur: some such as *Waptia ovata* and *Isoxys auritus* are nektonic and would have had a wide distribution regardless of bottom water conditions. However, the dysoxic-dominated seabed was not entirely lifeless, as evidenced by the greater abundance of sponges in background beds than occur in event beds (Zhao et al., 2009), and the abundance of taxa that would have lived close to the seabed such as *Kunmingella douvillei* (Hou

et al., 2010). This seems counterintuitive, however, experimentally, sponges have been shown to tolerate and live in oxygen levels that would kill most familiar benthic groups (Mills et al., 2014). The precise ecology of *Kunmingella douvillei* is yet to be studied in detail but its morphology is suggestive of a substrate crawler or a nektobenthic swimmer (Hou et al., 2010). Elsewhere this taxon has been found in sediments interpreted to be suboxic or dysoxic (Yang et al., 2007; Chen et al., 2013). So it is possible that *Kunmingella* was adapted to low oxygen conditions. Alternatively, it is possible that, whilst conditions were dominantly dysoxic during background bed deposition, occasional oxic incursions occurred allowing brief colonization of the seafloor by *Kunmingella*. Notwithstanding this, the background beds have a distinct community that we interpret was controlled by unfavorable redox conditions, and not by preservation bias. Thus, oxygen-depletion limited the ecological expansion of the Chengjiang Biota from the oxygenated shallower-water into deep-water settings (Fig. 6); again a conclusion reached by Hammarlund et al. (2017) through consideration of geochemistry.

Our new data from the event beds indicate that they were deposited initially in an oxic offshore transitional and shallower-water environment, which was adjacent to the dysoxic-dominated offshore depositional environment (Fig. 6). Within this environment the Chengjiang community flourished. Periodically live animals, or their carcasses were rapidly transported just a short distance into a deep-water, and low oxygen depositional environment (Zhang and Hou, 2007; Hammarlund et al., 2017). It is the spatial proximity of these two sharply different redox environments which enhanced the likelihood of exceptional preservation.

Our interpretation for the Chengjiang Biota is consistent with the idea that oxygen levels controlled the ecological structure and early animal distribution in the Ediacaran-early Cambrian oceans (e.g., Li et al., 2015; Jin et al., 2016; Li et al., 2017). It also demonstrates the importance

of a holistic approach to interpretation of ancient ecosystems: the depositional context of fossils must be understood before investigations on ecology and community analyses.

5. Conclusions

Using the most complete core through the Chengjiang fossiliferous units, we were able for the first time to carry out a systematic geochemical study to compare the palaeo-redox conditions between the background beds and the intercalated event beds. Our analysis results on iron speciation, $\delta^{34}\text{S}_{\text{py}}$, $\delta^{13}\text{C}_{\text{carb}}$, $\delta^{13}\text{C}_{\text{TOC}}$ and molybdenum abundance demonstrates that the background beds represent deep-water environments, which were dominated by dysoxic conditions; while the event beds were from shallower shelf and offshore-transitional environments and almost persistently oxic. The difference in redox condition could also have controlled the distribution of Chengjiang animal communities, thus the Chengjiang sediments record two distinct palaeocommunities within the background and event beds. While the diverse Chengjiang Biota flourished in the shallower shelf and offshore-transitional environments, sponge communities tolerant of low-oxygen conditions, lived intermittently in the deep-water environments. Our findings demonstrate that spatial redox heterogeneity had a significant impact on the distribution and preservation of the Chengjiang Biota, providing a valuable case study in our understanding of how ecological composition and exceptional preservation are impacted by environmental context.

Supplement

Supplementary material (Table DR1 Redox proxy data for Jinning Core).

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Fig. 1. Paleogeography of the Yangtze Platform during the Fortunian Age (A) and Age 2–3 (B) of the Cambrian period and contemporary stratigraphy and lithology around Jinning County, Kunming area (C), and representative event beds intercalated with background beds of Maotianshan Shale Member in Jinning Core which contains an enriched Chengjiang Biota (D). Note that Mb.: Member. Fig. 1A and 1B are modified after Wang et al. (2012 and 2015).

