New and extraordinary Early Cambrian sponge spicule assemblage from China

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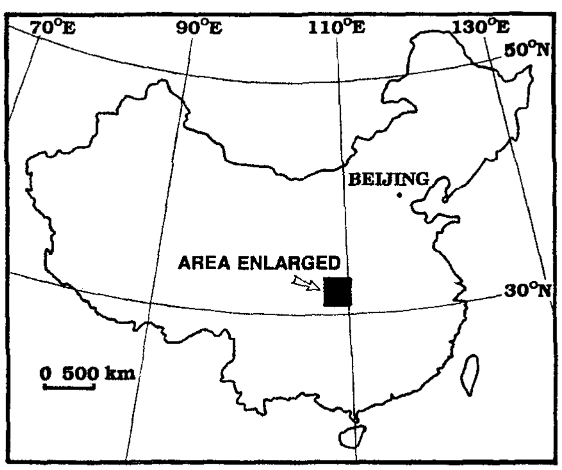
ABSTRACT

The fossil record of siliceous sponges, compared with that of other skeleton-secreting Metazoa, is poorly known, based as it is on disarticulated spicules and sporadically preserved body fossils. Abundant spicules recovered from Lower Cambrian strata in Shaanxi, China, essentially double the known morphological diversity of siliceous sponges for that interval of geologic time. These fossils, along with a comparable coeval fauna from South Australia, have a remarkably modern aspect, thereby demonstrating that the principal siliceous sponge groups and styles of body architecture were established quickly in the earliest Phanerozoic as part of the Cambrian "explosion" and that they inhabited a variety of low-energy, relatively deep water settings. The similarity of spicule shape and variation to that of younger assemblages reflects a conservative architecture for the siliceous sponges.

INTRODUCTION

Sponges have been a highly successful group throughout the Phanerozoic, colonizing most marine and some freshwater environments. Siliceous sponges have been important constituents in reefs since the Early Ordovician (Pratt and James, 1982), and calcareous sponges, as archaeocyathans and stromatoporoids, were primary reef builders even in the Early Cambrian (Pratt, 1990; Wood, 1991). Knowledge of the fossil record of siliceous sponges is based on whole, relatively rigid skeletons, compressed molds, casts, or films of once-flexible spicular networks, or isolated spicules seen in thin section or recovered as insoluble residues. Sponge body fossils with simple spicular morphology and architecture preserved in the Chengjiang and Burgess Shale faunas (Lower and Middle Cambrian, respectively) provide the only reliable foundation for classification for these early taxa, and show their rapid diversification in nonreefal environments (Rigby, 1986; Chen et al., 1989). However, such outstanding fossil Lagerstätten ("lode places") are mere glimpses, and the most common evidence of past sponges is isolated spicules.

Most Cambrian siliceous sponges were composed of relatively simple spicules, such as monaxons, stauractines, hexactines, or pen-



