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Diverse biomineralizing animals in the terminal Ediacaran Period herald the Cambrian explosion

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ABSTRACT

The origin and radiation of biomineralizing metazoans represents an important evolutionary innovation in the history of life. The earliest known skeletal metazoans are dominated by four genera in the terminal Ediacaran Period (ca. 550–539 Ma), followed by the diversification of new and diverse shelly fossils in the early Cambrian Period (ca. 539–510 Ma). Thus, terminal Ediacaran skeletal fossils and early Cambrian shelly fossils are commonly regarded as two distinct assemblages, with little overlap in stratigraphic distribution and taxonomic composition, implying a possible extinction event and a subsequent radiation event at the Ediacaran-Cambrian boundary. However, it has been shown recently that some Ediacaran skeletal taxa may have extended into the early Cambrian, indicating evolutionary continuity between these two assemblages. Here we document an assemblage of diverse skeletal fossils from the terminal Ediacaran Dengying Formation in South China. This assemblage is dominated by terminal Ediacaran taxa such as *Cloudina* and *Sinotubulites*, but also contains rare elements that morphologically resemble early Cambrian shelly fossils. This finding suggests that terminal Ediacaran skeletal animals are more diverse than previously thought and further reinforces the evolutionary continuity of biomineralizing animals across the Ediacaran-Cambrian transition.

INTRODUCTION

The origin of biomineralizing animals in the terminal Ediacaran (ca. 550–539 Ma) is a transformative evolutionary event with global impact on the Earth system (Wood et al., 2017). This event is represented by the appearance of at least four genera of weakly biomineralized forms, including *Cloudina*, *Sinotubulites*, *Namacalathus*, and *Namapoikia* (Germs, 1972; Chen et al., 1981; Grotzinger et al., 1995, 2000; Wood et al., 2002; Penny et al., 2014). Immediately above the Ediacaran-Cambrian boundary (ECB), a more diverse assemblage of new shelly fossils appears in the basal Cambrian (Zhuravlev and Wood, 2018). It was thought that the terminal Ediacaran skeletal animals may have gone extinct near the ECB (Amthor et al., 2003). Recent reports, however, have shown that cloudinids may extend above the ECB (Yang et al., 2016; Han et al., 2017; Zhu et al., 2017). This evolutionary continuity hints that elements of early Cambrian shelly fossils may extend below the ECB (Zhu et al., 2017), but this has not been thoroughly tested against the fossil record. Here, we document a diverse assemblage of biomineralizing tubular fossils from the terminal Ediacaran Dengying Formation in South China. Although this assemblage is dominated by classical terminal Ediacaran skeletal fossils such as *Cloudina* and *Sinotubulites*, several rare elements show similarities to early Cambrian shelly fossils. This finding indicates that terminal Ediacaran skeletal fossils are more diverse than previously thought. Further, the new data show that, although there is a taxonomic turnover across the ECB, the evolutionary connection between terminal Ediacaran and early Cambrian biomineralizing animal assemblages is stronger than previously thought.

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METHODS

Samples were collected from a 2 m interval (70.8–72.8 m in Fig. 1A) in the terminal Ediacaran Beiwan Member, upper Dengying Formation, Lijiagou section (Fig. 1; Figs. DR1 and DR2 in the GSA Data Repository[1]; also see the Data Repository for section location, sample horizon, and age constraints). Phosphatized microfossils were extracted from clastic dolostone of the Beiwan Member using a maceration technique with 5%–8% acetic acid. Fossils were handpicked from maceration residues and mounted on aluminum stubs for observation on a FEI Quanta 600 field-emission scanning electron microscope. Fossils illustrated in this paper are reposited in the Department of Geology, Northwest University (Xi'an, China).

RESULTS

Approximately 5220 kg of dolostone samples were collected from a 2 m interval that is 5–7 m below the top of the Beiwan Member and ~1.25 m below a $\delta^{13}C$ feature identified as the basal Cambrian negative carbon isotope excursion (BACE in Fig. 1A; Zhu et al., 2007). A total of 8782 fossils (*Cloudina* = 6029; *Sinotubulites* = 1964; others = 789; Table DR1) were extracted from these samples using the acetic acid maceration technique. Common elements include previously recognized tubular fossils such as *Cloudina hartmannae* (Fig. 2A), *C. ningqiangensis* (Fig. 2B), *Sinotubulites baimatuoensis* (Fig. 2C), *S. triangularis* (Fig. 2D), *Protolagena limbata* (Fig. 2E), and *Multiconotubus chinensis* (Fig. 2F). *Cloudina* and *Sinotubulites* are the most abundant genera, accounting for 68.65% and 22.36%, respectively, of the recovered specimens (Table DR1).