Fig. 2. Typical occurrence of fossils in event beds and background beds (A–E: event beds; F–H: background beds). All scales bars = 1 cm except A and F = 0.5 cm. A: *Kunmingella douvillei* (arthropod). B: *Leanchoilia illecebrosa* (arthropod). C: *Cricocosmia jinningensis* (priapulid). D: *Mafangsclex sinensis* (priapulid). E: *Diandongia pista* (brachiopod). F: *Kunmingella douvillei* (arthropod). G: *Saetaspongia densa* (poriferan). H: *Isoxys auritus* (arthropod). Note that G photo was taken by Derek Siveter.

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523 **Fig. 3.** First occurrence of hummocky cross-stratification (HCS) at 119.80 m of Jinning Core. Note
524 that E bed: event bed; B bed: background bed. Scales bar = 2 cm.

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Fig. 4. Burrows in the interval 120–100 m of Jinning Core. A: burrows (white arrows) at 119.42 m; B: burrows (white arrows) at 112.55 m. Note that bioturbations can be found in B beds (A and B). Abbreviation: E Bed, event bed; B Bed, background bed. Scales bars = 0.5 cm.

Fig. 5. Stratigraphy and Sedimentology (A) and Fe-S-Mo-C variations with depth (B) for Jinning core. Fm.: Formation; Mb.: Member; SYT Fm.: the Shiyantou Formation; BS Mb.: the Black Siltstone Member; BCS Mb.: the Black Carbonaceous Shale Member; E bed(s): event bed(s); B bed(s): background bed(s). Ichnofabric Index (i.i.) (Droser and Bottjer, 1991) indicates the abundance of bioturbation from no bioturbation (1 = green) to high bioturbation (5 = pink).

Fig. 6. Model for redox conditions and ecology of the Chengjiang Biota. Deep-waters (indicated in pink) were dominated by dysoxic conditions, where sponge communities were intermittently present; while the shallower shelf and offshore-transitional environments (indicated in blue) were almost persistently oxic, representing the living environment of most Chengjiang taxa. background beds and event beds represent deposits from the deep-water and shallow-water environments, respectively. Event beds are the result of sediments transported by turbidity currents from shallow shelf and offshore-transitional environments.

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571 **Table 1**

572 Measured values of standards and duplicates for iron speciation and sulfur isotopes of pyrites.

Sample number	Depth (m)	Lithology	Fe _{carb} (%)	Fe _{ox} (%)	Fe _{mag} (%)	Fe _{py} (%)	δ ³⁴ S _{py} (‰)
Duplicates for Fe _{py} and δ ³⁴ S _{py}							
GC87 _{p1}	158.88	claystone	-	-	-	1.06	-1.13
GC87 _{p2}	158.88	claystone	-	-	-	1.00	-0.81
GC103 _{p1}	144.24	claystone	-	-	-	0.69	7.49
GC103 _{p2}	144.24	claystone	-	-	-	0.66	8.04
Duplicates for Fe _{carb} , Fe _{ox} and Fe _{mag}							
GC126 _{p1}	127.61	claystone	0.29	0.16	0.18	-	-
GC126 _{p2}	127.61	claystone	0.27	0.17	0.15	-	-
GC147 _{p1}	110.45	claystone	0.34	0.18	0.19	-	-
GC147 _{p2}	110.45	claystone	0.34	0.19	0.19	-	-
GC163 _{p1}	95.70	silty claystone	0.36	0.23	0.23	-	-
GC163 _p	95.70	silty claystone	0.35	0.22	0.26	-	-
Internal lab standards							
CUG-2	-	-	0.12	0.24	0.14	-	-
CUG-3	-	-	1.19	0.18	0.59	-	-
<i>Note: Sample_{p1} and Sample_{p2} are duplicates.</i>							

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