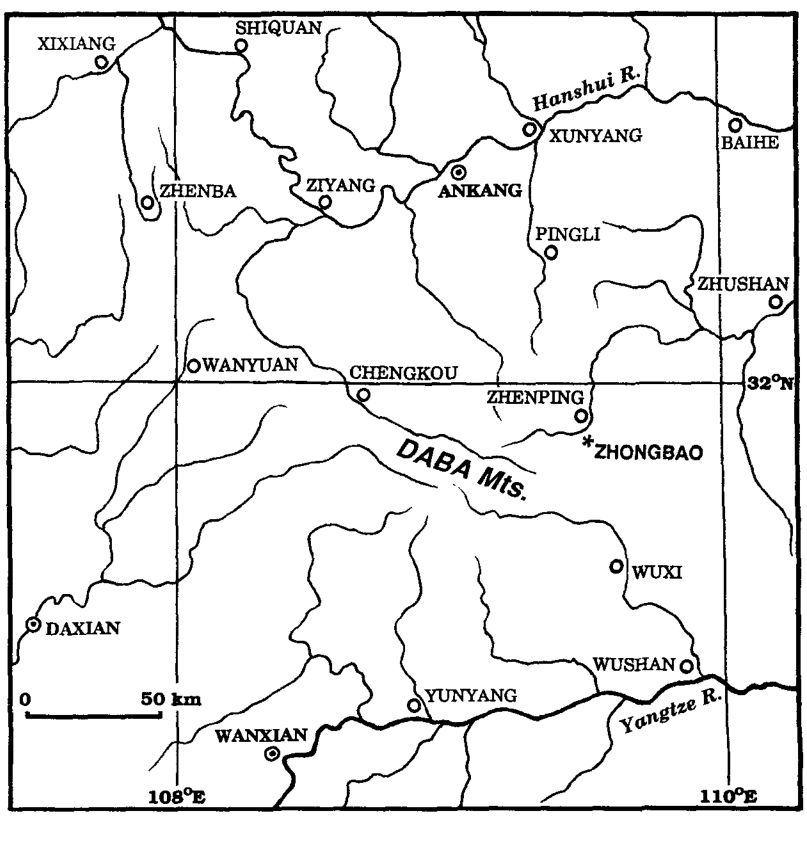


Figure 1. Location map. Fossils for this study were collected from Lower Cambrian Qiongzhusi Formation in Zhongbao (asterisk), small town 10 km south of Zhenping, southern Shaanxi, China.