[1]GSA Data Repository item 2019128, section location, sample horizon, age constrains, and taxonomic identification, is available online at http://www.geosociety.org/datarepository/2019/, or on request from editing@geosociety.org.

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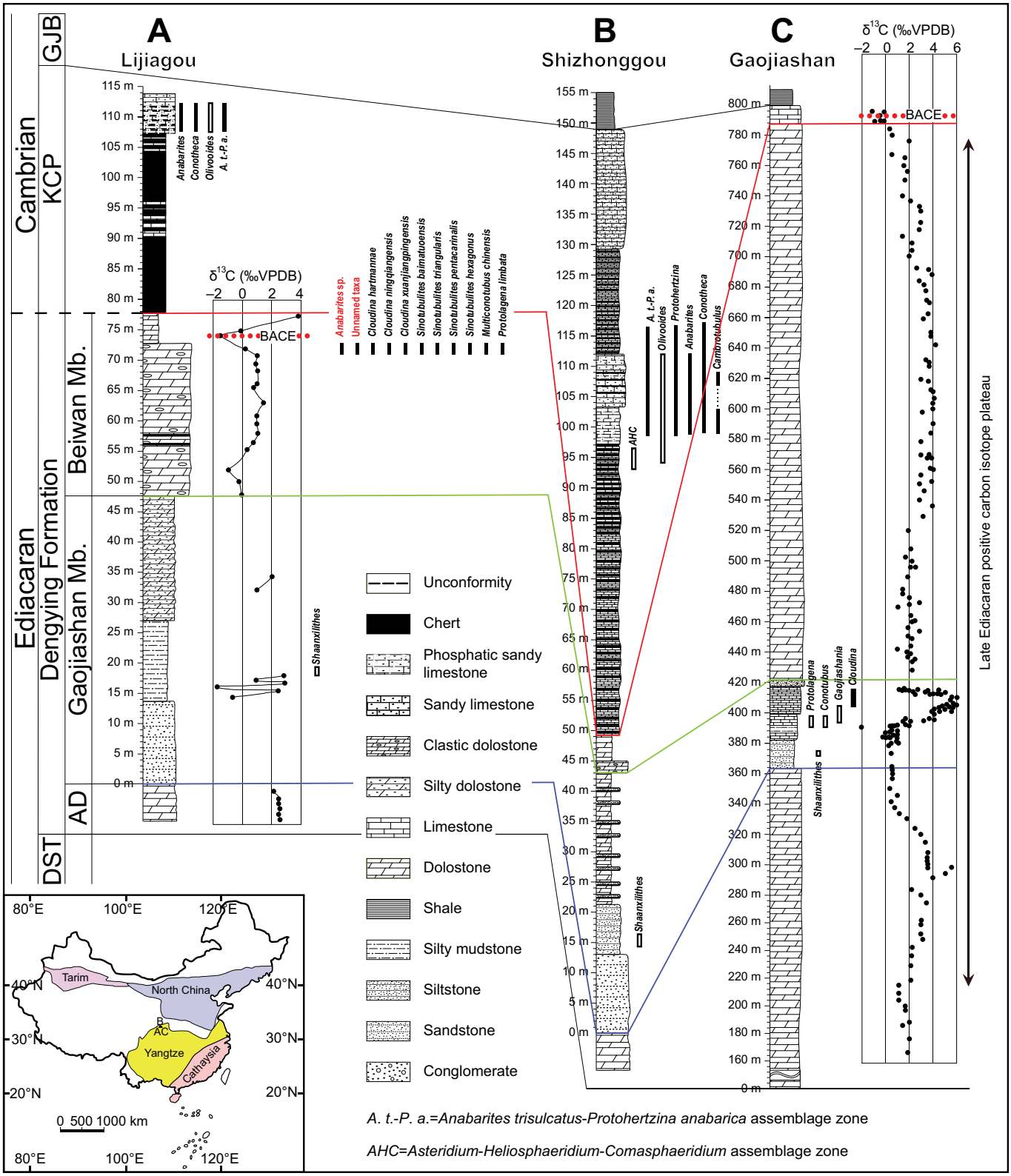


