Article

Earliest spicule fossils (550 Ma old) indicate radiation of Porifera Demospongiae sponges at end of Neoproterozoic

塔里木板块最早的（新元古代末）骨针化石说明5.5亿年前多孔动物门普通海绵纲的辐射

Hong-Xia Jiang (姜红霞) [1], Ya-Sheng Wu (吴亚生) [*2,3], Ying Li (李莹)[2, 3],
Guo Yang (杨果) [4], Wen-Qing Pan (潘文庆) [4]

[1] Hebei International Joint Research Center for Paleoanthropology, College of Earth Science, Hebei GEO University, Shijiazhuang 050000, China.
[2] University of Chinese Academy of Sciences, Beijing 100049
[3] Institute of Geology and Geophysics, Chinese Academy of Sciences, Beijing 100029
[4] Research Institute of Petroleum Exploration and Development, Tarim Oilfield Company, PetroChina, Korla, China
*Corresponding author: Ya-Sheng Wu. Email: wys@mail.igcas.ac.cn, jianghx@hgu.edu.cn

Abstract

Abundant silica sponge spicules were recovered from an argillaceous silicalite bed at the base of the Yuertusi Formation in the Tarim Basin, Xinjiang, China. Their features are in accordance with the spicules of Porifera Demospongiae. Small shelly fossils and carbon isotope curve indicate the spicules have an age of 550 Ma, are younger than the spicules reported from the Yangtze plate. The abundant occurrence of the Demospongiae spicules in both of the Tarim and Yangtze plates indicates radiation of Demospongiae sponges in the end of the Neoproterozoic.

Key words: Demospongiae, demosponges, sponges, porifera, Tarim, Yuertusi Formation, silica spicules.

1. Introduction

Sponges are regarded as the most primitive multicellular animals (Halanych, 2004; Taylor et al.,

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2007; Srivastava et al., 2010), and are one of the critical groups in understanding the early evolution of animals. Because sponges were among the first animals to build mineralized skeletons through biologically controlled processes, they provide key insights into the origins of animal biomineralization (Xiao, 2020). Sponges have a simple wall-like body, typically like a wine-cup, with abundant tiny holes within their body, which make water flow through them and filter the microbes from the water for food.

Sponges often have needle-like skeletons, spicules, in their body, which are composed of silica minerals in most sponges, but are carbonate in some sponges. Not all sponges have spicules. The sponges without spicules are difficult to preserve as fossils. In most cases, the spicules of the spiculate sponges can preserve as fossils.

Sponge spicules are regarded as the earliest skeletons of animals. The first appearance of spicules is not only an important event in animal evolution, but also a sign of a major change in ocean chemistry. Thus, to determine the times when the sponges appeared and when the sponge spicules appeared is an important task for paleontologists.

Molecular divergence estimates asserted that siliceous spicules should be present since the Precambrian (Sperling et al., 2010). Mitogenomic data using relaxed molecular clock techniques and likelihood-evaluated fossil calibration strategies show that the first appearance of silica spicules should have occurred about 633 (616–648) Ma ago (Ma and Yang, 2016).

The biomarker of a main group of sponges (Demospongiae), 24-isopropylcholestanes, has been found from the 635 Myr ago Cryogenian rock in South Oman Salt Basin (Love et al., 2009). And the three-dimensional body fossil of sponge has been recovered from the 600-million-year (Myr)-old horizon of the Doushantuo Formation in Guizhou Province, southern China (Yin et al., 2015).

Although spicule-like fossils were found from some Precambrian strata (Tang et al., 1978; Steiner et al., 1993; Brasier et al., 1997; Li et al., 1998), they were all questioned by later researchers (Yin et al., 2001; Zhou et al., 1998; Antcliffe et al., 2014). Currently the unequivocal earliest spicule fossils were from the Early Cambrian (Bengtsonet al., 1990; Yuan et al., 2002; Xiao et al., 2005) and Ediacaran-Cambrian transition (Chang et al., 2017, 2019). The silica spicules from the Ediacaran-Cambrian transition strata in Hubei (Chang et al., 2017, 2019) are mainly uniaxons, and were considered responsible for the formation of the silica rocks of this time. However, due to the lack of critical fossils and high-quality carbon isotope data, the age of the spicules was not yet accurately determined.

