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### ► To cite this version:

Xu Dai, Zhiwei Yuan, Arnaud Brayard, Mingtao Li, Xiaokang Liu, et al.. Calibrating the late Smithian (Early Triassic) crisis: new insights from the Nanpanjiang Basin, South China.. *Global and Planetary Change*, 2021, 201, pp.103492. 10.1016/j.gloplacha.2021.103492 . hal-03236935

**HAL Id: hal-03236935**

**<https://hal.science/hal-03236935v1>**

Submitted on 6 Oct 2021

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## 3 **Calibrating the late Smithian (Early Triassic) crisis: new** 4 **insights from the Nanpanjiang Basin, South China**

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6 **Published in: Global and Planetary Change, 2021, 201, 103492**

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16

### 17 **ABSTRACT**

18 The biotic recovery following the Permian/Triassic boundary mass extinction was  
19 influenced by several secondary extinctions during the Early Triassic, of which the late  
20 Smithian crisis is the most severe known for some nekto-pelagic organisms such as  
21 ammonoids. The Smithian-Spathian transition is characterized by successive global biotic  
22 and environmental changes, including a dramatic positive carbon isotopic excursion, oceanic  
23 anoxia and a cooling event beginning in the late Smithian. However, the tempo, modalities  
24 and the causal relationships among these various events remain poorly constrained. Here we  
25 synthesized paleontological, sedimentological, and geochemical data from three sections  
26 (Motianling, Nafang, and Shanggang) within the Nanpanjiang Basin, representing platform  
27 slop to basinal deposits spanning the Smithian/Spathian boundary. High-resolution analyses  
28 of thin sections show a sudden decrease in richness and abundance of fossil grains at the

29 middle/upper Smithian boundary in all three sections, coinciding with the onset of a positive  
30 shift in  $\delta^{13}\text{C}_{\text{carb}}$ . It also slightly precedes the beginning of the late Smithian cooling. At  
31 Shanggang, a change in dominance from bivalve-rich to ostracod-rich strata is also recorded  
32 at the middle/upper Smithian boundary. Overall, our results therefore indicate that a first  
33 major biotic crisis and turnover happened during the beginning of the late Smithian in the  
34 Nanpanjiang Basin, rather than around the Smithian/Spathian boundary. Complementary  
35 analyses on pyrite framboid size indicate that these observed biotic changes are concurrent  
36 with oxygen depletion in the studied sections, supporting the hypothesis that oceanic anoxia  
37 also played an important role in the late Smithian crisis in combination with climate cooling  
38 and oceanic acidification.

39

## 40 1. INTRODUCTION

41 After the largest known mass extinction at the Permian/Triassic boundary (PTB), the  
42 subsequent biotic recovery during the Early Triassic was a period characterized by recurrent  
43 deleterious environmental conditions (Song et al., 2012; Sun et al., 2012; Grasby et al., 2013a;  
44 Romano et al., 2013) and several secondary extinctions (Stanley, 2009; Jattiot et al., 2016;  
45 Foster et al., 2017), among which the late Smithian crisis (LSC, ~249.6 million years ago;  
46 Widmann et al., 2020) was probably the most severe. The LSC corresponds to climatic and  
47 marine environmental upheavals coeval to marked extinctions and turnovers in nekto-pelagic  
48 organisms such as ammonoids and conodonts (Orchard, 2007; Brayard et al., 2009;  
49 Goudemand et al., 2019; Song H.Y. et al., 2019). During this event, ammonoids suffered  
50 diversity and disparity bottlenecks, with e.g., the disappearance of ~80% of families and the  
51 transient loss of sphaeroconic forms (Brayard et al., 2009; Brühwiler et al., 2010a; Brosse et  
52 al., 2013; Zhang et al., 2019b). At the same time, ammonoids exhibit a marked change in  
53 paleogeographic distribution, becoming highly cosmopolitan (Brayard et al., 2006, 2007; Dai  
54 and Song, 2020). During the early late Smithian, ammonoid assemblages were dominated  
55 worldwide by iconic prionitids such as *Anasibirites* and *Wasatchites* (Tozer, 1981; Brayard et  
56 al., 2006; Brayard et al., 2007; Jattiot et al., 2016, 2018). Conodonts also show marked  
57 turnovers as well as size changes in segminate P1 elements during the late Smithian or near  
58 the Smithian/Spathian boundary (Orchard, 2007; Chen et al., 2013; Leu et al., 2019; Zhang et

59 al., 2019b). Overall, the LSC had a severe impact on nekton almost rivalling in intensity with  
60 that of the PTB mass extinction (Orchard, 2007; Brayard et al., 2009; Jattiot et al., 2016).  
61 However, this major event did not markedly delay the biotic recovery. For instance,  
62 ammonoids and conodonts show a remarkable diversification during the early Spathian  
63 (Orchard, 2007; Brayard et al., 2019). Benthos also shows a significant recovery in the  
64 Spathian (Song et al., 2011; Hofmann et al., 2014, 2015; Foster et al., 2017). In addition, a  
65 diverse and complex marine biota was recently documented from the earliest Spathian of the  
66 western USA basin (Brayard et al., 2017). Another key late Smithian change in the marine  
67 realm corresponds to the shift in taxonomic composition of marine predatory guilds, from  
68 fish/amphibian- to fish/reptile-dominated higher trophic levels (Scheyer et al., 2014).

69 From a geochemical point of view, this event corresponds to a marked, global,  
70 positive carbon isotope excursion beginning near the middle/upper Smithian boundary up to  
71 the lower Spathian, indicating large environmental perturbations during this interval (Payne  
72 et al., 2004; Tong et al., 2007; Song et al., 2013). Sun et al. (2012) initially postulated that  
73 lethally hot temperatures caused the LSC. However, new high-resolution oxygen isotope  
74 measurements from the Salt Range show a rapid climate cooling during the latest Smithian  
75 (Goudemand et al., 2019). Spore-pollen analyses show a rapid transition from the middle  
76 Smithian spore-dominated floras to the latest Smithian gymnosperm-dominated assemblages,  
77 reflecting a change from a humid, warm climate in the middle Smithian to a drier, cooler  
78 climate during the latest Smithian (Galfetti et al., 2007b; Hermann et al., 2012). This  
79 observation is also consistent with oxygen isotope trends. Apart from temperature changes,  
80 upper Smithian and Smithian/Spathian boundary dysoxic to anoxic deposits were often  
81 documented worldwide, including South China (Song et al., 2012; Sun et al., 2015; Song H.Y.  
82 et al., 2019), the Salt Range (Hermann et al., 2011), Arctic Canada (Grasby et al., 2013a),  
83 Iran (Zhang et al., 2018), Oman (Clarkson et al., 2016) and USA (Brayard et al., 2019).  
84 However, the exact timing, extent, and triggers of these anoxic deposits remain controversial  
85 (Clarkson et al., 2016; Song H.Y. et al., 2019; Zhang et al., 2019a). For instance, it has been  
86 hypothesized that the pre-late Smithian ocean potentially highly stagnated (Song et al., 2013)  
87 and that the late Smithian cooling restarted the global oceanic circulation and upwellings on  
88 continental margins, leading to transient local increases in marine productivity, expansion of

89 oceanic oxygen-minimum zones, and shelf acidification (Lyu et al., 2019; Song HY et al.,  
90 2019; Song et al., 2021). Another hypothesis is that the cooling event also generated a  
91 glacio-eustatic regression and consequently enhanced the deposit of anoxic sediments  
92 (Goudemand et al., 2019; Hammer et al., 2019).

93 Thus, the relationships between the LSC and coeval environmental and climate  
94 changes remain not completely constrained. Analyses of the biotic responses to the LSC are  
95 mainly derived from compilations of ammonoid and conodont diversity at a regional or  
96 global scale (Tozer, 1981; Orchard, 2007; Brayard et al., 2009; Brühwiler et al., 2010a; Zhang  
97 et al., 2019b). In this work, we synthesized paleontological, paleoredox and  $\delta^{13}\text{C}$  analyses  
98 from three sections (Motianling, Shanggang, and Nafang) of the Nanpanjiang Basin, South  
99 China, to highlight the position of the first biotic changes corresponding to the LSC and to  
100 provide new insights on the potential relationships between the LSC and coeval  
101 environmental upheavals.

102

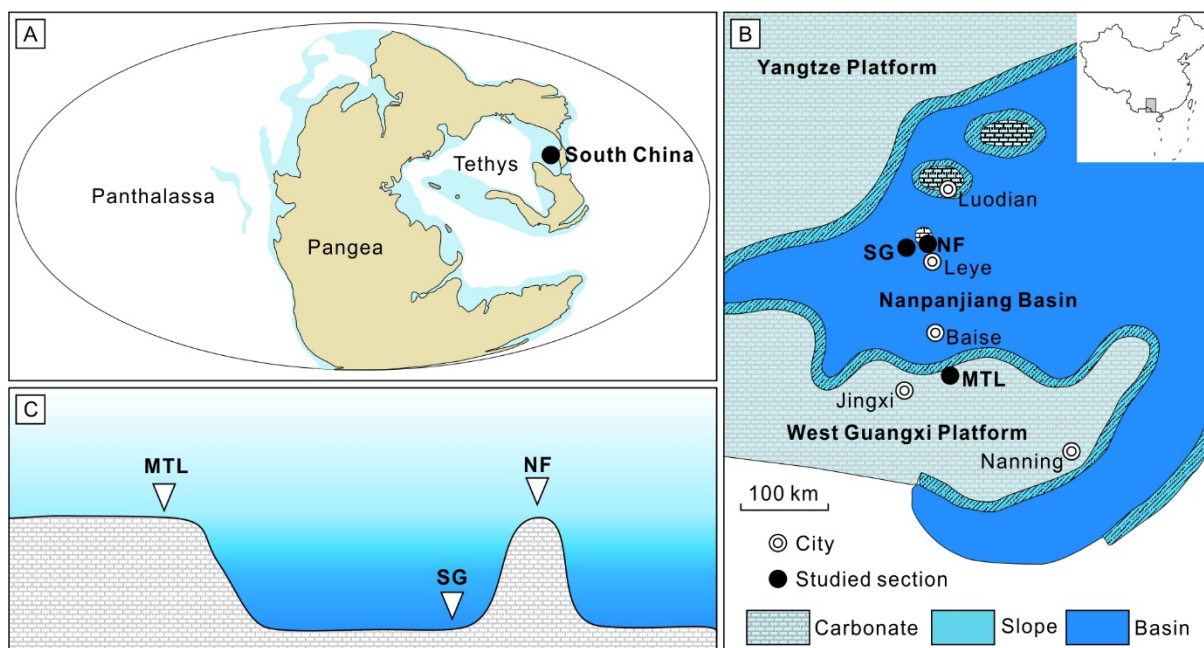
## 103 **2. GEOLOGICAL BACKGROUND**

104

### 105 **2.1. Regional paleogeography and stratigraphy**

106 The South China Block formed a stable paleogeographic element from the Late  
107 Proterozoic to the Late Triassic, mainly dominated by shallow-water carbonates during much  
108 of this time (Enos et al., 1998). Lower Triassic rocks are well exposed throughout South  
109 China (Yang et al., 1987; Tong et al., 2018). During the Early Triassic, the South China block  
110 was located at equatorial latitudes, at the interface between the Panthalassa and Tethys  
111 (Scotese, 2014). A large carbonate platform, the Yangtze Platform, was located in its center.  
112 The Nanpanjiang Basin embayed its southern margin. Several isolated carbonate platforms  
113 such as the Luodian Platform developed within the basin (Feng et al., 1997). Shallow-water  
114 limestones and dolostones dominate the Early Triassic deposits of the Yangtze Platform,  
115 whereas carbonates and siliciclastic series represented by the Luolou Formation dominate in  
116 the Nanpanjiang Basin. The lowermost deposits of the Luolou Formation include the iconic  
117 thick microbialite deposits of Griesbachian age, developed on carbonate platforms and  
118 representing the shallowest environments of the Luolou Formation (Galfetti et al., 2008;

119 Lehrmann et al., 2015; Bagherpour et al., 2017; Fang et al., 2017). The overlaying  
 120 carbonate-siliciclastic unit is made of dark, thin-bedded, laminated mudstones alternating  
 121 with organic-rich shales of Dienerian to Smithian age, suggesting oxygen-restricted and  
 122 low-energy basin environments (Galfetti et al., 2008). Some sites on carbonate platforms  
 123 were not influenced by massive siliciclastic inputs and showed a continuous carbonate  
 124 succession, such as at the Motianling (Wu et al., 2019) and Nafang sections (this work). The  
 125 carbonate-siliciclastic unit is overlain by massive nodular limestones of Spathian age, formed  
 126 in well-oxygenated, medium- to high-energy environments (Galfetti et al., 2008).



127  
 128 Figure 1. (A) Early Triassic paleogeographic map, modified from Scotese (2014). (B) Early  
 129 Triassic paleogeographic map of the Nanpanjiang Basin, modified from Feng et al. (1997). (C)  
 130 Schematic paleogeographic settings of the three studied sections. MTL—Motianling section;  
 131 SG—Shanggang section; NF—Nafang section.

132

## 133 2.2. General Smithian biostratigraphy

134 The Early Triassic is officially divided into two stages, the Induan and Olenekian  
 135 (Ogg, 2012). The latter is further subdivided into two substages, the Smithian and Spathian,  
 136 based on ammonoid biostratigraphy (Tozer, 1965). This subdivision is widely used by the  
 137 Early Triassic workers as the Smithian/Spathian boundary corresponds to the largest known  
 138 intra-Early Triassic event (e.g., Brayard et al., 2009). However, the Smithian/Spathian

139 boundary has not been officially defined (e.g., Zhang et al., 2019). Based on ammonoids, it is  
140 commonly assumed that the Smithian/Spathian boundary can be placed between the late  
141 Smithian *Glyptohiceras/Xenoceltites* assemblage and the early Spathian *Bajarunia/Tirolites*  
142 assemblage (Brayard et al., 2019; Zhang et al., 2019b). Recently, Widmann et al. (2020)  
143 proposed a new latest Smithian ammonoid zone based on data from Nevada, western USA,  
144 which is younger than the *Glyptohiceras/Xenoceltites* assemblage. They therefore suggested  
145 that the Smithian/Spathian boundary should be placed within the separation interval between  
146 this new zone and the Tirolitidae n. gen. A zone. Zhao et al. (2007) claimed the use of the  
147 conodont *Novispathodus pingdingshanensis* as a marker for the Smithian/Spathian boundary.  
148 However, this proposal is still intensively debated (see e.g. discussion in Zhang et al., 2019a  
149 and Widmann et al., 2020). In this work, the biostratigraphic framework and the definition of  
150 the Smithian/Spathian boundary is mainly based on ammonoids, supplemented with recent  
151 conodont works conducted in the Nanpanjiang basin (Wu et al., 2019; Widmann et al., 2020).

152 The Smithian ammonoid biostratigraphy is presently the most well-constrained one  
153 among the four substages of the Early Triassic, benefiting from several recent extensive  
154 bed-by-bed fieldworks and detailed taxonomic revisions in the last decade (Brayard and  
155 Bucher, 2008; Shigeta et al., 2009, 2014; Brühwiler et al., 2010b, 2010c, 2011, 2012a, 2012b,  
156 2012c; Brayard et al., 2013; Jattiot et al., 2016, 2017, 2020; Jenks and Brayard, 2018). Based  
157 on these works, the Smithian can be further subdivided into three parts: early, middle and late  
158 (Brühwiler et al., 2010a). These Smithian subdivisions can also be applied to the Nanpanjiang  
159 basin (Brayard and Bucher, 2008; Jenks et al., 2015).