Figure 1. Litho-, bio-, and chemo-stratigraphic data from Lijiagou (A), Shizhonggou (B), and Gaojiashan (C) sections in the southern Shaanxi Province, South China (see Fig. DR1 [see footnote 1] for section location). Terminal Ediacaran non-biomineralized (open vertical bars) and weakly biomineralized (filled bars, new taxa in red) fossils are present in the Beiwan Member of the Dengying Formation at Lijiagou (A; this study), as well as in the Gaojiashan Member at Shizhonggou and Gaojiashan (B–C; Cai et al., 2010). Basal Cambrian shelly fossil *Anabarites trisulcatus–Protohertzina anabarica* assemblage zone (*A.t.-P.a.*) (Steiner et al., 2007) and acritarch *Asteridium-Heliosphaeridium-Comasphaeridium* assemblage zone (*AHC*) (Yao et al., 2005; Yin, 1987) have been reported from the Kuanchuanpu Formation at Lijiagou and Shizhonggou. Basal Cambrian negative carbon isotope excursion (BACE) has been reported from the uppermost Beiwan Member at Lijiagou (Zhu et al., 2007) and lower Kuanchuanpu Formation at Gaojiashan (Cui et al., 2016). Lines linking sections represent lithostratigraphic correlation, and are not necessarily exact time lines because of lateral facies changes. Inset map shows approximate location of sections (triangles). DST—Doushantuo Formation; AD—Algal Dolomite Member; Mb.—Member; KCP—Kuanchuanpu Formation; GJB—Guojiaba Formation.

Figure 2. Typical terminal Ediacaran skeletal fossils (A–F) and newly discovered Cambrian-style skeletal fossils (G–K) from the Beiwan Member of the Dengying Formation at Lijiagou, South China. A: *Cloudina hartmannae*. B: *C. ningqiangensis*. C: *Sinotubulites baimatuoensis*. D: *S. triangularis*. E: *Protolagena limbata*. F: *Multiconotubus chinensis*. G–K: Internal molds of *Anabarites* sp. Arrows indicate longitudinal sulci, which initiate apically (J–K) or subapically (I). K is an enlargement of J. See Table DR2 (see footnote 1) for museum catalog numbers.

A variety of new but rare tubular fossils were also recovered (Figs. 2G–2K and 3), and they share morphological similarities with some Cambrian shelly fossils. Importantly, these fossils include forms that can be assigned to *Anabarites* (Figs. 2G–2K)—a genus characterized by three longitudinal sulci and that occurs widely in the basal Cambrian (Kouchinsky et al., 2009)—as well as a number of unnamed and morphologically simple tubular fossils that resemble some Cambrian taxa (Fig. 3).

DISCUSSION

The ECB marks the decline of the Ediacara biota characterized by soft-bodied macrofossils such as rangeomorphs and erniettomorphs (Xiao and Laflamme, 2009) and the initial diversification of bioturbating and biomineralizing animals (Droser et al., 2017; Chen et al., 2018; Darroch et al., 2018). Whether this evolutionary transition was triggered by environmental or ecological factors is a matter of current debate (Laflamme et al., 2013; Smith et al., 2016; Darroch et al., 2018; Tarhan et al., 2018). To resolve the competing hypotheses about the triggers, it is critical to have a more nuanced picture of the evolutionary pattern across the ECB. In this regard, the recent reports of cloudinids and possible rangeomorphs in early Cambrian rocks (Yang et al., 2016; Han et al., 2017; Zhu et al., 2017; Hoyal Cuthill and Han, 2018) indicate that the extent of the taxonomic turnover across the ECB may have been overestimated. The new discovery of tubular fossils from the terminal Ediacaran Beiwan Member that morphologically resemble some early Cambrian shelly fossils further reinforces the evolutionary continuity across the ECB. Together, these fossils suggest not only that cloudinid skeletal fossils, which were previously regarded as exclusively terminal Ediacaran taxa, may extend into the basal Cambrian, but also that a small number of lineages of basal Cambrian shelly taxa may have had their origins in the terminal Ediacaran Period (e.g., *Anabarites* and *Cambrotubulus*; see also Zhu et al., 2017). We emphasize that, despite the evolutionary continuity, there is also evolutionary turnover across the ECB in both soft-bodied and skeletal animals. Currently available data indicate that most erniettomorphs and rangeomorphs likely went extinct at the ECB, and a large number of Fortunian (earliest Cambrian Period) shelly fossils have no counterparts in the terminal Ediacaran Period. Even for those skeletal fossils that do cross the ECB, their relative abundance is drastically different on either side of the boundary. For example, *Cloudina* is the dominant genus in terminal Ediacaran strata (e.g., accounting for 68.65% of all fossil specimens in our collection) but is relatively rare in basal Cambrian rocks. Similarly, tubular microfossils resembling basal Cambrian taxa are numerically rare in terminal Ediacaran strata (no more than 8.23% of all Beiwan fossils recovered in this study; Table DR1). This further highlights the need to process large amounts of material (~5220 kg in our case) in order to recover the rare elements of Cambrian-style tubular fossils from terminal Ediacaran rocks.