In this study, abundant siliceous sponge spicules were recovered from the end of the Neoproterozoic in Tarim, Xinjiang, China. Based on small shelly fossils and high-quality carbon isotopic data, the age of the spicules was precisely determined.

2. Stratigraphy of the Study Area

The studied section is located at the western part of the Tarim Basin, about 20 km southwest of Aksu, Xinjiang, China (Fig. 1: Shiairike). The terminal Ediacaran to Early Cambrian succession in the study area (Fig. 2-A) is divided into two formations, the Qigebulak, and the overlying Yuertusi (**Huang et al., 2017; Li et al., 2021; Wu et al., 2021**). The Qigebulak Formation consists of thin- to medium-bedded dolostones. The Yuertusi Formation consists of the basal phosphatic and silica rocks and the above shale and dolostones.

3. Research Methods

In this study, an outcrop section spanning the terminal Ediacaran and the basal Cambrian at Shiairi-

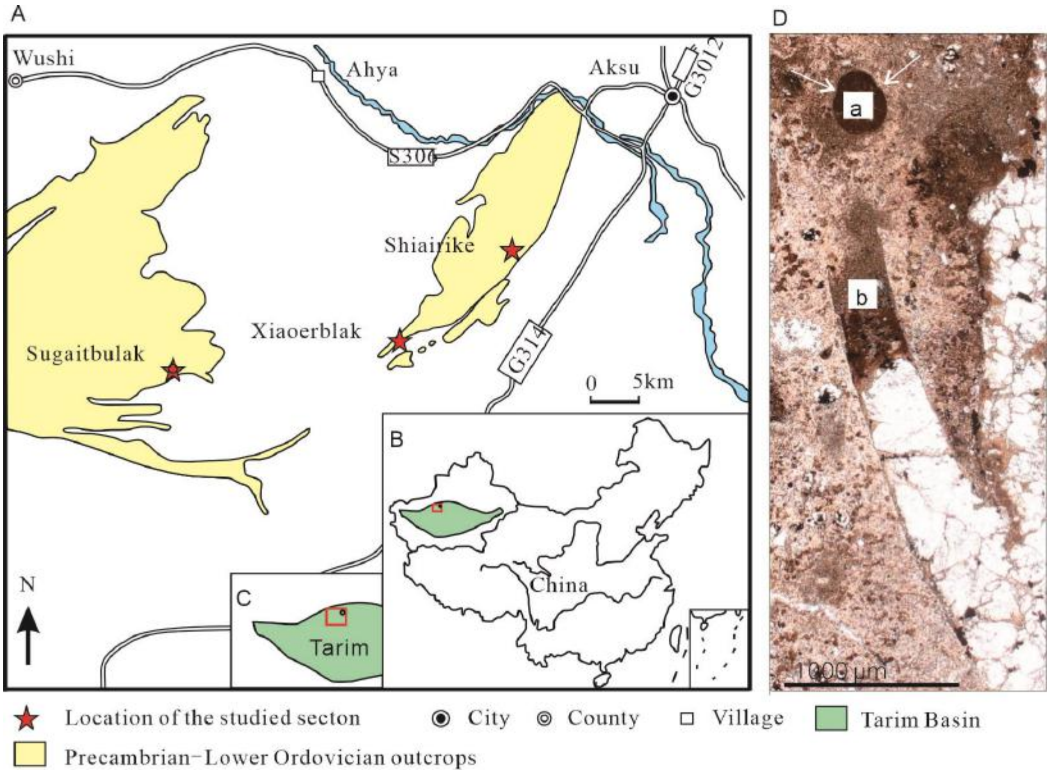

Fig. 1 A, Location of the studied section at Shiairike, in northwest of the Tarim Basin, China. B, Location of the Tarim Basin in China. C, Position of map A in the Tarim Basin. D, Photomicrograph of *Anabarites trisulcatus* recovered in this study, a key fossil whose first appearance is used considered the beginning of the Cambrian. (a) and (b) in D are the cross and oblique sections of the fossil respectively.

ke was measured. 99 rock samples were collected at intervals of 0.01-1.5 m from the section and thin sections and slabs were made from them. Microscopic examination was conducted to determine the lithology and evaluate the degree of diagenetic alternation. For carbon and oxygen isotopic analyses, 37 powder samples were taken using a micro drill from the microcrystalline parts of the slabs. Coarsely recrystallized areas and cement were avoid in the sampling process. The powder samples were analyzed on a Finnigan MAT-252 mass spectrometer at Institute of Geology and Geophysics, Chinese Academy of Sciences for $\delta^{13}C$ and $\delta^{18}O$ compositions. The $\delta^{13}C$ and $\delta^{18}O$ values are reported in ‰ relative to the standard Vienna Pee Dee Belemnite (VPDB). The reproducibility for $\delta^{13}C$ is better than 0.01%. The data were used to form the curve in Figure 2.