160

### 161 **2.3. Regional Smithian biostratigraphy**

162 Chao (1959) conducted the first extensive study on Early Triassic ammonoids from  
163 the Nanpanjiang Basin. He established a preliminary zonation including eight ammonoid  
164 zones for the entire Early Triassic. In the last 15 years, Early Triassic ammonoid scales with a  
165 higher resolution were proposed for the Nanpanjiang Basin (Galfetti et al., 2007a; Mu et al.,  
166 2007; Brühwiler et al., 2008; Brayard and Bucher, 2008; Dai et al., 2019). Brayard and  
167 Bucher (2008) recognized four main ammonoid “beds” for the Smithian, i.e., *Kashmirites*  
168 *kapila* beds, *Flemingites rursiradiatus* beds, *Owenites koeneni* beds, and *Anasibirites*

169 *multiformis* beds, which can be further subdivided into successive horizons that can be  
170 correlated worldwide (e.g., Jenks et al., 2015).

171 Early Triassic conodont biostratigraphy is still in progress for the Nanpanjiang Basin.  
172 Although still debated, it often comprises more than ten zones for the entire Early Triassic  
173 (Wu et al., 2019). Recently, eight conodont Unitary Association zones were proposed for the  
174 early Smithian–early Spathian interval (Widmann et al., 2020). Some of these conodont zones  
175 being only of regional significance with some uncertainty in long-distance correlation, we  
176 consequently use the Smithian ammonoid biostratigraphic scale in this work.

177

#### 178 **2.4. Studied sections**

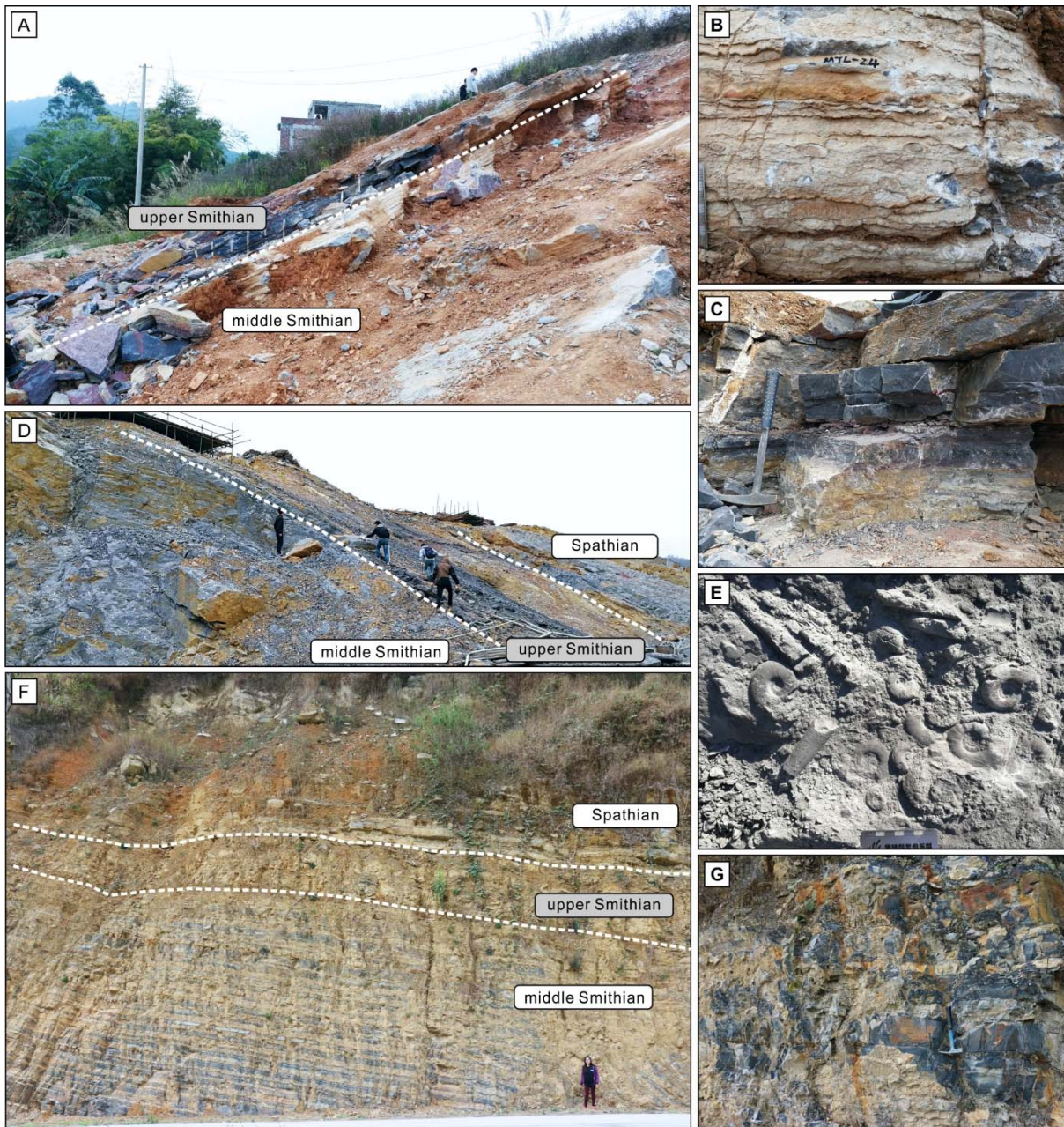
179 The Motianling section (23°26'04"N, 106°57'17"E) was located in the northern  
180 margin of the western Guangxi Platform during the Early Triassic (Fig. 1B, C). A late  
181 Permian-Middle Triassic succession is well exposed at this site. The upper Permian Heshan  
182 Formation is dominated by massive, gray, bioclastic limestones containing abundant  
183 foraminifers, sponges, brachiopods and calcareous algae, representing a well-developed  
184 shallow-water carbonate platform (Wu et al., 2019). The lower Triassic Luolou Formation is  
185 composed of two main lithological units. The basal unit is made of microbialites. The  
186 overlying unit is characterized by light gray, medium- to thick- bedded, argillaceous  
187 limestones (Fig. 2A), with occasional occurrences of ash beds. This unit contains abundant  
188 ammonoids (Fig. 2B). Wu et al. (2019) provided a comprehensive conodont biostratigraphical  
189 scale for this section, including eleven conodont zones for the Luolou Formation. However,  
190 only one conodont zone was recognized at this site for the entire Smithian.

191 The Nafang section (24°48'48"N, 106°32'56"E) is located about 3 km north of Leye  
192 County (Fig. 1B). The lithological succession at Nafang is relatively similar to the Motianling  
193 section (Fig. 2D). The base of the Luolou Formation is also characterized by microbial  
194 deposits, overlain by massive, light gray limestones, which contain abundant ammonoids and  
195 occasionally bivalve-rich beds (Fig. 2E). These calcareous deposits do not interfinger with  
196 siliciclastic deposits. This suggests that the Nafang section was located on a rather isolated  
197 highland within the Nanpanjiang Basin during the Early Triassic (Fig. 1C).

198 The Shanggang section (24°48'45"N, 106°32'32"E) is located 700 m west of the



199 Nafang section (Fig. 1B, C). The upper Permian Heshan Formation, lower Triassic Luolou  
200 Formation, and the middle Triassic Baifeng Formation are well exposed along a newly built  
201 road. The Heshan Formation is composed of massive, dark-gray bioclastic limestones  
202 showing centimetric to decametric irregular, dark chert concretions. The succession  
203 corresponding to the Luolou Formation is similar to the one already described by Galfetti et  
204 al. (2008) and Widman et al. (2020). The faunal content of the Griesbachian-Dienerian strata  
205 was documented in Brühwiler et al. (2008), Hautmann et al. (2010) and Kaim et al. (2010).  
206 The Smithian deposits are characterized by thin-bedded limestones alternating with dark  
207 shales. Part of their ammonoid content was preliminarily described by Brayard and Bucher  
208 (2008). The Spathian is mainly composed of massive nodular limestones (Fig. 2F), as  
209 thoroughly described in Galfetti et al. (2008). Widmann et al. (2020) provided a synthetic  
210 study of the Smithian-Spathian succession at Shanggang, including conodont biostratigraphy,  
211 U-Pb dating and carbon isotopes. These recent data thus provide a robust basis for  
212 stratigraphic correlation among studied sections.



213

214 Figure 2. Field photos of the studied sites: (A) Motianling section, (B) bed MTL-24,  
 215 containing abundant ammonoids at Motianling, (C) late Smithian strata at Motianling,  
 216 showing dark limestones, (D) Nafang section, (E) abundant ammonoids from the *Xenoceltites*  
 217 *variocostatus* Zone at Nafang, (F) Shanggang section, (G) black shales alternating with dark  
 218 limestones and characterizing the late Smithian interval at Shanggang.

219

### 220 3. MATERIAL AND METHODS

221

#### 222 3.1. Ammonoid study

223 Ammonoid specimens were collected bed-by-bed. However, some beds are highly  
224 cemented, preventing an easy excavation on the field. Careful preparation was performed  
225 using air tools to workout morphological details and thereby facilitate taxonomic assignment.  
226 Specimens were photographed using a Canon 70D camera with a Micro EF lens with 100  
227 mm focal length and f/2.8 aperture. Taxonomic assignment mainly follows the classification  
228 proposed by Brayard and Bucher (2008) and refined by Jenks and Brayard (2018).

### 230 **3.2. Carbon isotope analyses**

231 Widmann et al. (2020) recently provided a high-resolution carbon isotope profile from  
232 Shanggang. We thus did not replicate similar analyses on Shanggang section. The Nafang  
233 succession is nearly identical to Motianling, both representing shallow-water settings. Thus,  
234 we only analyzed samples from the Motianling section. Thirty-eight limestone samples were  
235 collected from a ~5 m interval, covering the Smithian-Spathian transition, for carbon isotope  
236 analyses. Carbon isotopes were analyzed at the State Key Laboratory of Biogeology and  
237 Environmental Geology, China University of Geosciences, Wuhan. Powders were drilled  
238 using a dental drill after removing minor and weathered surfaces. About 300  $\mu\text{g}$  powder was  
239 sealed into a 10 mL round-bottomed borosilicate vials, and reacted with 0.05 mL 99%  
240 orthophosphoric acid (Merck, Darmstadt, Germany, cat. #1.00565) at 72 °C after purged with  
241 99.999% helium. The extracted  $\text{CO}_2$  was then transported in a MAT253 isotope ratio mass  
242 spectrometer via a coupled Finnigan GasBench II interface to determine the carbon and  
243 oxygen isotope compositions. Isotopic values are reported as per mil notation (‰) with  
244 respect to the Vienna Pee Dee Belemnite (VPDB) standard, calibrated against laboratory  
245 standards GBW04416 ( $\delta^{13}\text{C}=1.61\text{‰}$ ) and GBW04417 ( $\delta^{13}\text{C}=-6.06\text{‰}$ ). The reproducibility of  
246 replicate analyses for standards and samples was better than  $\pm 0.1\text{‰}$  for  $\delta^{13}\text{C}$ .

### 248 **3.3. Thin section analyses and statistics of fossil grains**

249 A total of 45, 39 and 46 thin sections were made for facies analysis and fossil grains  
250 statistics. Due to the highly cemented nature of the studied limestones, the extraction of  
251 macrofossils is often difficult, except in a few beds with abundant ammonoids. We therefore  
252 used grid counts of thin sections to quantitatively evaluate the abundance and richness of

253 fossil grains. This approach often sacrifices precise taxonomic identification, and thus,  
254 involves a taxonomic work only performed at a high rank, such as the order or the class.  
255 However thin section counts can quantitatively track the changes in abundance and richness  
256 of high taxonomic-level organisms. It can also be performed at a high stratigraphic resolution,  
257 which is often difficult for specimen-based taxonomic works. Additionally, the highly  
258 cemented nature of the rocks does not significantly bias this approach.

259 To carry out the grid count, we follow several steps. First, we set a standard 10×10  
260 grid transparent slice with a single cell size of 1×1 mm. Then, we put this slice on a thin  
261 section and count the abundance of each kind of fossil grains under the microscope. We count  
262 1 if they occur in a given cell and 0 if not. Finally, we sum their total number of occurrences  
263 within the one hundred cells. To avoid artificial count biases, the analyzed area was chosen  
264 randomly. We additionally choose two different areas to count twice in each thin section and  
265 calculate an average abundance for each identified group. The identification of biotic grains  
266 was performed with the help of the deep learning classifier of microfacies  
267 ([www.ai-fossil.com](http://www.ai-fossil.com), Liu and Song, 2020; website under construction).

268

### 269 **3.4. Pyrite framboid analyses**

270 Paleoredox conditions were tentatively reconstructed by pyrite framboid size analyses,  
271 following the approach of Bond and Wignall (2010) and Tian et al. (2014). These  
272 investigations complement sedimentological observations made on the field and thin section  
273 analyses. Fourteen and seventeen samples from the Motianling and Shanggang sections,  
274 respectively, were thus used to measure the size distribution of pyrite framboids potentially  
275 present in each sample. Samples were cut and polished at a size of  $\sim 2 \times 2$  cm. Pyrite  
276 framboid measurements were performed using a Zeiss reflection microscope at the School of  
277 Earth Sciences, China University of Geosciences (Wuhan). A minimum of 100 pyrite  
278 framboids was measured for each sample when possible.

279

## 280 **4. RESULTS**

281

### 282 **4.1. Ammonoid biostratigraphy**



283           Based on bed-by-bed sampling and the previous work of Brayard and Bucher (2008)  
284 in Guangxi, we illustrate a high-resolution ammonoid framework for the three studied  
285 sections, spanning the middle to late Smithian and including four successive ammonoid zones.  
286 Two zones correspond to the middle Smithian: the *Flemingites rursiradiatus* and *Owenites*  
287 *koeneni* zones, and the other two are late Smithian: the *Anasibirites kingianus* and  
288 *Xenoceltites variocostatus* zones, in ascending order (Fig. 3). This succession is nearly  
289 identical to the one proposed by Brayard and Bucher (2008), except their initial *A.*  
290 *multiformis* beds, which are here further subdivided into two distinct zones, i.e., the lower *A.*  
291 *kingianus* Zone and the upper *X. variocostatus* Zone, which can be correlated worldwide (e.g.,  
292 Jenks et al., 2015; Jattiot et al., 2017).