The data presented in this paper show that although the terminal Ediacaran and earliest Cambrian faunas remain distinct, emerging data—including those presented here—suggest that the evolutionary connection between these two faunas may be stronger than previously thought. At one level, such a connection would be expected unless life started anew after the ECB (Xiao and Laflamme, 2009). What is important, however, is that paleontologists can now distinguish animal taxa that survived the ECB from those that failed. This development is key to demonstrating the survival and extinction selectivity across the ECB and to testing the various environmental and ecological processes behind the Ediacaran-Cambrian turnover.

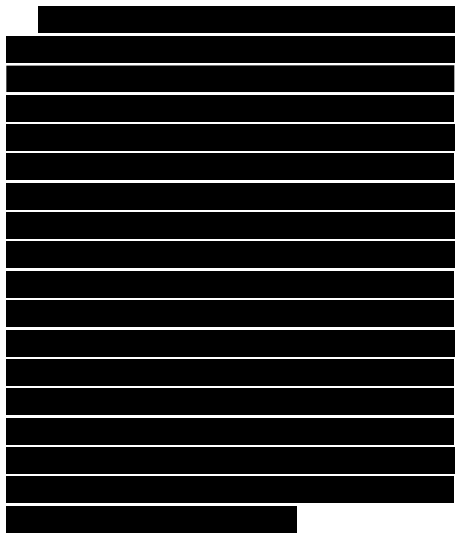
Among all tubular microfossils described in this paper, the anabaritids with triradial sulci (Figs. 2G–2K) stand out in their remarkable resemblance to *Anabarites trisulcatus*, which is present in abundance in basal Cambrian strata (Kouchinsky et al., 2009). Rare specimens of *A. trisulcatus* have been previously reported from strata of possible terminal Ediacaran age (Zhuravlev et al., 2012; Rogov et al., 2015; Zhu et al., 2017; Zhuravlev and Wood, 2018), and the new data enhance the possibility that anabaritids first appeared in the terminal Ediacaran Period. With representatives in the terminal Ediacaran Period, it is possible to chart the morphological and evolutionary trends of anabaritids across the ECB. In this regard, we note that, despite the common presence of triradial sulci, the Beiwan anabaritids are subtly different from Cambrian specimens of *A. trisulcatus* (Kouchinsky et al., 2009). The three longitudinal sulci of Cambrian *A. trisulcatus* initiate a short distance from the apex (Kouchinsky et al., 2009; Shao et al., 2015), whereas the sulci start apically in some Beiwan anabaritids (Fig. 2K) but subapically in others (Fig. 2I). These fossils cast doubt on the proposition that anabaritids

Figure 3. New skeletal fossils from the Beiwan Member of the Dengying Formation at Lijiagou, South China. A–C: Conical tube with round apex and subapical constriction (arrows). D–E: Incompletely preserved cylindrical tubes. Note triangular cross section (lower end of E). F–G: Incompletely preserved cylindrical tubular fossils with poorly defined transverse annulations or undulations. H–I: Slightly tapering tubular fossils with round apex but no constrictions. J–K: Conotubular and cylindrical fossils with thin and faintly preserved transverse annulations. L: Incompletely preserved tube. M–N: Cylindrical or slightly conotubular tube with broad and round apex. O: Incompletely preserved tube with transverse annulations and ridges (arrows). P: Incompletely preserved cylindrical tube with poorly defined transverse annulations. See Table DR2 (see footnote 1) for museum catalog numbers.

originated from a cylindrical tubular ancestor and progressively developed their triradial sulci from the aperture to the apex (Chen and Peng, 2005; Shao et al., 2015).

The Beiwan anabaritids join a number of other terminal Ediacaran tubular fossils (e.g., *S. triangularis*, *S. pentacarinalis*, and *S. hexagonus* [Cai et al., 2015]) in exhibiting triradial, pentaradial, and hexaradial symmetry characteristic of some Cambrian fossils (e.g., *Emeiconularia amplicanalis* [Liu et al., 2005], *Eopriapulites sphinx* [Liu et al., 2014], and *A. sexalox* [Bengtson et al., 1990]). Although the phylogenetic links among these fossils remain to be established, the broad similarities in body symmetry further echo the possible evolutionary continuity across the ECB. Thus, although iconic elements of the Ediacara biota disappear at the ECB, a number of skeletal taxa may have persisted through this geological divide and later diversified into the Cambrian shelly fauna. These terminal Ediacaran skeletal animals represent a prelude to the Cambrian explosion of shelly animals, echoing recent views that an early phase of the Cambrian explosion may have actually started in the terminal Ediacaran Period (Darroch et al., 2018).

CONCLUSIONS



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