4. Lithology of the Shiairike section

As shown in Figure 2, the Yuertusi Formation in the Shiairike section is 38 m thick, and consists of six lithological intervals (Fig. 2), in ascending order, (1) the basal silica and phosphatic rocks, (2) the thin-bedded silicalite with black shale interbeds, (3) the blackish shale and calcareous shale, (4) the blackish massive dolostone, (5) the blackish shale and alternative medium-bedded dolostone, and (6) the greenish thin-bedded argillaceous dolostone.

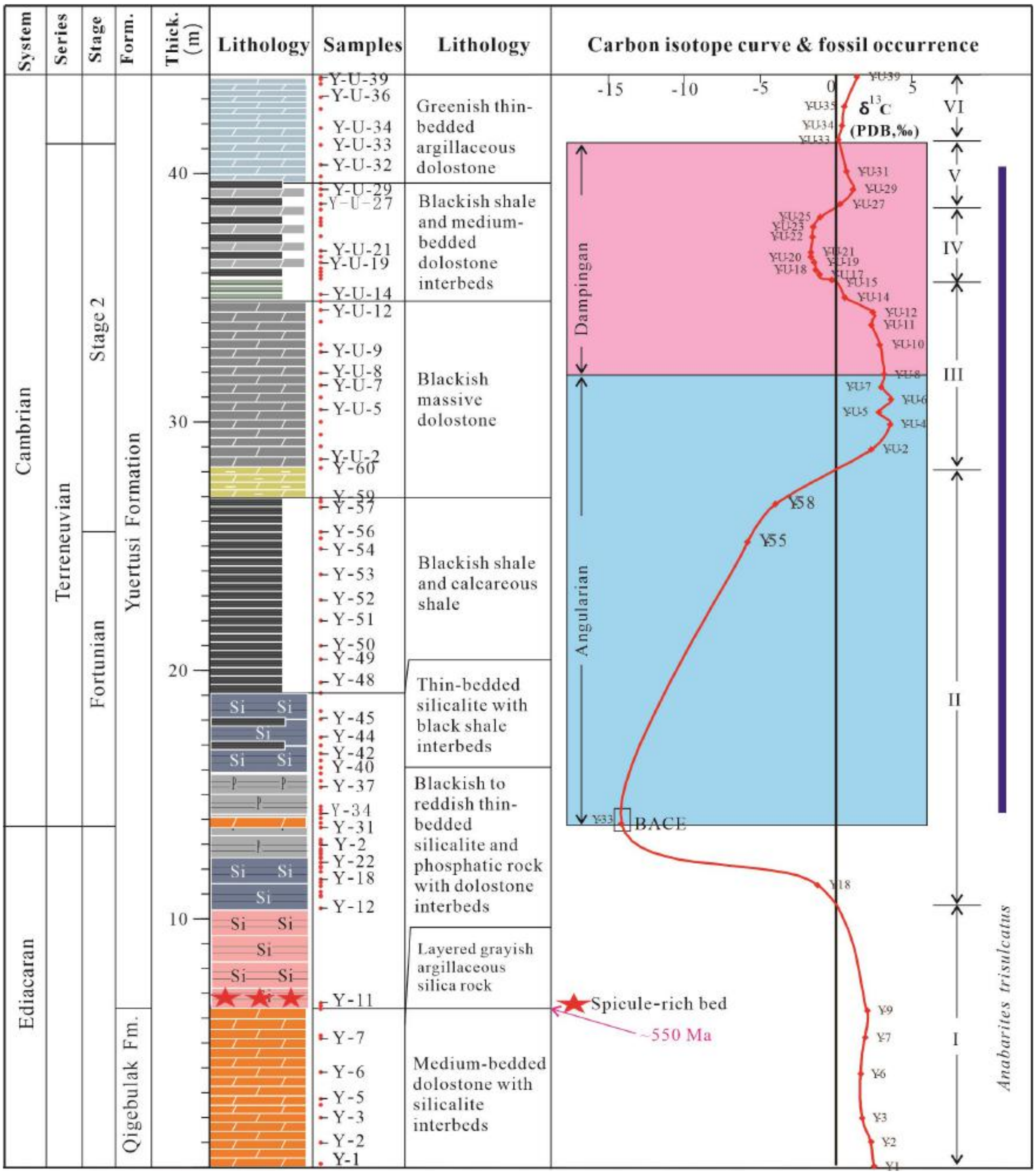

Fig. 2 The stratigraphy and lithology of the terminal Ediacaran to early Cambrian transition in the Shiairike section and the occurrence of the silica spicules from Samples Y-9, 10 and 11, and the key small shelly fossil for the Ediacaran-Cambrian boundary, *Anabarites trisulcatus* from Sample Y-34. The carbon isotope curve is divided into four segments (I to VI), showing an excursion (BACE) and two variation patterns (Angularian timely equals Furtunian and the lower part of Stage 2 of the Cambrian, and Dampingian equals the upper part of Stage 2, *see* Wu et al., 2021).

5. Characteristics of the silica spicules

Microscopic examination of 99 thin sections from Shiairike section revealed abundant needle-like