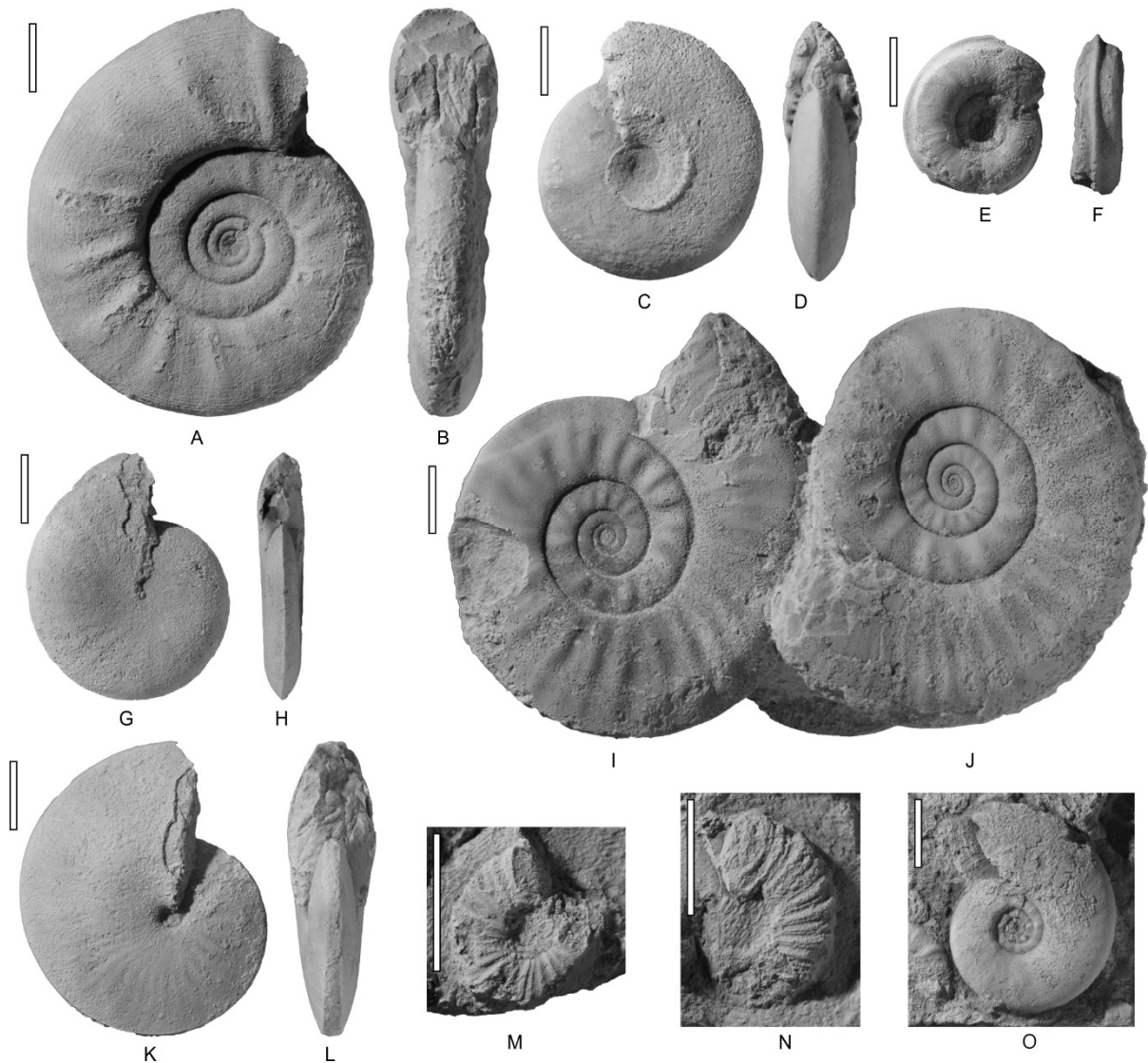
293           The *Flemingites rursiradiatus* Zone is defined on the occurrence of *F. rursiradiatus*. It  
294 contains a highly diversified ammonoid assemblage, including 24 genera (Chao, 1959,  
295 Brayard and Bucher, 2008). Common species are e.g., *Rohillites sobolevi*, *Submeekoceras*  
296 *mushbachanum*, *Pseudaspidites muthianus*, *Mesohedenstroemia kwangsiana* (Brayard and  
297 Bucher, 2008). At Shanggang, *F. rursiradiatus* was not found, but the occurrence of *Rohillites*  
298 sp. indet. and *S. mushbachanum* can be used for stratigraphic correlation, because the two  
299 genera are known so far only from the *F. rursiradiatus* zone in the Nanpanjiang Basin  
300 (Brayard and Bucher 2008). This zone corresponds to the lower *Novispathodus waageni*  
301 Zone at Motianling (Wu et al., 2019), and the conodont UAZ1 at Shanggang (Widmann et al.,  
302 2020).

303           The *Owenites koeneni* Zone is characterized by the occurrence of *O. koeneni*. This  
304 zone can be subdivided into three horizons, i.e., *Ussuria* horizon, *Hanielites* horizon and  
305 *Inyoites* horizon in ascending order (Brayard and Bucher, 2008). However, due to sporadic  
306 occurrence of these index genera in the studied sections, we are not able to use these detailed  
307 subdivisions. The *Owenites koeneni* Zone correlates well among sites from equatorial  
308 paleolatitudes and the North Indian Margin (e.g., Jenks et al., 2015). This ammonoid zone  
309 indicates a middle Smithian age and corresponds to the upper *Novispathodus waageni* Zone  
310 at Motianling (Wu et al., 2019), and the conodont UAZ2 at Shanggang (Widmann et al.,  
311 2020).

312           The *Anasibirites kingianus* Zone in the Nanpanjiang Basin contains the two genera

313 *Anasibirites* and *Hemiprionites* (Brayard and Bucher, 2008). This zone corresponds to the  
314 conodont UAZ4 at Shanggang (Widmann et al., 2020) and indicates an early late Smithian  
315 age. This low-diversity assemblage is represented by highly cosmopolitan ammonoid taxa  
316 that can be used for worldwide correlation (e.g., Brayard et al., 2006, 2007; Jattiot et al.,  
317 2018).

318         The *Xenoceltites variocostatus* Zone corresponds to the second zone of the late  
319 Smithian and is characterized by the association of *X. variocostatus*, *Pseudosageceras*  
320 *augustum*, and *Condensoceras youngi*. These taxa are also rather cosmopolitan and the *X.*  
321 *variocostatus* Zone can therefore be correlated worldwide (Brayard and Bucher, 2008;  
322 Shigeta et al., 2014; Jattiot et al., 2017; Jenks and Brayard, 2018). The *Xenoceltites*  
323 *variocostatus* Zone correlates with the conodont UAZ5 at Shanggang (Widmann et al., 2020).  
324 It can be noted that *Novispathodus pingdingshanensis* occurs in UAZ5, although this taxon  
325 has been claimed as marker for the Smithian/Spathian boundary (see e.g. discussion in  
326 Zhang et al., 2019 and Widmann et al., 2020). Its temporal distribution thus probably extends  
327 from the late Smithian to early Spathian and it is thus probably better not to consider this  
328 species as an appropriate marker for the Smithian/Spathian boundary. As this debate requires  
329 more data and is beyond the scope of this work, we follow the original definition of the  
330 Smithian and Spathian substage, proposed by Tozer (1965) based on ammonoid zones. Thus,  
331 the *Xenoceltites variocostatus* Zone is considered to represent the latest Smithian in South  
332 China.

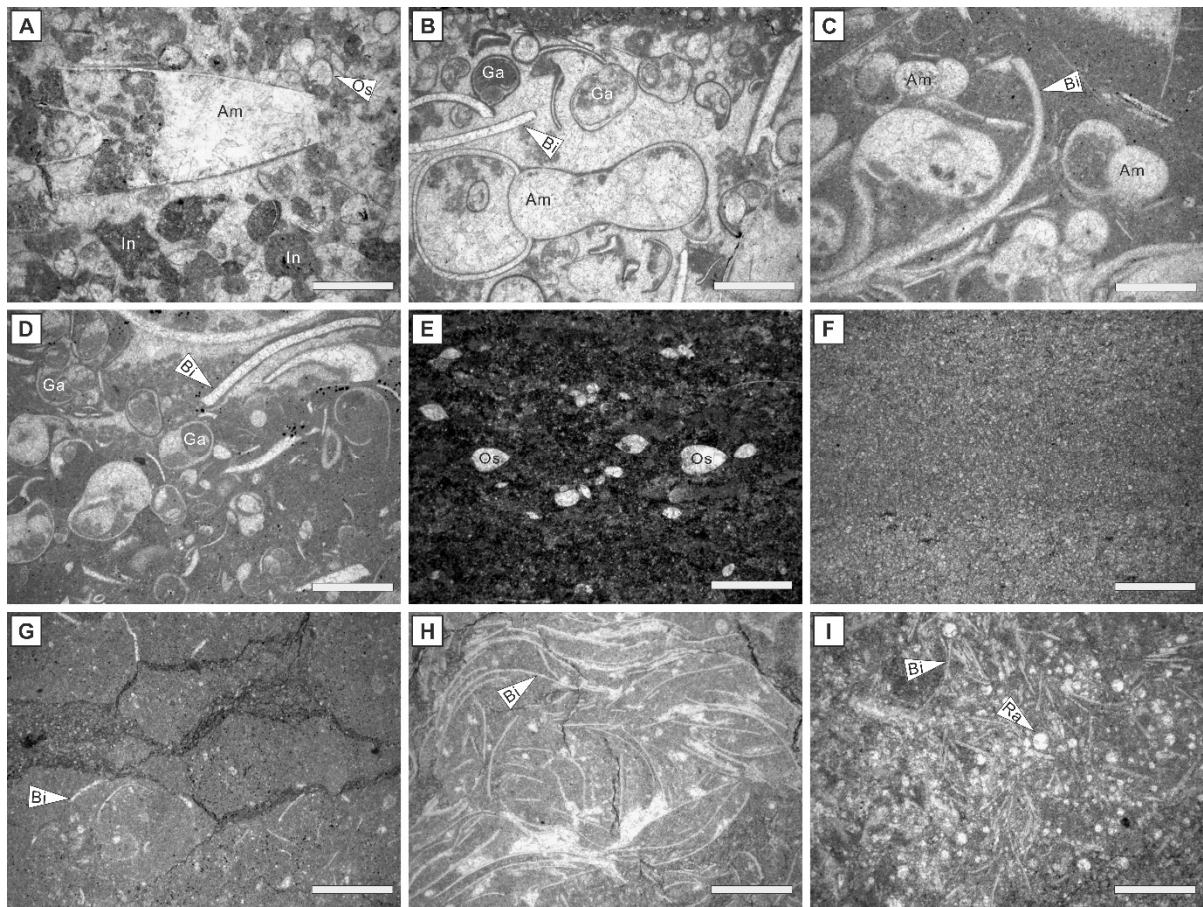


333  
 334 Figure 3. Typical middle and late Smithian ammonoids collected from the studied sections.  
 335 (A, B) *Flemingites rursiradius*. (C, D) *Owenites koeneni*. (E, F). *Proharpoceras*  
 336 *carinatitabulatum*. (G, H) *Aspenites acutus*. (I, J). *Rohillites sobolevi*. (K, L)  
 337 *Mesohedenstroemia kwangiana*. (M, N) *Anasibirites kingianus*. (O) *Xenoceltites*  
 338 *variocostatus*. All specimens from Nafang section, except for M-N, from Motianling section.  
 339 The scale bars represent 1 cm.

340

#### 341 4.2. Facies analysis

342 The Smithian-Spathian successions of Motianling, Nafang, and Shanggang consist of  
 343 seven facies that can be combined into three main facies associations, representing platform  
 344 slope, deep shelf, and basin settings (Table 1, Fig. 4). Facies associations of the platform and  
 345 deep shelf are prevalent in Motianling and Nafang, whilst deep basin settings occur only in



347  
 348 Figure 4. Photomicrographs of observed microfacies in the studied sections. (A)  
 349 Intraclast-rich grainstone (MF2); Motianling, Sample MTL-35b. (B) Gastropod-rich  
 350 grainstone (MF2); Motianling, Sample MTL-26b. (C) Bioclastic packstone with diverse  
 351 fossils (MF3). Nafang, Sample NF-139. (D) Bioclastic packstone with diverse fossils (MF3);  
 352 Motianling, Sample MTL-25b. (E) Bioclastic wackestone (MF4), the bioclasts are  
 353 represented by ostracods. Shanggang, Sample SG-144. (F) Lime mudstone (MF5);  
 354 Motianling, Sample MTL-30b. (G) Bioclastic wackestone showing nodular structure;  
 355 Motianling, Sample MTL-41. (H) Thin-shelled bivalve packstone; Shanggang, Sample  
 356 SG-157. (I) Calcispheres packstone with the occurrence of thin-shelled bivalves;  
 357 Shanggang, sample SG-125. Scale bar: 1 mm.

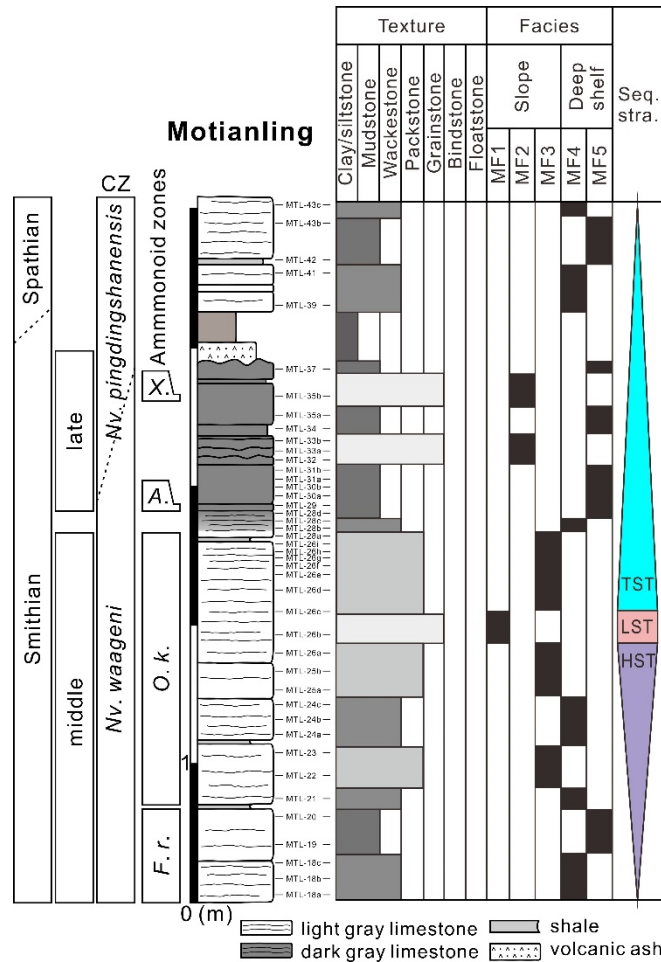
358

#### 359 4.2.1. Motianling section

360 **Description:** The middle Smithian interval in Motianling comprises greyish-banded  
 361 limestone and yellowish marlstone. Banded limestone mainly consists of gastropod-rich



362 grainstone (MF1, Fig. 4B), bioclastic packstone (MF3), and nodular bioclastic wackestone  
 363 (MF4). The upper Spathian succession consists of dark grey limestone and is characterized  
 364 by its macrofossil paucity. Bioclasts are rare in the dark grey limestones excepting two levels  
 365 that consist of intraclast grainstone (MF2) in which ostracods are abundant. The overlying  
 366 lower Spathian succession is composed of nodular limestone that is mainly represented by  
 367 low energy facies, including bioclastic wackestone (MF4) and lime mudstone (MF5) (Fig. 5).



368  
 369 Figure 5. Sequence stratigraphy and microfacies evolution from the middle Smithian to the  
 370 lower Spathian at Motianling. Abbreviations: CZ—conodont zones. Nv.—*Novispathodus*. X.  
 371 —*Xenoceltites variocostatus*. A.—*Anasibirites kingianus*. O. k.—*Owenites koeneni*. F. r.—  
 372 *Flemingites rursiradiatus*. Seq. stra.—Sequence stratigraphy. TST—transgressive systems  
 373 tract. LST—lowstand systems tract. HST—highland systems tract.