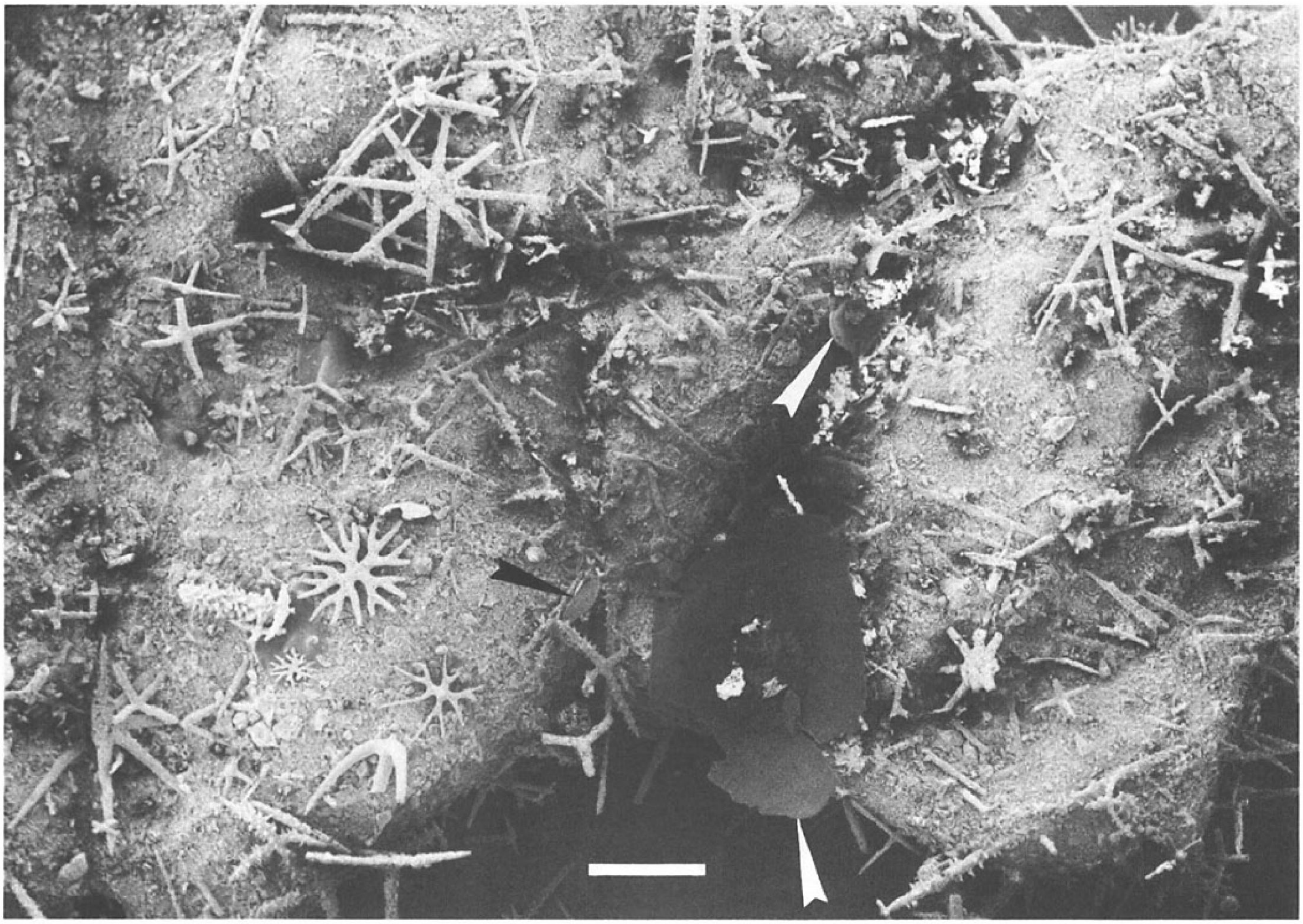


Figure 2. Partially acid-digested limestone from Lower Cambrian Qiongzhusi Formation in Zhenping, southern Shaanxi, China, showing varied densely accumulated sponge spicules (ZP 0010). White arrows indicate two bradoriid ostracodes; black arrow indicates inarticulate brachiopod. Scale bar (middle bottom) = 1 mm.

tactines (Sdzuy, 1969; Mostler and Mosleh-Yazdi, 1976; Ding and Qian, 1988; Wrona, 1989; Mehl, 1991). However, an Upper Cambrian spicule assemblage from Queensland (Bengtson, 1986) and the recently described Early Cambrian spicules from South Australia (Bengtson, 1990) indicate a much higher diversity and complexity than previously recognized and provide evidence that early siliceous sponges are comparable to some extent to Mesozoic and Cenozoic lithistids and hexactinellids. We report a somewhat similar but even more diverse sponge-spicule assemblage from approximately coeval Lower Cambrian strata in Zhenping, southern Shaanxi, China.

STUDY AREA

Spicules were recovered by dilute (5%) acetic-acid digestion of a thin-bedded, black argillaceous limestone of the Qiongzhusi (Chiungchussu) Formation in Zhenping, Shaanxi (Chön-p'ing-hien, Shensi) (Fig. 1); Blackwelder (1907) conducted the first stratigraphic study of the area during 1903–1904. This limestone was deposited in relatively deep water in a slope setting. The area is structurally complex, however, and no continuous section can be measured. The associated fauna, including bradoriid ostracodes, inarticulate brachiopods, and redlichiid trilobites, belongs to the Early Cambrian *Eoredlichia-Wutingaspis* Zone, Qiongzhusi Stage (Xiang et al., 1981), which is roughly equivalent to the upper Atdabanian of Siberia.

The Qiongzhusi Formation is widespread in southwestern China, but only the single unit at this locality has so far yielded such a spicule assemblage. The spicules are disorganized but concentrated in thin layers and mixed with other bioclasts (Fig. 2), indicating that, although derived from many disintegrated sponge skeletons, they underwent minimal transport. The variety of spicules present indicates that the benthic sponge community consisted of several coexisting species. Petrographic observations of the limestone indicate that only some of the spicules retain their primary silica mineralogy. Most of the others are found as calcite cement-filled molds because of the tendency of opaline silica to dissolve in seawater and during early burial (Land, 1976; Brasier, 1992). The Shaanxi siliceous sponge-spicule assemblage thus represents fortuitous preservation, and we suspect that siliceous sponges were more widely distributed than the current fossil record suggests.

SPONGE SPICULES

The spicule network of some sponges is constructed of only one spicule type, but most contain more, either interlocked or fused into networks. Spicule form in many extant and fossil sponges is complex and variable, difficult to use by itself in classification (Bergquist, 1978). Most isolated stauractines or hexactines from Cambrian rocks, which have been traditionally identified as *Protospongia*, for example, also exist in many other taxa (Rigby, 1981). In most cir-