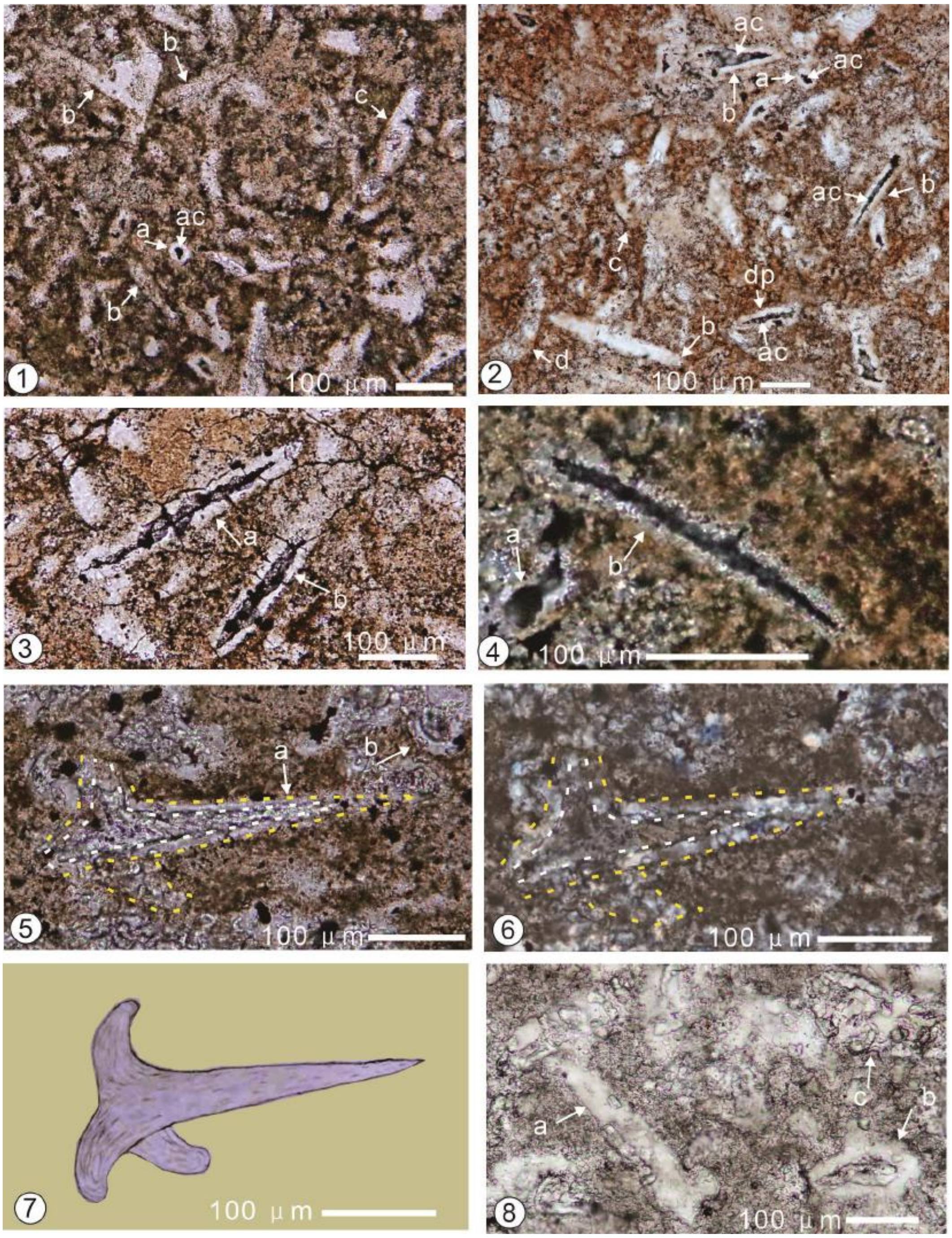

Fig. 3 Photomicrographs of the silica spicules from the basal 10 cm of the Yurertusi Formation at Shiairike, Aksu, Xinjiang, China, dating terminal Ediacaran, 550 Ma old.

Most spicules are needle-like, with one or two aciform. Some spicules are anchor-like. Most needle-like and anchor-like structures have an axial canal ("ac"). 1-6, 8: thin sections. 1-5, 8: in plane polarized light all spicules show a grayish color. 6: in cross-polarized light the spicules showed a first order gray interference color. 5 and 6 are of the same spicule. 7 is the restored figure of the anchor-like structure in 6.

1, 2: The rock consisting of the whitish silica spicules and the brownish interstitial clays. The spicule cross section (a) is rounded and shows an axial cavity (ac). Longitudinal sections of the spicules (b) are needle-like, some in 2 showing axial cavities. A few spicules have a thicker middle part (c). Some spicules (c, d) are probably anchor-like.

3: Two needle-like spicules (a, b) with axial canals.

4: A spicule cross section (a) and a spicule longitudinal section (b) show axial canals.

5, 6: A longitudinal section of an anchor-like spicule (within the yellow dash-line) with an axial cavity (within the white dash-line), and a spicule cross section showing an oval cross section of an axial canal.

8: Many spicules, three maybe anchor-like (a, longitudinal section near surface; b, cross section of the base; c, longitudinal section showing an axial canal).

structures in the six thin sections from the lowest 10 cm of the basal silica and phosphatic rock interval of the Yuertusi Formation (Fig. 2).