<b>Microfacies</b>	<b>Biogenic content and texture</b>	<b>Sedimentary structure</b>	<b>Standard microfacies</b>	<b>Depositional setting</b>
MF1 Gastropod-rich grainstone	Abundant gastropods, common bivalves and ammonoids; Poorly sorted bioclasts cemented by sparry calcite.	Banded limestone intercalated with marls.	SMF 5	Platform slope
MF2 Intraclast grainstone	Abundant intraclasts with occasional ostracods; Moderately sorted bioclasts with sparry calcite.	Ripple laminated limestone	SMF 4	
MF3 Bioclastic packstone with diverse fossils	Common gastropods and bivalves, occasional ammonoids; Geopetal structures developed in shells of gastropods and ammonoids.	Massive limestone with thin banded marl intercalations.	SMF 5	
MF4 Ostracod wackestone	Occasional ostracods with rare thin-shelled bivalves.	Thin, fine laminated limestone	SMF 10	Deep shelf
MF5 Lime mudstone	Rare ostracods, thin-shelled bivalves.	Massive limestone	SMF 3	
MF6 Thin-shelled bivalve packstone	Abundant thin-shelled bivalves and rare ostracods or calcispheres.	Thin bedded limestone	SMF 12	Basin
MF7 Calcispheres-rich packstone/wackestone	Abundant calcispheres and common thin-shelled bivalves.	Horizontally laminated limestone	SMF 3	

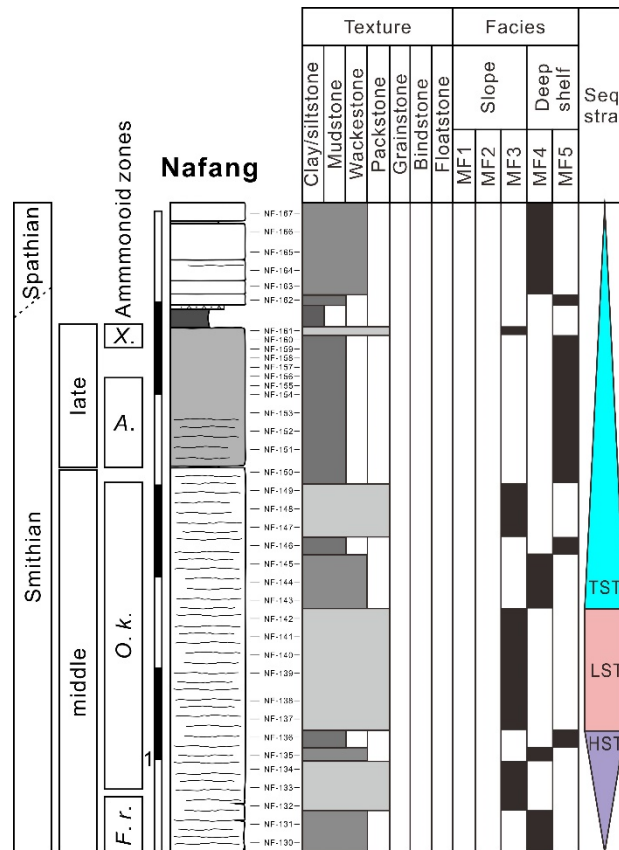
375 **Interpretation:** The vertical distribution of Smithian-Spathian microfacies in Motianling  
376 shows a gradual deepening-upward trend, a transition from carbonate platform slope to deep  
377 shelf. The Smithian sequence is characterized by the occurrence of gastropod-rich grainstone  
378 (MF1) and mollusk-dominated packstone (MF3). Allochthonous bioclasts (i.e., gastropods,  
379 bivalves, and ammonoids) in MF1 are poorly sorted and highly abraded, and show a  
380 fining-upward trend, as well as a sharp lower erosive boundary, suggesting they correspond  
381 to tempestite deposits (Flügel, 2010; Pérez-López and Pérez-Valera, 2012). The randomly  
382 oriented geopetal fabrics in the shells of MF3, indicate reworking and redeposition,  
383 supporting a middle Smithian sequence deposited in high-hydrodynamic settings of the  
384 platform slope to deep shelf. The upper Smithian interval mainly consists of nodular  
385 wackestone/lime mudstone (MF5). Two thin layers of intraclast-rich grainstone (MF2) are  
386 interbedded with MF5. The MF2 intraclasts are poorly rounded and weakly sorted, indicating  
387 they were probably formed near or in the storm wave base on the platform slope and rapidly  
388 transported into the deep shelf.

389

#### 390 **4.2.2. Nafang section**

391 **Description:** The middle Smithian succession in Nafang is mainly composed of massive  
392 limestones. Yellowish marlstones are absent. This differs from the Motianling succession.  
393 The massive limestone is rich in bioclasts including ammonoids and gastropods, which  
394 constitute the main component of bioclastic packstone (MF3). The upper Smithian interval is  
395 composed of dark grey limestone lacking macro- and micro-fossils, excepting one thin layer  
396 in which ostracods are abundant. The overlying lower Spathian interval is composed of  
397 thin-bedded bioclastic wackestone (MF4) (Fig. 6).

398 **Interpretation:** The middle Smithian succession corresponds to packstone-dominated  
399 limestones in which abundant macrofossils (especially gastropods and ammonoids) are well  
400 preserved. Geopetal fabrics are common but are oriented randomly, suggesting a reworking  
401 of shells after deposition by distal storm waves (Kidwell, 1991; Chatalov, 2013). The upper  
402 Smithian sequence is dominated by lime mudstones with very rare occurrences of fossils. A  
403 thin layer with abundant ostracods intercalated in the lime mudstones, similar ostracods rich  
404 beds also documented at Waili Fall section (Galfetti et al., 2008). The lower Spathian  
405 succession consists of monotonous bioclastic wackestones, indicating a stable deeper shelf  
406 setting. Overall, the Smithian-Spathian sequence shows a deepening-upward trend, similar to  
407 that of Motianling.



408

409 Figure 6. Sequence stratigraphy and microfacies evolution from the middle Smithian to the  
 410 lower Spathian at Nafang. Abbreviations: see Figure 5.

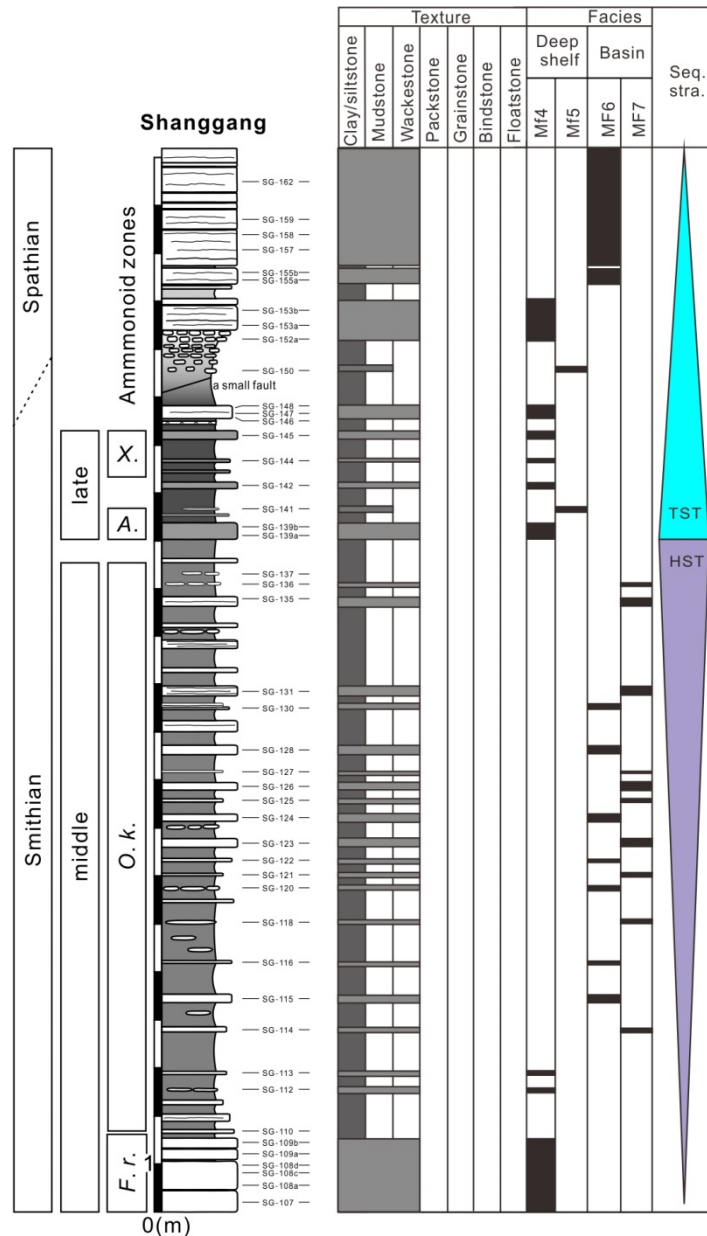
411

412 **4.2.3. Shanggang section**

413 **Description:** The middle Smithian succession is composed of planar laminated, greenish  
 414 mudstone intercalated with thin layers of limestone in which bioclasts are represented by  
 415 thin-shelled bivalves (MF6) and calcified calcispheres (MF7). The upper Smithian interval  
 416 consists of dark grey limestones embedded in black shales. The upper Smithian biofacies are  
 417 comparable with their counterparts in Motianling and Nafang, all of which are characterized  
 418 by their organic-rich levels and the concentration of ostracods in thin layers of dark grey  
 419 limestones. The overlying lower Spathian succession is dominated by nodular/ribbon  
 420 limestone consisted of densely packed thin-shelled bivalves (MF6) (Fig. 7).

421 **Interpretation:** The Smithian and Spathian successions of the shanggang section is identical  
 422 to the section from the Jinya/Waili area, mainly dominated by basinal facies (Galfetti et al.,  
 423 2008). Facies of the middle Smithian interval are interpreted as basinal deep-water facies  
 424 (Galfetti et al., 2008; Flügel, 2010; Li et al., 2019). It is noteworthy that the middle Smithian  
 425 lithofacies are highly similar to coeval deposits in the deep-water section of Xiukang, South  
 426 Tibet (Li et al., 2019). The Smithian-Spathian sequence only contains two system tracts with

427 the lack of lowstand system tract, a pattern that is different from that of Motianling and  
 428 Nafang. This is probably because that Shanggang was deposited in deeper settings, which  
 429 were less influenced by relative sea level fluctuations.  
 430

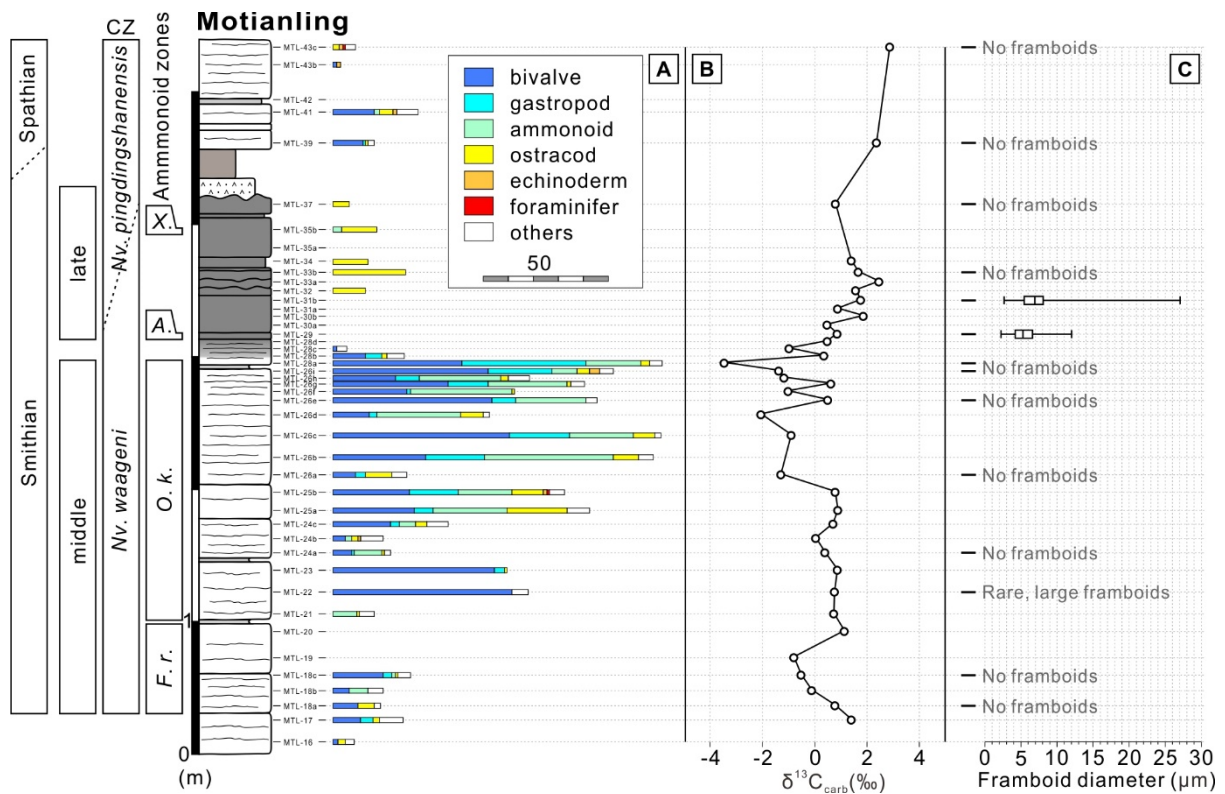


431  
 432 Figure 7. Sequence stratigraphy and microfacies evolution from the middle Smithian to the  
 433 lower Spathian at Shanggang. Abbreviations: see Figure 5.  
 434

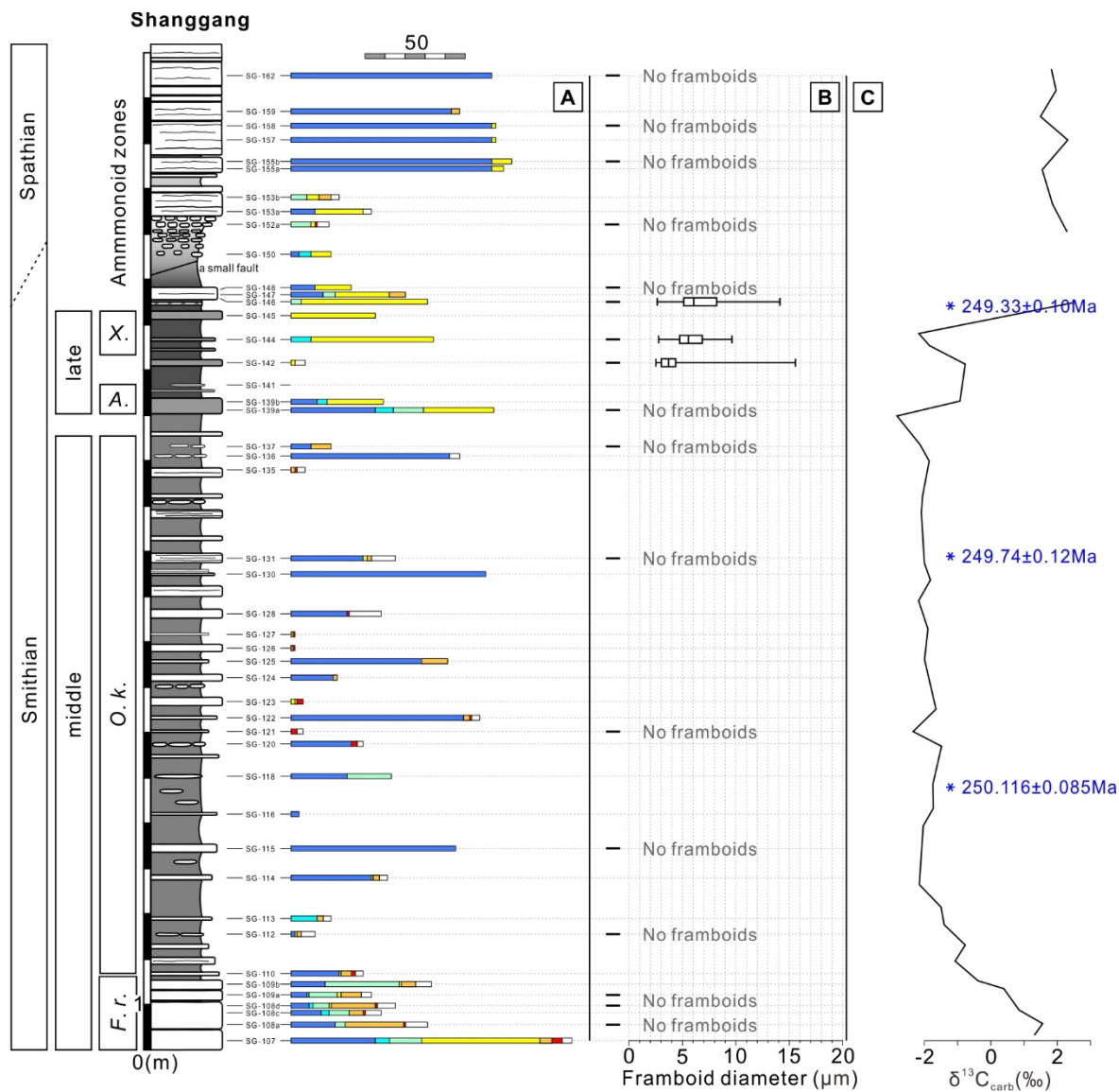
435 **4.3. Carbon isotope profile**

436 The carbon isotope signal obtained from the Motianling section displays an overall  
 437 variation from -3.5‰ to 2.8‰ during the middle Smithian to the earliest Spathian (Fig. 8). It  
 438 shows a gradual decrease across the *Flemingites rursiradiatus* Zone, followed by a slightly

439 positive shift at the top of this zone, and then, a plateau around 1‰ in the lower *Owenites*  
 440 *koeneni* Zone. A second drop is observed in the middle of the *O. koeneni* Zone, followed by a  
 441 fluctuating signal ranging from -3.5‰ to 0.5‰. A positive excursion is recorded from the  
 442 base of the late Smithian up to the early Spathian. This positive shift is also documented at  
 443 Shanggang (Widmann et al., 2020, their fig. 6), in neighboring sections (e.g., Galfetti et al.,  
 444 2007) and worldwide (e.g., Zhang et al., 2019).



445  
 446 Figure 8. Paleontological and environmental analyses from the Motianling section. (A) Count  
 447 of fossil grains: the bars represent the number of grid cells containing each kind of grains per  
 448 one hundred cells. (B) Carbon isotope curve. (C) Pyrite framboid size measurements.  
 449 Abbreviations: see Figure 5.



450

451 Figure 9. Paleontological and environmental analyses from the Shanggang section. (A) Fossil  
 452 grains. (B) Pyrite framboid measurements. (C) Carbon isotope curve and U-Pb ages,  
 453 modified from Widmann et al. (2020). Abbreviations: see Figure 5.

454

#### 455 4.4. Fossil grains

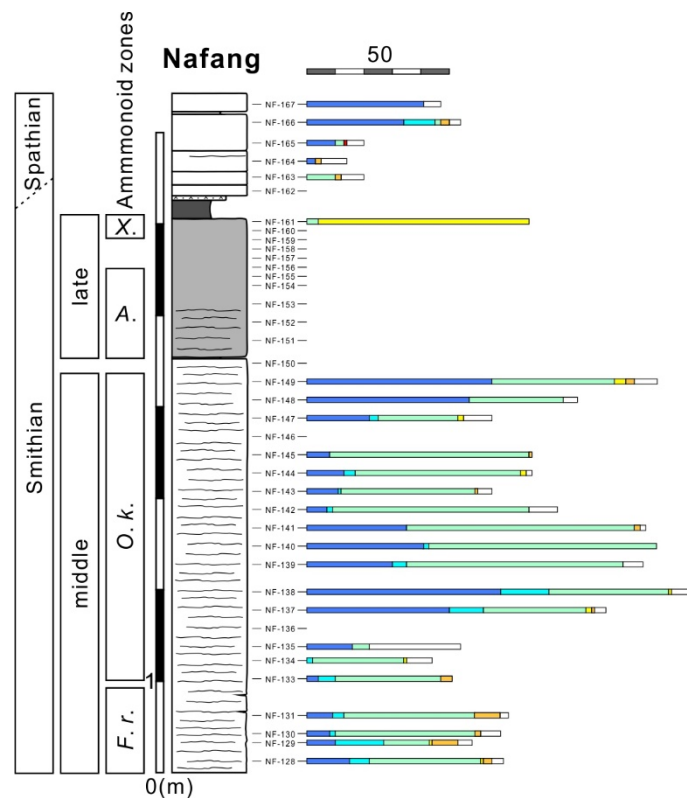
456 Overall, the middle Smithian strata mainly contain mollusk remains (i.e., bivalves,  
 457 ammonoids, and gastropods), whereas overlying late Smithian deposits are dominated by  
 458 ostracods in all studied sections (Figs. 8-10).

459 At Motianling and Nafang, strata corresponding to the *Flemingites rursiradiatus* and  
 460 *Owenites koeneni* Zones include abundant and diverse grains, dominated by mollusks (e.g.,  
 461 bivalves and ammonoids). At the middle/upper Smithian boundary, fossil grains show a  
 462 dramatic decrease in diversity and abundance. The late Smithian is here exclusively  
 463 characterized by occasional occurrences of ostracod grains. In the early Spathian, the



464 diversity and abundance of grains show a weak increase.

465 At Shanggang, fossil grains are abundant and diverse in the *Flemingites rursiradiatus*  
466 Zone. The *Owenites koeneni* Zone is exclusively dominated by bivalves. At the middle/upper  
467 Smithian boundary, fossil grains show a shift in dominance, from bivalves to ostracods.  
468 Across the Smithian/Spathian boundary, the abundance in ostracod grains decreased,  
469 followed by an abrupt increase of bivalve particles during the early Spathian.



470  
471 Figure 10. Temporal evolution of fossil grains at Nafang section. for Abbreviations: see  
472 Figure 5.

#### 473 474 **4.5. Paleoredox conditions**

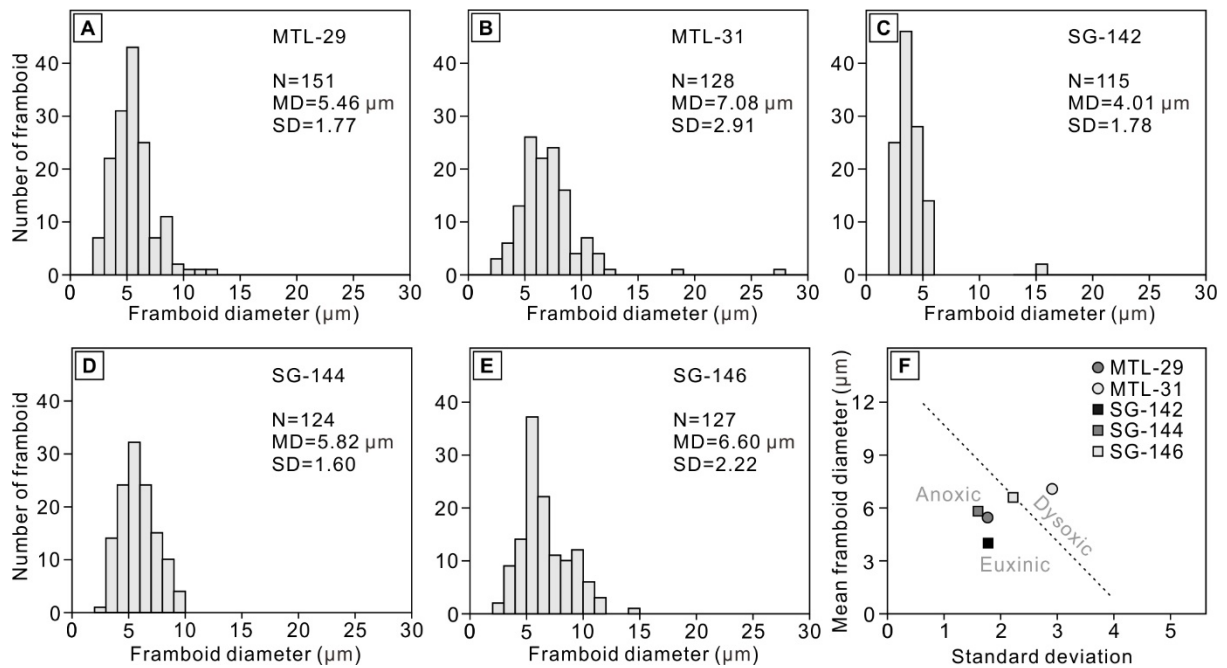
475 The reconstruction of paleoredox history is based on microfacies and pyrite framboid  
476 analyses. 14 and 17 samples from Motianling and Shanggang were polished for pyrite  
477 framboid analyses, respectively. Two samples from Motianling and three samples from  
478 Shanggang yield abundant pyrite framboids (Figs. 8, 9). Other samples contain a few large or  
479 no pyrite framboids.

480 At Motianling, the middle Smithian samples do not contain pyrite framboids. This  
481 interval is characterized by bioclastic packstones with abundant ammonoids and a few  
482 gastropods, corresponding to well-oxygenated slope facies (Figs. 2B, 5). Two (MTL-29 and  
483 MTL-31) of the four samples from the late Smithian show abundant framboids. The late



484 Smithian strata are made of dark finely-laminated mudstone intercalated with ostracod-rich  
485 grainstone, suggesting dysoxic to anoxic deep shelf settings (Figs. 2C, 5). The two samples  
486 from the early Spathian do not show any pyrite framboids. MTL-29 contains small framboids  
487 (mean diameter = 5.46  $\mu\text{m}$ ; Fig. 11A) with a small standard deviation (1.77), suggesting  
488 potential euxinic-anoxic conditions (Fig. 11F), based on the method of Bond and Wignall  
489 (2010) and Tian et al. (2014). Framboids in sample MTL-31 have a larger mean diameter  
490 (7.08  $\mu\text{m}$ ; Fig. 11B) and standard deviation (2.91), suggesting a dysoxic environment (Fig.  
491 11F). Pyrite framboids data are thus consistent with sedimentary observations.

492 At the Shanggang section, middle Smithian samples do not contain pyrite framboids.  
493 However, the middle Smithian interval at Shanggang is dominated by dark shales interbedded  
494 with thin limestones, likely corresponding to oxygen-poor deep shelf settings. Two (SG-142  
495 and SG-144) of the three samples from the late Smithian exhibit abundant framboids. The  
496 late Smithian interval is dominated by black shales and black finely-laminated ostracod-rich  
497 wackestones (Figs. 2G, 4E, 7), suggesting a deep shelf oxygen-poor environment, identical to  
498 the upper Unit IV described from the Luolou Formation by Galfetti et al. (2008). In the six  
499 remaining samples, only one near the Smithian/Spathian boundary contains pyrite framboids.  
500 Framboids from samples SG-142 and SG-144 exhibit small mean diameters (4.01  $\mu\text{m}$  and  
501 5.82  $\mu\text{m}$ , respectively; Figs. 11C, D) with small standard deviations (1.78, and 1.60,  
502 respectively). These values suggest potential euxinic-anoxic conditions for the corresponding  
503 beds (Fig. 11F). SG-146 contains large pyrite framboids (mean diameter = 6.60  $\mu\text{m}$ ; Figs.  
504 11E) with a large standard deviation (2.22), indicating a potential dysoxic environment (Fig.  
505 11F).



506

507 Figure 11. Size distributions of pyrite framboids in late Smithian strata of Motianling and

508 Shanggang (A-E) and corresponding interpreted redox conditions (F). MTL—Motianling; SG

509 —Shanggang.

510

## 511 5. DISCUSSION

512

### 513 5.1. Timing and modalities of the late Smithian crisis

514 The successive global events occurring near the Smithian/Spathian boundary were  
 515 often previously referred to as the “Smithian/Spathian boundary extinction” (Galfetti et al.,  
 516 2007b; Stanley, 2009; Sun et al., 2012; Chen et al., 2013; Sun et al., 2015; Grasby et al.,  
 517 2016). However, recent progresses in biostratigraphy showed that the first dramatic diversity  
 518 drop associated with changes in the spatial distribution of taxa is actually at the middle/upper  
 519 Smithian boundary, at least for some nekto-pelagic taxa (Orchard, 2007; Brayard et al., 2009;  
 520 Brühwiler et al., 2010a).

521 The LSC has an almost equal impact on ammonoids as the PTB mass extinction  
 522 (Brayard et al., 2009; Jattiot et al., 2016) eliminating ~75% ammonoid families (Zhang et al.,  
 523 2019b), coinciding with a severe disparity decrease (Brosse et al., 2013) and a marked  
 524 cosmopolitanism episode (Tozer, 1981; Brayard et al., 2006; Brayard et al., 2007; Jattiot et al.,  
 525 2018). Conodonts also exhibit a diversity bottleneck during this time interval (Orchard, 2007).  
 526 In addition, it corresponds to a size reduction in segminate P1 elements, and a gradual  
 527 increase in segminiplanate P1 elements (Chen et al., 2013; Leu et al., 2019). Apart from the

528 nekton crisis, data from western USA, Dolomites, Hungary, and Lombardy suggest that  
529 benthic ecosystems apparently do not show any remarkable changes during the late Smithian  
530 and the Smithian/Spathian transition, but a potential faunal turnover in the early Spathian  
531 (Hofmann et al., 2014, 2015; Foster et al., 2015, 2017, 2018). Foraminifer data from South  
532 China show a temporary pause in their diversification, but no marked extinctions or turnovers  
533 during the late Smithian (Song et al., 2011). Therefore, based on presently known data, the  
534 LSC has maybe only a few impacts on benthic ecosystems. Intrinsic factors (e.g.,  
535 evolutionary rates) or interspecific competition might be a plausible explanation of this  
536 discrepancy between benthic and nekto-pelagic organisms during the late Smithian (e.g.,  
537 Stanley, 2009; Hautmann et al., 2015). However, it should be noticed that the exact content of  
538 Early Triassic benthic ecosystems at that time is far to be well constrained (e.g., Brayard et al.,  
539 2017).