The rock of the six thin sections is composed of intercontact needle-like structures and the interstitial clays (Fig. 3). In addition to the needle-like structures, there are a few anchor-like structures (Fig. 3, E to H). In a PP light, the needle-like structures and the anchor-like structures show a white color, and in a XP light, they all show a first order gray interference color, a characteristic of quartz (Haldar, 2020), which indicates that these structures are all composed of quartz.

The needle-like structures have two sharp ends or one sharp end and another thickened end. The anchor-like structures consist of a long rod and about three short rods (Fig. 3, E, F, G). The needle-like structures and the long rods of the anchor-like structures generally range 280-300 μm length and 30-50 μm in outer diameter. Most needle-like and anchor-like structures have an inner canal in their longitudinal or cross sections (Fig. 3: ac), which is rounded or triangular in cross section, and is 15-35 μm in diameter.

6. Small Shelly Fossils and Carbon Isotope Results

Examination of the thin sections revealed abundant *Anabarites trisulcatus* (Fig. 1, D) in Sample Y-34, which is about 7.8 m from the bottom boundary of the Yuertusi Formation (Fig. 2).

One of the *Anabarites trisulcatus* fossils is 365 μm in diameter and at least 3,524 μm in length, and shows evidence of two distinct longitudinal grooves (Fig. 1, D: pointed by the arrows).

The 37 carbon isotope data produced a smooth curve (Fig. 2). The carbon isotope data vary from 2.85 to -14.39, and oxygen isotope data from -4.98 to -8.08.