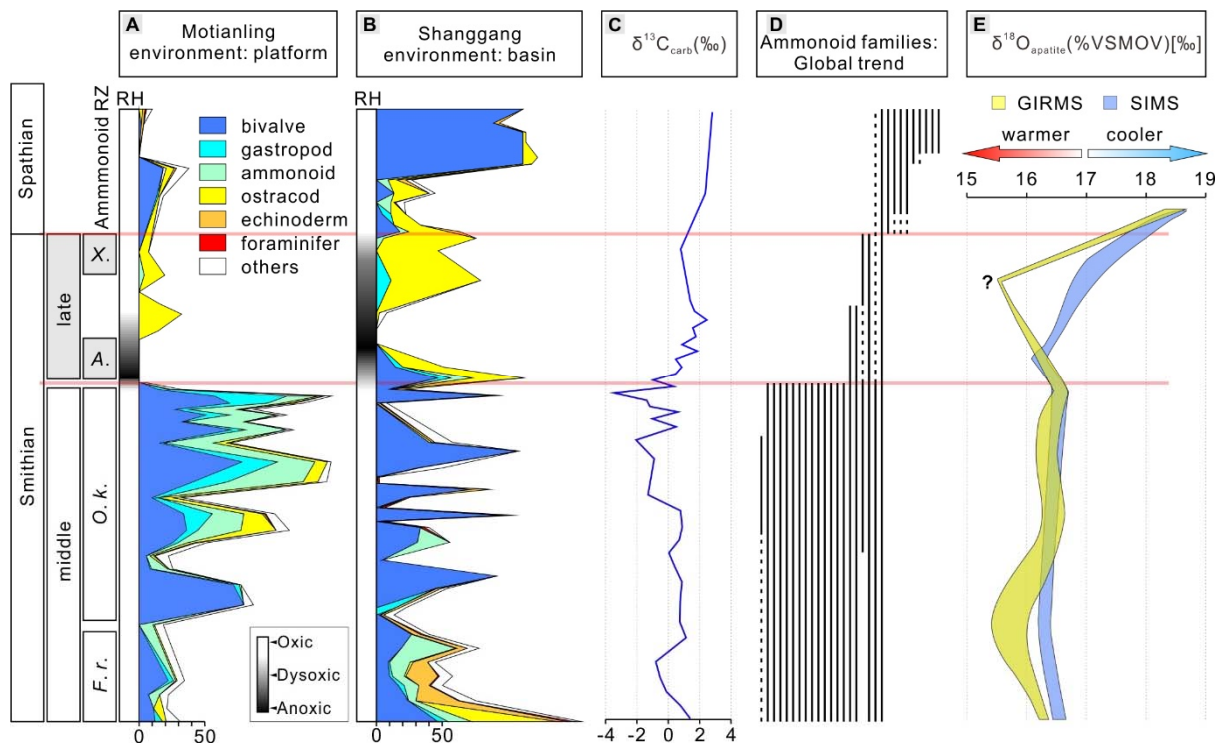
540 At Motianling (shallow-water environment), fossil grains are abundant and diverse  
541 during the middle Smithian (Fig. 8). This echoes the known concomitant remarkable  
542 diversification of e.g., ammonoids, conodonts, and foraminifers (Orchard, 2007; Brayard et  
543 al., 2009; Song et al., 2011). At Shanggang (deeper water settings), fossil grains show a  
544 clade-diversity loss between the *Flemingites rursiradiatus* and *Owenites koeneni* Zones (Fig.  
545 9). This decrease may result from facies change, corresponding to a transition from deep shelf  
546 to basin environment (Fig. 7).

547 A major turnover is visible at the boundary between the *Owenites koeneni* and  
548 *Anasibirites kingianus* Zones, i.e., at the middle/upper Smithian boundary, in the three  
549 studied sections. This turnover is not a result of a sedimentary facies change, as there are no  
550 significant facies change at Motianling and Shanggang. This boundary also coincides with  
551 the onset of the positive carbon isotopic excursion and disoxic/anoxic conditions (Fig. 12).

552 At Motianling and Nafang, the base of the late Smithian corresponds to a severe  
553 decrease in the abundance and diversity of fossil particles (Fig. 8, 10). The same time interval  
554 corresponds to a turnover from mollusk-dominated facies to ostracod-dominated facies in the  
555 deeper water settings of Shanggang. Ostracods notably show a bloom in both shallow and  
556 deep-water environments during the late Smithian. One potential explanation is that ostracods  
557 which often show a high tolerance to temperature changes and anoxia in modern contexts  
558 (Song et al., 2014), can have better survived to marked environmental fluctuations known for  
559 the LSC. Similar ostracod blooms are also reported from various Early Triassic exposures  
560 (Forel et al., 2013; Wan et al., 2019; Gliwa et al., 2020).

561 Our data suggest a potential heterogeneous impact of the LSC on benthic ecosystems

562 depending on their environmental settings. Hence, further studies at different  
 563 paleogeographic locations and in various paleoenvironments at a larger spatial scale are a  
 564 prerequisite to elucidate these differential effects.



565  
 566 Figure 12. Simplified trends of local fossil grain count, global ammonoid family richness and  
 567 environmental proxies around the late Smithian. (A) Count of fossil grains at Motianling. (B)  
 568 Count of fossil grains at Shanggang. (C) Carbon isotope curve from Motianling section. (D)  
 569 Global ammonoid family trend, modified from Zhang et al. (2019b). (E) Oxygen isotope  
 570 curves, modified from Goudemand et al. (2019). RH—redox history. Abbreviations: see  
 571 Figure 5.

572

## 573 5.2. Insights on environmental triggers of the late Smithian events.

574 A series of environmental upheavals were documented around the middle/upper  
 575 Smithian boundary, mainly including: (i) a warm episode during the middle Smithian  
 576 followed by a cooling event during the late Smithian (Goudemand et al., 2019), (ii) the  
 577 occurrence of dysoxic to anoxic deposits in several basins (Grasby et al., 2013a; Song et al.,  
 578 2014; Song H.Y. et al., 2019), and more recently (iii) Hg poisoning (Grasby et al., 2016).  
 579 These changes were assumed to have triggered the LSC or to have been a consequence of this  
 580 event (e.g., Grasby et al., 2013a; Goudemand et al., 2019). Causal relationships among these  
 581 different parameters therefore remain partly unclear.

582

### 583 **5.2.1. Oceanic anoxia and acidification**

584 The studied sections show an anoxic/dysoxic event in both shallow- and deep-water  
585 settings during the late Smithian (Fig. 12A, B). The onset of this anoxic event in  
586 shallow-water settings is coeval with the reduction of fossil grains, suggesting a causal  
587 relationship.

588 Anoxia is a potential killing mechanism in many past extinctions, e.g., at the PTB  
589 (Wignall and Twitchett, 1996) and during the Toarcian (Bailey et al., 2003). Late  
590 Smithian-earliest Spathian anoxic deposits were also documented in e.g., Salt Range  
591 (Hermann et al., 2011), North Vietnam (Komatsu et al., 2016), Arctic Canada (Grasby et al.,  
592 2013a), South China (Song et al., 2012; Sun et al., 2015; Song H.Y. et al., 2019; Zhao et al.,  
593 2020). Recent calcium isotope analyses suggested a shelf acidification event associated with  
594 the anoxia event during the late Smithian-earliest Spathian interval (Song et al., 2021). This  
595 widespread anoxia as well as potential acidification thus could have contributed to the LSC.  
596 In this hypothesis, benthic organisms should have been more vulnerable than nekto-pelagic  
597 organisms, who can supposedly benefit from their higher mobility (Bambach et al., 2002;  
598 Song et al., 2018). However, ammonoids and conodonts show a marked extinction (Orchard,  
599 2007; Brayard et al., 2009; Hofmann et al., 2014; Hofmann et al., 2015). In addition, no  
600 evidence for anoxia was found at some places and on isolated highs (e.g., Clarkson et al.,  
601 2016), although ammonoids also exhibit here a diversity drop like in any other locations  
602 (Brühwiler et al., 2012a). This thus suggests that anoxia and acidification probably  
603 contributed to the LSC but were likely not the main driver of nektonic taxa extinction.

604

### 605 **5.2.2. Temperature change**

606 Changes in sea surface temperature (SST) is commonly suggested to be one of the  
607 main triggers of the late Smithian events. Sun et al. (2012) initially reported a thermal  
608 maximum at the Smithian/Spathian boundary. However, after revision of used  
609 biostratigraphical markers and new sensitive high-resolution ion microprobe analyses, this  
610 thermal maximum is now suggested to occur near the middle/upper Smithian boundary or at  
611 the beginning of the early late Smithian (Goudemand et al., 2013, 2019; Zhang et al., 2019b).  
612 The late Smithian thus mainly corresponds to a marked SST decrease event from this thermal  
613 maximum. The LSC nekton diversity drop is consequently associated with complex SST  
614 changes, and notably with a marked decrease, preventing a simple causal relationship  
615 between high-SST and biotic extinction, as initially proposed by Sun et al. (2012).

616 The evolutionary rates of ammonoids and conodonts were very high during the

617 Smithian (Orchard, 2007; Stanley, 2009; Brühwiler et al., 2010a). These high intrinsic  
618 evolutionary rates can have helped to some extent these organisms to display rapid  
619 rediversification during the Early Triassic (Stanley, 2009). Based on data from Pakistan, the  
620 late Smithian cooling mainly occurred from the *Wasatchites distractus* Zone to the earliest  
621 Spathian (Goudemand et al., 2019). This short time interval (~500 kyr; Widmann et al., 2020)  
622 with such relatively rapid SST decrease after a marked warm climate during the middle  
623 Smithian, may have been beyond the physiological tolerances of most ammonoids and  
624 conodonts. So, the rate of the SST change is potentially as crucial as its magnitude to lead to  
625 biotic extinction (Mathes et al., 2021).

626

### 627 **5.2.3. Hg poisoning**

628 Mercury anomalies are usually associated with releases of large igneous provinces.  
629 They were thus used as a putative signal of volcanic activities during the geological past  
630 (Thibodeau et al., 2016; Charbonnier and Follmi, 2017; Grasby et al., 2017; Wang et al.,  
631 2018). Hg poisoning generated by volcanism was recently proposed to be an additional  
632 killing mechanism participating in the LSC (Grasby et al., 2016). These authors documented  
633 Hg enrichments, assumed to be toxic to the ecosystem, during the early late Smithian in  
634 shallow-water settings from western Spitsbergen. However, Hammer et al. (2019) reported  
635 Hg anomalies mainly occurring within the middle Smithian of central Spitsbergen. This casts  
636 doubt on a direct link between Hg anomalies and the late Smithian crisis. Additionally, Hg  
637 contents in Chaohu (South China), Guryul Ravine (Kashmir), and Arctic Canada do not show  
638 any remarkable increase during the late Smithian (Grasby et al., 2013b; Wang et al., 2019).  
639 To sum up, only a few sections recorded so far mercury anomalies during the late Smithian,  
640 suggesting that volcanism poisoning, if real, had only a very limited geographic impact  
641 (Wang et al., 2019). Overall, there is no direct evidence supporting a causal relationship of  
642 Hg anomaly to the late Smithian crisis.

643 In summary, global temperature fluctuations secondarily associated with oceanic  
644 anoxia most likely caused the LSC (Song et al., 2014). Volcanic activities were probably only  
645 responsible for some local to regional stresses (Wang et al., 2019). Further studies combining  
646 primary productivity, eustatic fluctuations, with high-resolution biostratigraphic constraints  
647 could be helpful to fully decipher the primary causes of the LSC.

648

### 649 **5.3. Recovery from the LSC**

650 The LSC corresponds to a relatively short interval spanning the two ammonoid zones

651 of the late Smithian in the Nanpanjiang Basin (Fig. 12). Above the Smithian/Spathian  
652 boundary, fossil grains show a small rebound in diversity and abundance in both shallow and  
653 deeper water settings (Figs. 8-10). This increase does not result from sedimentary facies shift  
654 (Figs. 5-7). This therefore probably suggests a rather rapid restoration of regional  
655 communities after the LSC. Ammonoids and conodonts also show a rather rapid  
656 diversification during the early Spathian (Orchard, 2007; Brayard et al., 2009; Brayard et al.,  
657 2019). In addition, the Paris Biota from the earliest Spathian of southeastern Idaho highlights  
658 the existence of highly diversified and complex marine ecosystems in the immediate  
659 aftermath of the LSC (Brayard et al., 2017). Based on presently known data, the LSC  
660 apparently did not have a profound effect on benthic communities. The anoxic settings  
661 recorded during the late Smithian reduced considerably above the Smithian/Spathian  
662 boundary, potentially due to the cooling event and a renewed oceanic circulation (Lyu et al.,  
663 2019; Song H.Y. et al., 2019) and carbonate factory (Galfetti et al., 2008). The recovery after  
664 the LSC probably also benefited from the potentially more stable and less deleterious marine  
665 environments at the beginning of the Spathian (Zhang et al., 2015). The Spathian interval  
666 recorded a profound worldwide reconstruction of marine ecosystems from the tropics to the  
667 poles (Song et al., 2020), including the renewed increase in diversity of many clades  
668 (Orchard, 2007; Bottjer et al., 2008; Brayard et al., 2009; Song et al., 2011; Hofmann et al.,  
669 2013; Chen et al., 2015; Tu et al., 2016; Foster et al., 2017), the occurrence of complex  
670 marine ecosystems (Brayard et al., 2017), and potentially the return of more standard marine  
671 functional pyramid (Song et al., 2018).

672

## 673 **6. CONCLUSIONS**

674 Four ammonoid zones were identified in the three studied sections from the  
675 Nanpanjiang Basin, South China. They include the middle Smithian *Flemingites*  
676 *rursiradiatus* and *Owenites koeneni* Zones, and the late Smithian *Anasibirites kingianus* and  
677 *Xenoceltites variocostatus* Zones. Our combined analyses show that the late Smithian crisis  
678 likely started at the middle/upper Smithian boundary, coinciding with the onset of the positive  
679 carbon isotopic excursion. Grain count in thin sections indicates a sudden decrease in  
680 richness and abundance in shallow-water settings at the middle/upper Smithian boundary,  
681 while deeper water settings show a turnover from bivalve-dominated to ostracod-dominated  
682 benthic assemblages. The diversity and abundance of various taxa began to increase again  
683 during the early Spathian in shallow-water settings. This was coeval to the rapid resurgence  
684 of bivalve-dominated assemblages in deeper basin settings. Overall, these observations

685 support a rapid regional recovery after the LSC. Size analyses of pyrite framboids and  
686 sedimentological field observations support the existence of a relatively short-term  
687 disoxic/anoxic event coeval with the LSC, suggesting a potential causal relationship. The  
688 known fluctuations of temperatures together with contemporaneous oceanic anoxia and  
689 acidification most likely caused the late Smithian crisis.

690

## 691 **ACKNOWLEDGEMENTS**

692 We thank Jun Wang, Yiran Cao, Luyi Miao and Yan Feng for their help in the field.  
693 This research was supported by the Natural Science Foundation of China (41821001,  
694 41872033), the Strategic Priority Research Program of Chinese Academy of Sciences  
695 (XDB26000000), the Research Program the State Key Laboratory of Palaeobiology and  
696 Stratigraphy (143106); the French “Investissements d’Avenir” program, project ISITE-BFC  
697 (ANR-15-IDEX-03), and the Fundamental Research Funds for National University, China  
698 University of Geosciences (Wuhan).

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## 700 **REFERENCES CITED**

- 701 Bagherpour, B., Bucher, H., Baud, A., Brosse, M., Vennemann, T., Martini, R., and Guodun,  
702 K., 2017, Onset, development, and cessation of basal Early Triassic microbialites  
703 (BETM) in the Nanpanjiang pull-apart Basin, South China Block: *Gondwana*  
704 *Research*, v. 44, p. 178–204.
- 705 Bailey, T. R., Rosenthal, Y., McArthur, J. M., Van de Schootbrugge, B., and Thirlwall, M. F.,  
706 2003, Paleooceanographic changes of the Late Pliensbachian–Early Toarcian interval: a  
707 possible link to the genesis of an Oceanic Anoxic Event.: *Earth and Planetary Science*  
708 *Letters*, v. 212, no. 3–4, p. 307–320.
- 709 Bambach, R. K., Knoll, A. H., and Sepkoski, J. J., 2002, Anatomical and ecological  
710 constraints on Phanerozoic animal diversity in the marine realm: *Proceedings of the*  
711 *National Academy of Sciences*, v. 99, no. 10, p. 6854–6859.
- 712 Bottjer, D. J., Clapham, M. E., Fraiser, M. L., and Powers, C. M., 2008, Understanding  
713 mechanisms for the end-Permian mass extinction and the protracted Early Triassic  
714 aftermath and recovery: *GSA Today*, v. 18, no. 9, p. 4-10.
- 715 Brühwiler, T., Brayard, A., Bucher, H., and Guodun, K., 2008, Griesbachian and Dienerian  
716 (Early Triassic) Ammonoid Faunas from Northwestern Guangxi and Southern  
717 Guizhou (South China): *Palaeontology*, v. 51, no. 5, p. 1151–1180.
- 718 Brühwiler, T., Bucher, H., Brayard, A., and Goudemand, N., 2010a, High-resolution



719 biochronology and diversity dynamics of the Early Triassic ammonoid recovery: The  
720 Smithian faunas of the Northern Indian Margin: *Palaeogeography Palaeoclimatology*  
721 *Palaeoecology*, v. 297, no. 2, p. 491–501.

722 Brühwiler, T., Bucher, H., and Goudemand, N., 2010b, Smithian (Early Triassic) ammonoids  
723 from Tulong, South Tibet: *Geobios*, v. 43, no. 4, p. 403–431.

724 Brühwiler, T., Bucher, H., Goudemand, N., and Galfetti, T., 2012a, Smithian (Early Triassic)  
725 ammonoid faunas from Exotic Blocks from Oman: taxonomy and biochronology:  
726 *Palaeontographica Abteilung A*, p. 13–107.

727 Brühwiler, T., Bucher, H., and Krystyn, L., 2012b, Middle and late Smithian (Early Triassic)  
728 ammonoids from Spiti, India: *Special papers in Palaeontology Series*, no. 88, p. 115–  
729 174.

730 Brühwiler, T., Bucher, H., Roohi, G., Yaseen, A., and Rehman, K., 2011, A new early  
731 Smithian ammonoid fauna from the Salt Range (Pakistan): *Swiss Journal of*  
732 *Palaeontology*, v. 130, no. 2, p. 187–201.

733 Brühwiler, T., Bucher, H., Ware, D., Herrmann, E., Hochuli, P. A., Roohi, G., Rehman, K.,  
734 and Yaseen, A., 2012c, Smithian (Early Triassic) ammonoids from the Salt Range:  
735 *Special papers in Palaeontology Series*, v. 88, p. 1–114.

736 Brühwiler, T., Ware, D., Bucher, H., Krystyn, L., and Goudemand, N., 2010c, New Early  
737 Triassic ammonoid faunas from the Dienerian/Smithian boundary beds at the  
738 Induan/Olenekian GSSP candidate at Mud (Spiti, Northern India): *Journal of Asian*  
739 *Earth Sciences*, v. 39, no. 6, p. 724–739.

740 Brayard, A., and Bucher, H., 2008, Smithian (Early Triassic) ammonoid faunas from  
741 northwestern Guangxi (South China): taxonomy and biochronology: *Fossils and*  
742 *Strata*, v. 55, p. 1–184.

743 Brayard, A., Bucher, H., Escarguel, G., Fluteau, F., Bourquin, S., and Galfetti, T., 2006, The  
744 Early Triassic ammonoid recovery: Paleoclimatic significance of diversity gradients:  
745 *Palaeogeography Palaeoclimatology Palaeoecology*, v. 239, no. 3–4, p. 374–395.

746 Brayard, A., Bylund, K. G., Jenks, J. F., Stephen, D. A., Olivier, N., Escarguel, G., Fara, E.,  
747 and Vennin, E., 2013, Smithian ammonoid faunas from Utah: implications for Early  
748 Triassic biostratigraphy, correlation and basinal paleogeography: *Swiss Journal of*  
749 *Palaeontology*, v. 132, no. 2, p. 141–219.

750 Brayard, A., Escarguel, G., and Bucher, H., 2007, The biogeography of early Triassic  
751 ammonoid faunas: Clusters, gradients, and networks: *Geobios*, v. 40, no. 6, p. 749–  
752 765.

753 Brayard, A., Escarguel, G., Bucher, H., Monnet, C., Brühwiler, T., Goudemand, N., Galfetti,  
754 T., and Guex, J., 2009, Good genes and good luck: ammonoid diversity and the  
755 end-Permian mass extinction: *Science*, v. 325, no. 5944, p. 1118–1121.

756 Brayard, A., Jenks, J. F., Bylund, K. G., and the Paris Biota team 2019, Ammonoids and  
757 nautiloids from the earliest Spathian Paris Biota and other early Spathian localities in  
758 southeastern Idaho, USA: *Geobios*, v. 54, p. 13–36.

759 Brayard, A., Krumenacker, L. J., Botting, J. P., Jenks, J. F., Bylund, K. G., Fara, E., Vennin,  
760 E., Olivier, N., Goudemand, N., Saucedo, T., Charbonnier, S., Romano, C.,  
761 Doguzhaeva, L., Ben, T., Hautmann, M., Stephen, D. A., Thomazo, C., and Escarguel,  
762 G., 2017, Unexpected Early Triassic marine ecosystem and the rise of the Modern  
763 evolutionary fauna: *Science Advances*, v. 3, no. 2, p. e1602159.

764 Brosse, M., Brayard, A., Fara, E., and Neige, P., 2013, Ammonoid recovery after the  
765 Permian-Triassic mass extinction: a re-exploration of morphological and phylogenetic  
766 diversity patterns: *Journal of the Geological Society, London*, v. 170, p. 225–236.

767 Charbonnier, G., and Follmi, K. B., 2017, Mercury enrichments in lower Aptian sediments  
768 support the link between Ontong Java large igneous province activity and oceanic  
769 anoxic episode 1a: *Geology*, v. 45, no. 1, p. 63–66.

770 Chatalov, A., 2013, A Triassic homoclinal ramp from the Western Tethyan realm , Western  
771 Balkanides , Bulgaria : Integrated insight with special emphasis on the Anisian outer  
772 to inner ramp facies transition: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v.  
773 386, p. 34–58.

774 Chen, J., Tong, J., Song, H., Luo, M., Huang, Y., and Xiang, Y., 2015, Recovery pattern of  
775 brachiopods after the Permian–Triassic crisis in South China: *Palaeogeography,*  
776 *Palaeoclimatology, Palaeoecology*, v. 433, p. 91–105.

777 Chen, Y., Twitchett, R. J., Jiang, H., Richoz, S., Lai, X., Yan, C., Sun, Y., Liu, X., and Wang,  
778 L., 2013, Size variation of conodonts during the Smithian–Spathian (Early Triassic)  
779 global warming event: *Geology*, v. 41, no. 8, p. 823–826.

780 Clarkson, M. O., Wood, R. A., Poulton, S. W., Richoz, S., Newton, R. J., Kasemann, S. A.,  
781 Bowyer, F., and Krystyn, L., 2016, Dynamic anoxic ferruginous conditions during the  
782 end-Permian mass extinction and recovery: *Nature Communications*, v. 7, p. 12236.

783 Dai, X., Song, H., Brayard, A., and Ware, D., 2019, A new Griesbachian–Dienerian (Induan,  
784 Early Triassic) ammonoid fauna from Gujiao, South China: *Journal of Paleontology*, v.  
785 93, no. 1, p. 48–71.

786 Dai, X., and Song, H., 2020, Toward an understanding of cosmopolitanism in deep time: a

787 case study of ammonoids from the middle Permian to the Middle Triassic:  
788 *Paleobiology*, v. 46, no. 4, p. 533–549.

789 Enos, P., Jiayong, W., and Lehrmann, D. J., 1998, Death in Guizhou — Late Triassic  
790 drowning of the Yangtze carbonate platform: *Sedimentary Geology*, v. 118, no. 1998,  
791 p. 55–76.

792 Fang, Y., Chen, Z. Q., Kershaw, S., Yang, H., and Luo, M., 2017, Permian–Triassic boundary  
793 microbialites at Zuodeng section, Guangxi Province, South China: geobiology and  
794 palaeoceanographic implications: *Global and planetary change*, v. 152, p. 115–128.

795 Feng, Z., Bao, Z., and Liu, S., 1997, *Lithofacies Palaeogeography of Early and Middle*  
796 *Triassic of South China*, Beijing, Petroleum Industry Press, 222 p.

797 Flügel, E., 2010, *Microfacies of Carbonate Rocks*, Berlin Heidelberg, Springer, 929 p.

798 Forel, M. B., Crasquin, S., Kershaw, S., and Collin, P. Y., 2013, In the aftermath of the end-P  
799 ermanian extinction: the microbialite refuge?: *Terra Nova*, v. 25, no. 2, p. 137–143.

800 Foster, W. J., Danise, S., Price, G. D., and Twitchett, R. J., 2017, Subsequent biotic crises  
801 delayed marine recovery following the late Permian mass extinction event in northern  
802 Italy: *PloS one*, v. 12, no. 3, p. e0172321.

803 Foster, W. J., Danise, S., Price, G. D., and Twitchett, R. J., 2018, Paleocological analysis of  
804 benthic recovery after the Late Permian mass extinction event in eastern Lombardy,  
805 Italy: *Palaios*, v. 33, no. 6, p. 266–281.

806 Foster, W. J., Danise, S., Sedlacek, A., Price, G. D., Hips, K., and Twitchett, R. J., 2015,  
807 Environmental controls on the post-Permian recovery of benthic, tropical marine  
808 ecosystems in western Palaeotethys (Aggtelek Karst, Hungary): *Palaeogeography,*  
809 *Palaeoclimatology, Palaeoecology*, v. 440, p. 374–394.

810 Galfetti, T., Bucher, H., Martini, R., Hochuli, P. A., Weissert, H., Crasquin-Soleau, S.,  
811 Brayard, A., Goudemand, N., Brühwiler, T., and Guodun, K., 2008, Evolution of  
812 Early Triassic outer platform paleoenvironments in the Nanpanjiang Basin (South  
813 China) and their significance for the biotic recovery: *Sedimentary Geology*, v. 204, no.  
814 1–2, p. 36–60.

815 Galfetti, T., Bucher, H., Ovtcharova, M., Schaltegger, U., Brayard, A., Bruehwiler, T.,  
816 Goudemand, N., Weissert, H., Hochuli, P. A., Cordey, F., and Guodun, K., 2007a,  
817 Timing of the Early Triassic carbon cycle perturbations inferred from new U-Pb ages  
818 and ammonoid biochronozones: *Earth and Planetary Science Letters*, v. 258, no. 3–4,  
819 p. 593–604.

820 Galfetti, T., Hochuli, P. A., Brayard, A., Bucher, H., Weissert, H., and Vigran, J. O., 2007b,

821 Smithian-Spathian boundary event: Evidence for global climatic change in the wake  
822 of the end-Permian biotic crisis: *Geology*, v. 35, no. 4, p. 291–294.

823 Gliwa, J., Ghaderi, A., Leda, L., Schobben, M., Tomás, S., Foster, W. J., Forel, M. B., Tabrizi,  
824 N. G., Grasby, S. E., Struck, U., Ashouri, A. R., and Korn, D., 2020, Aras Valley  
825 (northwest Iran): high-resolution stratigraphy of a continuous central Tethyan  
826 Permian–Triassic boundary section: *Fossil Record*, v. 23, no. 1, p. 33–69.

827 Goudemand, N., Romano, C., Brayard, A., Hochuli, P. A., and Bucher, H., 2013, Comment  
828 on "Lethally hot temperatures during the Early Triassic greenhouse": *Science*, v. 339,  
829 no. 6123, p. 1033–1033.

830 Goudemand, N., Romano, C., Leu, M., Bucher, H., Trotter, J. A., and Williams, I. S., 2019,  
831 Dynamic interplay between climate and marine biodiversity upheavals during the  
832 early Triassic Smithian-Spathian biotic crisis: *Earth-Science Reviews*, v. 195, p. 169–  
833 178.

834 Grasby, S. E., Beauchamp, B., Bond, D. P., Wignall, P. B., and Sanei, H., 2016, Mercury  
835 anomalies associated with three extinction events (Capitanian crisis, latest Permian  
836 extinction and the Smithian/Spathian extinction) in NW Pangea: *Geological magazine*,  
837 v. 153, no. 2, p. 285–297.

838 Grasby, S. E., Beauchamp, B., Embry, A., and Sanei, H., 2013a, Recurrent Early Triassic  
839 ocean anoxia: *Geology*, v. 41, no. 2, p. 175–178.

840 Grasby, S. E., Sanei, H., Beauchamp, B., and Chen, Z. H., 2013b, Mercury deposition  
841 through the Permo-Triassic Biotic Crisis: *Chemical Geology*, v. 351, p. 209–216.

842 Grasby, S. E., Shen, W., Yin, R., Gleason, J. D., Blum, J. D., Lepak, R. F., Hurley, J. P., and  
843 Beauchamp, B., 2017, Isotopic signatures of mercury contamination in latest Permian  
844 oceans: *Geology*, v. 45, no. 1, p. 55–58.

845 Hammer, Ø., Jones, M. T., Schneebeli-Hermann, E., Hansen, B. B., and Bucher, H., 2019,  
846 Are Early Triassic extinction events associated with mercury anomalies? A  
847 reassessment of the Smithian/Spathian boundary extinction: *Earth-Science Reviews*, v.  
848 195, p. 179–190.

849 Hermann, E., Hochuli, P. A., Mehay, S., Bucher, H., Brühwiler, T., Ware, D., Hautmann, M.,  
850 Roohi, G., ur-Rehman, K., and Yaseen, A., 2011, Organic matter and  
851 palaeoenvironmental signals during the Early Triassic biotic recovery: The Salt Range  
852 and Surghar Range records: *Sedimentary Geology*, v. 234, no. 1–4, p. 19–41.

853 Hofmann, R., Hautmann, M., Brayard, A., Nüetzel, A., Bylund, K. G., Jenks, J. F., Vennin, E.,  
854 Olivier, N., and Bucher, H., 2014, Recovery of benthic marine communities from the

855 end-Permian mass extinction at the low latitudes of eastern Panthalassa:  
856 *Palaeontology*, v. 57, no. 3, p. 547–589.

857 Hofmann, R., Hautmann, M., and Bucher, H., 2015, Recovery dynamics of benthic marine  
858 communities from the Lower Triassic Werfen Formation, northern Italy: *Lethaia*, v. 48,  
859 no. 4, p. 474–196.

860 Hofmann, R., Hautmann, M., Wasmer, M., and Bucher, H., 2013, Palaeoecology of the  
861 Spathian Virgin Formation (Utah, USA) and its implications for the Early Triassic  
862 recovery: *Acta Palaeontologica Polonica*, v. 58, no. 1, p. 149–173.

863 Jattiot, R., Brayard, A., Bucher, H., Vennin, E., Caravaca, G., Jenks, J. F., Bylund, K. G., and  
864 Escarguel, G., 2018, Palaeobiogeographical distribution of Smithian (Early Triassic)  
865 ammonoid faunas within the western USA basin and its controlling parameters:  
866 *Palaeontology*, v. 61, no. 6, p. 881–904.

867 Jattiot, R., Bucher, H., and Brayard, A., 2020, Smithian (Early Triassic) ammonoid faunas  
868 from Exotic Blocks from Timor: taxonomy and biochronology: *Palaeontographica*  
869 *Abteilung A*, v. 317, no. 1–6, p. 1–137.

870 Jattiot, R., Bucher, H., Brayard, A., Brosse, M., and Jenks, J. F. B., K.G, 2017, Smithian  
871 ammonoid faunas from northeastern Nevada: implications for Early Triassic  
872 biostratigraphy and correlation within the western USA basin: *Palaeontographica*  
873 *Abteilung A*, v. 309, p. 1–89.