7. Interpretations

7.1 Identification of spicules

Present-day sponges are divided into four groups, Demospongiae, Hexactinellida, Homoscleromorpha and Calcispongia, and most of the former three groups have silica spicules, which vary in shape and size. The Calcispongia sponges have calcareous spicules (Borchiellini et al., 2004; Botting and Muir, 2018). The silica spicules can be needle-like (called monaxons), or consist of three rods in a plane with adjacent two rods at 120 ° (called triactines) or four rods in four directions with two adjacent at 120° (called tetractines). The silica spicules in Demospongiae and Hexactinellida sponges have an axial canal. The axial canals in Demospongiae sponges are triangular or hexagonal in cross section, which is regarded as a key characteristic of demosponge spicules. The silica spicules in Homoscleromorpha sponges do not have an axial canal (Botting and Muir, 2018), or have an axil canal that has an irregular cross section (Uriz et al., 2003).

The silica spicules in the Hexactinellida sponges can be needle-like, or consist of two (called stauractines) or three rods (called triaxonal or pentactines, triaxonal hexactines) at 90°. The key characteristic of the Hexactinellida spicules is the angle between any two adjacent rods is 90°. The spicules in the Homoscleromorpha sponges include monaxons, tritriactines and tetractines, and all lack an axial canal, which makes them distinguishable from demospongiae spicules. The spicules of the Calcispongia are calcareous and include monaxons, triaxons and tetraxons.

The spicules in modern Demospongiae sponges is 0.1-1mm in length, maximally 10 mm, and vary from 0.05 to 0.15 mm in diameter. The calcisponge spicules are 0.03-0.4 mm in diameter and 0.3-2.5 mm in length.

The silica (quartz) composition of the Shiairike needle-like and anchor-like structures rules out the possibility that they belong to Calcispongia.

The sizes of the Shiairike needle-like and anchor-like structures are within the sizes of the Demospongiae, Hexaspongiae and Homoscleromorpha sponges.

The anchor-like structures are interpreted as tetraxons (Fig. 3: 5, 6, 7). The angle between any two adjacent rods may be 120°. There is no structure that has adjacent rods at 90°, which rule out the possibility that the silica structures belong to Hexaspongiae. Since some of axial canals are triangular in cross section (Fig.3: 1, a), some of the spicules may belong to Demospongiae sponges.

7.2 The Ediacaran–Cambrian (E–C) Boundary

7.2.1 Based on fossils

The Ediacaran–Cambrian (E–C) boundary is officially placed at the first appearance data (FAD) of the trace fossil *Treptichnus* (*Phycodes*) *pedum* (Brasier et al., 1994). However, this trace fossil is generally absent in carbonate strata. In its absence, the E–C boundary was placed at the first appearance data of the small shelly fossil *Anabarites trisulcatus* (Qian et al., 2001; Peng et al., 2012; Zhu et al., 2019), or at the peak of the large negative excursion in carbon isotope curve defined as BACE (Zhu et al., 2006; Wu et al., 2021).

The occurrence of *Anabarites trisulcatus* at 7.8 m above the bottom of the Yuertusi Formation may represent the first appearance datum of this fossil. Thus, the E-C boundary in this area can be placed 7.8 m above the bottom of the Yuertusi Formation.

7.2.2 Based on Carbon Isotope curve

Since the carbon isotope curve of the Shiairike section (Fig. 2) is smooth and the oxygen isotope data are greater than -10‰ (PDB), the carbon isotope data may represent the original carbon isotope composition of the seawater at that time (Hendy & Wilson, 1968; Wu et al., 2021), and can be used for correlation of strata.

The peak of the segment II (Fig. 2: "BACE") at the horizon of Sample Y-33 is similar to and correlated with the BACE excursion (Zhu et al., 2006), and the Ediacaran–Cambrian can be placed at the horizon of Sample Y-33, which is 0.2 m below Sample Y-34.

The carbon isotope curve is very similar to that of the Xiaoerbulak section (Wu et al., 2021: Fig. 2), and consists of 6 segments, (I) A positive straight part, (II) A large triangular negative part, (III) A small arc positive part, (IV) A smaller hill-like negative part, (V) A much smaller positive part, and (VI) The following positive part.