874 Jattiot, R., Bucher, H., Brayard, A., Monnet, C., Jenks, J. F., and Hautmann, M., 2016,  
875 Revision of the genus *Anasibirites* Mojsisovics (Ammonoidea): an iconic and  
876 cosmopolitan taxon of the late Smithian (Early Triassic) extinction: *Papers in*  
877 *Palaeontology*, v. 2, no. 1, p. 155–188.

878 Jenks, J. F., and Brayard, A., 2018, Smithian (Early Triassic) ammonoids from Crittenden  
879 Springs, Elko County, Nevada: taxonomy, biostratigraphy and biogeography: *New*  
880 *Mexico Museum of Natural History and Science Bulletin*, v. 78, p. 1–175.

881 Jenks, J. F., Monnet, C., Balini, M., Brayard, A., and Meier, M., 2015, Biostratigraphy of  
882 Triassic Ammonoids, *in* Klug, C., Kruta, I., Korn, D., Mapes, R. H., and Baets, K. D.,  
883 eds., *Ammonoid Paleobiology: From macroevolution to paleogeography*, Volume 44:  
884 Netherlands, Springer, p. 329–388.

885 Kidwell, S. M., 1991, Taphonomic feedback (live/dead interactions) in the genesis of  
886 bioclastic beds: keys to reconstructing sedimentary dynamics: *Cycles and events in*  
887 *stratigraphy*, p. 268–281.

888 Komatsu, T., Takashima, R., Shigeta, Y., Maekawa, T., Tran, H. D., Cong, T. D., Sakata, S.,

889 Dinh, H. D., and Takahashi, O., 2016, Carbon isotopic excursions and detailed  
890 ammonoid and conodont biostratigraphies around Smithian-Spathian boundary in the  
891 Bac Thuy Formation, Vietnam: *Palaeogeography Palaeoclimatology Palaeoecology*, v.  
892 454, p. 65-74.

893 Lehrmann, D. J., Bentz, J. M., Wood, T., Goers, A., Dhillon, R., Akin, S., Li, X. W., Payne, J.  
894 L., Kelley, B. M., Meyer, K. M., Schaal, E. K., Suarez, M. B., Yu, M. Y., Qin, Y. J., Li,  
895 R. X., Minzoni, M., and Henderson, C. M., 2015, Environmental controls on the  
896 genesis of maerle microbialites and dissolution surface associated with the  
897 end-Permian mass extinction: new sections and observations from the Nanpanjiang  
898 Basin, South China: *Palaios*, v. 30, no. 7, p. 529–552.

899 Leu, M., Bucher, H., and Goudemand, N., 2019, Clade-dependent size response of conodonts  
900 to environmental changes during the late Smithian extinction: *Earth-Science Reviews*,  
901 v. 195, no. 52–67.

902 Li, M., Song, H., Woods, A. D., Dai, X., and Wignall, P. B., 2019, Facies and evolution of the  
903 carbonate factory during the Permian–Triassic crisis in South Tibet, China:  
904 *Sedimentology*, v. 59, p. 646–678.

905 Liu, X., and Song, H., 2020, Automatic identification of fossils and abiotic grains during  
906 carbonate microfacies analysis using deep convolutional neural networks:  
907 *Sedimentary Geology*, v. 410, p. 105790.

908 Lyu, Z. Y., Zhang, L., Algeo, T. J., Zhao, L. S., Chen, Z. Q., Li, C., Ma, B. A., and Ye, F. H.,  
909 2019, Global-ocean circulation changes during the Smithian-Spathian transition  
910 inferred from carbon-sulfur cycle records: *Earth-Science Reviews*, v. 195, p. 114–132.

911 Mathes, G. H., van Dijk, J., Kiessling, W., and Steinbauer, M. J., 2021, Extinction risk  
912 controlled by interaction of long-term and short-term climate change: *Nature Ecology  
913 & Evolution*. doi:10.1038/s41559-020-01377-w.

914 Mu, L., Zakharov, Y., Li, W.-Z., and Shen, S.-Z., 2007, Early Induan (Early Triassic)  
915 cephalopods from the Daye Formation at Guiding, Guizhou Province, South China:  
916 *Journal Information*, v. 81, no. 5, p. 858–872.

917 Orchard, M. J., 2007, Conodont diversity and evolution through the latest Permian and Early  
918 Triassic upheavals: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 252, no.  
919 1–2, p. 93–117.

920 Pérez-López, A., and Pérez-Valera, F., 2012, Tempestite facies models for the epicontinental  
921 Triassic carbonates of the Betic Cordillera (southern Spain): *Sedimentology*, v. 59, p.  
922 646–678.

923 Payne, J. L., Lehrmann, D. J., Wei, J., Orchard, M. J., Schrag, D. P., and Knoll, A. H., 2004,  
924 Large perturbations of the carbon cycle during recovery from the end-Permian  
925 extinction: *Science*, v. 305, no. 5683, p. 506–509.

926 Romano, C., Goudemand, N., Vennemann, T. W., Ware, D., Schneebeli-Hermann, E., Hochuli,  
927 P. A., Bruehwiler, T., Brinkmann, W., and Bucher, H., 2013, Climatic and biotic  
928 upheavals following the end-Permian mass extinction: *Nature Geoscience*, v. 6, no. 1,  
929 p. 57–60.

930 Scheyer, T. M., Romano, C., Jenks, J., and Bucher, H., 2014, Early Triassic marine biotic  
931 recovery: the predators' perspective: *PLoS One*, v. 9, no. 3, p. e88987.

932 Scotese, C. R., 2014, Atlas of Middle & Late Permian and Triassic Paleogeographic maps,  
933 maps 43–48 from volume 3 of the PALEOMAP Atlas for ArcGIS (Jurassic and  
934 Triassic) and maps 49–52 from volume 4 of the PALEOMAP PaleoAtlas for ArcGIS  
935 (Late Paleozoic): Mollweide Projection, PALEOMAP Project, Evanston, IL.

936 Shigeta, Y., Komatsu, T., Maekawa, T., and Tran, H. D., 2014, Olenekian (Early Triassic)  
937 stratigraphy and fossil assemblages in northeastern Vietnam: *National Museum of  
938 Nature and Science*, v. 45, p. 1–309.

939 Shigeta, Y., Zakharov, Y. D., Maeda, H., and Popov, A. M., 2009, The Lower Triassic System  
940 in the Abrek Bay Area, South Primorye, Russia, Tokyo, National Museum of Nature  
941 and Science, 218 p.

942 Song, H., Tong, J., Algeo, T. J., Horacek, M., Qiu, H., Song, H., Tian, L., and Chen, Z.-Q.,  
943 2013, Large vertical  $\delta^{13}\text{C}$  DIC gradients in Early Triassic seas of the South China  
944 craton: implications for oceanographic changes related to Siberian Traps volcanism:  
945 *Global and Planetary Change*, v. 105, p. 7–20.

946 Song, H., Huang, S., Jia, E., Dai, X., Wignall, P. B., and Dunhill, A. M., 2020, Flat latitudinal  
947 diversity gradient caused by the Permian–Triassic mass extinction: *Proceedings of the  
948 National Academy of Sciences*, v. 117, no. 30, p. 17578-17583.

949 Song, H., Song, H., Tong, J., Gordon, W. G., Wignall, B. P., Tian, L., Zheng, W., Algeo, J. T.,  
950 Liang, L., Bai, R., Wu, K., and Ariel, A. D., 2021, Conodont calcium isotopic  
951 evidence for multiple shelf acidification events during the Early Triassic: *Chemical  
952 Geology*, v. 562, p. 120038.

953 Song, H., Wignall, P. B., Chen, Z. Q., Tong, J., Bond, D. P. G., Lai, X., Zhao, X., Jiang, H.,  
954 Yan, C., Niu, Z., Chen, J., Yang, H., and Wang, Y., 2011, Recovery tempo and pattern  
955 of marine ecosystems after the end-Permian mass extinction: *Geology*, v. 39, no. 8, p.  
956 739–742.

957 Song, H., Wignall, P. B., Chu, D., Tong, J., Sun, Y., Song, H., He, W., and Tian, L., 2014,  
958 Anoxia/high temperature double whammy during the Permian-Triassic marine crisis  
959 and its aftermath: *Scientific Reports*, v. 4.

960 Song, H., Wignall, P. B., and Dunhill, A. M., 2018, Decoupled taxonomic and ecological  
961 recoveries from the Permo-Triassic extinction: *Science Advances*, v. 4, no. 10, p.  
962 eaat5091.

963 Song, H., Wignall, P. B., Tong, J., Bond, D. P., Song, H., Lai, X., Zhang, K., Wang, H., and  
964 Chen, Y., 2012, Geochemical evidence from bio-apatite for multiple oceanic anoxic  
965 events during Permian–Triassic transition and the link with end-Permian extinction  
966 and recovery: *Earth and Planetary Science Letters*, v. 353, p. 12–21.

967 Song, H., Wignall, P. B., and Dunhill, A. M., 2018, Decoupled taxonomic and ecological  
968 recoveries from the Permo-Triassic extinction: *Science Advances*, v. 4, no. 10, p.  
969 eaat5091.

970 Song, H. Y., Du, Y., Algeo, T. J., Tong, J. N., Owens, J. D., Song, H. J., Tian, L., Qiu, H., Zhu,  
971 Y., and Lyons, T. W., 2019, Cooling-driven oceanic anoxia across the  
972 Smithian/Spathian boundary (mid-early Triassic): *Earth-Science Reviews*, v. 195, p.  
973 133–146.

974 Stanley, S. M., 2009, Evidence from ammonoids and conodonts for multiple Early Triassic  
975 mass extinctions: *Proceedings of the National Academy of Sciences of the United*  
976 *States of America*, v. 106, no. 36, p. 15264–15267.

977 Sun, Y., Joachimski, M. M., Wignall, P. B., Yan, C., Chen, Y., Jiang, H., Wang, L., and Lai, X.,  
978 2012, Lethally Hot Temperatures During the Early Triassic Greenhouse: *Science*, v.  
979 338, no. 6105, p. 366–370.

980 Sun, Y. D., Wignall, P. B., Joachimski, M. M., Bond, D. P. G., Grasby, S. E., Sun, S., Yan, C.  
981 B., Wang, L. N., Chen, Y. L., and Lai, X. L., 2015, High amplitude redox changes in  
982 the late Early Triassic of South China and the Smithian–Spathian extinction:  
983 *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 427, p. 62–78.

984 Thibodeau, A. M., Ritterbush, K., Yager, J. A., West, A. J., Ibarra, Y., Bottjer, D. J., Berelson,  
985 W. M., Bergquist, B. A., and Corsetti, F. A., 2016, Mercury anomalies and the timing  
986 of biotic recovery following the end-Triassic mass extinction: *Nature*  
987 *Communications*, v. 7. p. 11147.

988 Tong, J., Chu, D., Liang, L., Shu, W., Song, H., Song, T., Song, H., and Wu, Y., 2018, Triassic  
989 integrative stratigraphy and timescale of China: *Science China Earth Sciences*, v. 62,  
990 no. 1, p. 189–222.



- 991 Tong, J., Zuo, J., and Chen, Z. Q., 2007, Early Triassic carbon isotope excursions from South  
992 China: Proxies for devastation and restoration of marine ecosystems following the  
993 end-Permian mass extinction: *Geological Journal*, v. 42, no. 3–4, p. 371–389.
- 994 Tozer, E. T., 1965, Lower Triassic stages and Ammonoid zones of Arctic Canada: Paper of  
995 the Geological Survey of Canada, v. 65-12, p. 1–14.
- 996 Tozer, E. T., 1981, Triassic Ammonoidea: geographic and stratigraphic distribution, *in* House,  
997 M. R., and Senior, J. R., eds., *The ammonoidea: the evolution, classification, mode of*  
998 *life and geological usefulness of a major fossil group*: London, The Systematics  
999 Association, p. 397–431.
- 1000 Tu, C. Y., Chen, Z. Q., and Harper, D. A. T., 2016, Permian-Triassic evolution of the Bivalvia:  
1001 Extinction-recovery patterns linked to ecologic and taxonomic selectivity:  
1002 *Palaeogeography Palaeoclimatology Palaeoecology*, v. 459, p. 53–62.
- 1003 Wan, J., Yuan, A., Crasquin, S., Jiang, H., Yang, H., and Hu, X., 2019, High-resolution  
1004 variation in ostracod assemblages from microbialites near the Permian-Triassic  
1005 boundary at Zuodeng, Guangxi region, South China: *Palaeogeography,*  
1006 *Palaeoclimatology, Palaeoecology*, v. 535, p. 109349. Wang, X. D., Cawood, P. A.,  
1007 Zhao, H., Zhao, L. S., Grasby, S. E., Chen, Z. Q., Wignall, P. B., Lv, Z. Y., and Han,  
1008 C., 2018, Mercury anomalies across the end Permian mass extinction in South China  
1009 from shallow and deep water depositional environments: *Earth and Planetary Science*  
1010 *Letters*, v. 496, p. 159–167.
- 1011 Wang, X. D., Cawood, P. A., Zhao, H., Zhao, L. S., Grasby, S. E., Chen, Z. Q., and Zhang, L.,  
1012 2019, Global mercury cycle during the end-Permian mass extinction and subsequent  
1013 Early Triassic recovery: *Earth and Planetary Science Letters*, v. 513, p. 144–155.
- 1014 Widmann, P., Bucher, H., Leu, M., Vennemann, T., Bagherpour, B., Schneebeil-Hermann, E.,  
1015 Goudemand, N., and Schaltegger, U., 2020, Dynamics of the Largest Carbon Isotope  
1016 Excursion During the Early Triassic Biotic Recovery: *Frontiers in Earth Science*, v. 8,  
1017 no. 196.
- 1018 Wignall, P. B., and Twitchett, R. J., 1996, Oceanic anoxia and the end Permian mass  
1019 extinction: *Science*, v. 272, no. 5265, p. 1155–1158.
- 1020 Wu, K., Tian, L., Liang, L., Metcalfe, I., Chu, D., and Tong, J., 2019, Recurrent biotic  
1021 rebounds during the Early Triassic: biostratigraphy and temporal size variation of  
1022 conodonts from the Nanpanjiang Basin, South China: *Journal of the Geological*  
1023 *Society*, v. 176, no. 6, p. 1232–1246.
- 1024 Yang, Z., Yin, H., Wu, S., Yang, F., Ding, M., and Xu, G., 1987, Permian-Triassic boundary

1025 stratigraphy and faunas of South China, Beijing, Geological Publishing House, 379 p.:

1026 Zhang, F., Algeo, T. J., Cui, Y., Shen, J., Song, H., Sano, H., Rowe, H., and Anbar, A. D.,

1027 2019a, Global-ocean redox variations across the Smithian-Spathian boundary linked

1028 to concurrent climatic and biotic changes: *Earth-Science Reviews*, v. 195, p. 147–168.

1029 Zhang, F., Romaniello, S. J., Algeo, T. J., Lau, K. V., Clapham, M. E., Richoz, S., Herrmann,

1030 A. D., Smith, H., Horacek, M., and Anbar, A. D., 2018, Multiple episodes of extensive

1031 marine anoxia linked to global warming and continental weathering following the

1032 latest Permian mass extinction: *Science Advances*, v. 4, no. 4, p. e1602921.

1033 Zhang, L., Orchard, M. J., Brayard, A., Algeo, T. J., Zhao, L., Chen, Z.-Q., and Zhengyi, L.,

1034 2019b, The Smithian/Spathian boundary (late Early Triassic): A review of ammonoid,

1035 conodont, and carbon-isotopic criteria: *Earth-Science Reviews*, v. 195, p. 7–36.

1036