The curve from the peak of (II) to the midpoint of (III) is correlated with the Angularian pattern of the Carbon Isotope Pattern Curve defined in Wu et al. (2021), correspondent to the Fortunian and the lower half of Stage 2 of the Cambrian, and has an age of 541 to 525 Ma. The curve from the midpoint of (III) to the end of (V) is correlated with the Dampingan pattern, which is correspondent to the upper half of Stage 2, and has an age of 525 to 520 Ma. The Ediacaran–Cambrian (E–C) boundary is placed at the peak of the Angularian pattern, that is, the peak of the BACE.

7.3 Estimating the Age of the Spicules

The spicules occur in the lowest 10 cm of the Yuertusi Formation, and is 7.8 m below the Ediacaran -Cambrian boundary. The interval correlated with the Fortunian and Stage 2 is 27.5 m. The time of the interval is 20.7 Ma, implying that 1 m roughly represents 0.75 Ma. The occurrence of the spicules is 7.8 m below the E-C boundary. 7.8 m represents about 5.9 Ma. Thus, the age of the spicules is about 550 Ma.

8. Discussion: a radiation of Demospongiae ?

The silica spicules from Shiairike are very similar to the silica spicules from the E-C transition in Hubei, China (Chang et al., 2019, Fig. 2) in shape and size. The Hubei spicules are dominated by needle-like types, and most of them have a thicker middle part. Similarly, the silica spicules from Shiairike are also dominated by needle-like types that generally have a thick middle part. For example, one of the spicules in Fig. 3 (1, c) has a length of 0.2 mm and width of 0.06 mm, resembling the fifth spicule in Figure 9 of Chang et al. (2019) in shape and size. The needle-like spicules from Hubei are generally 150 to 350 μm in length, and the needle-like spicules from Shiairike are in the similar size.

Even though the age of the Hubei spicules were not accurately determined, they may not younger much than the Shiairike spicules, considering that the Hubei spicules occur a height above the bottom of the silica and phosphate rock interval, but the Shiairike spicules occur at the bottom of the silica and phosphate rock interval of the Yuertusi Formation.

During the Ediacaran, Hubei was located at the South China tectonic plate, and Shiairike at the Tarim tectonic plate, and these two plates were separated by the Australian plate (Li and Jiang, 2013, Fig. 1, page 3).

Sponges are benthic animals. The expansion in the distribution of benthic animals is generally a slow process. The occurrence of the same or similar spicules in the two plates indicates a radiation in demosponges (Croteau, 2010). The occurrence of the same or similar demosponge faunas represented by the Shiairike and Hubei spicules at two far apart tectonic plates at nearly the same time represents a radiation of Demospongiae. The expansion from the birthplace to the two plates might have taken a very long time. So, the first appearance of the sponges at their birthplace may be much earlier than 550 Ma.

9. Conclusions

The first appearance of spiculate Demospongiae sponges is a major event in the evolutionary history of animals. Previously it is believed to happen in the Early Cambrian. This study, however, based on fossils and carbon isotope data, determined that it happened at the end of the Ediacaran, perhaps much earlier than 550 Ma. Because similar demosponge faunas occurred in both of the South China plate and Tarim plate, they represent the first radiation of Demospongiae in its evolutionary history.

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内容亮点

（1）在塔里木盆地550Ma前的地层中发现了丰富的多孔动物门普通海绵纲的硅质骨针化石；

（2）当时塔里木板块和华南板块都有普通海绵纲硅质海绵动物繁盛，代表了其第一次大幅射。

详细摘要

（1）此研究通过薄片分析，在新疆塔里木盆地什艾日克早寒武世玉尔吐斯组最底部10 cm地层中，发现了丰富的单轴单射、单轴双射、锚状的硅质海绵骨针；根据形态和结构，将这些骨针鉴定为多孔动物门普通海绵纲；

（2）根据小壳化石的首现面、高密度碳酸盐岩碳同位素数据，确定玉尔吐斯组下部这段34. 5 m厚的地层属于寒武系纽芬兰统幸运阶和第二阶；由于这段地层岩性均一，结合地层厚度估算出这些海绵骨针的时代为550 Ma；

（2）这些骨针的特征与前人报道自华南寒武系底部的硅质海绵骨针非常相似。当时普通海绵在华南板块和塔里木板块的繁盛，代表了多孔动物门普通海绵纲的第一次大辐射。这种辐射可能与生物演化进程和古海洋环境有关。

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