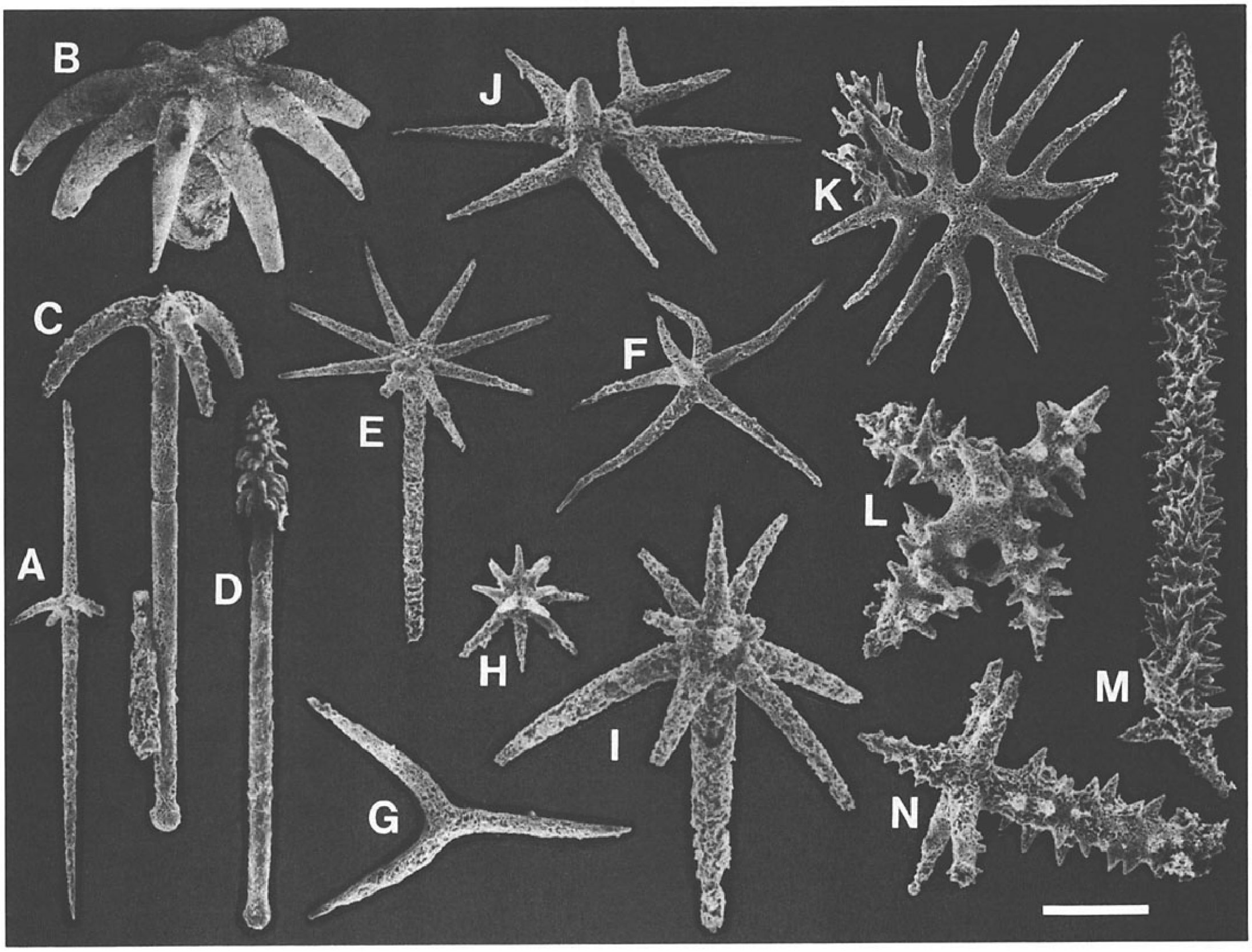


Figure 3. Isolated sponge spicules from Lower Cambrian Qiongzhusi Formation in Zhenping, southern Shaanxi, China. A: Hexactine oxea (ZP 0011). B: Tylostyle (ZP 0012). C: Triaene tylostyle (ZP 0013). D: Modified tylostyle (ZP 0014). E: Orthopolyaene (ZP 0015). F: Curved-clad hexactine (ZP 0016). G: Triactine (ZP 0017). H, I: Oxyasters (ZP 0018, ZP 0019). J: Dichopentactine (ZP 0020). K: Dichostauract (ZP 0021). L: Curved-clad acanthopentactine (ZP 0022). M: Swollen-rhabdome acanthopentactine (ZP 0023). N: Acanthohexactine (ZP 0024). Scale bar (bottom right) = 0.4 mm for A–F and K; 0.3 mm for H–J, M, and N; 0.2 mm for G and L.

cumstances, it is impossible to reconstruct the network or even recognize the assemblage belonging to an individual taxon on the basis of isolated spicules. We therefore consider it premature to apply formal taxonomy to the Shaanxi spicules.

Because classificatory terms for spicule morphology are many and no common scheme has been agreed to, we have attempted to use the simplest terms plus descriptors and have grouped the Shaanxi sponge spicules into seven categories.

1. Oxeas (monaxons pointed at both ends) are the simplest elements. Acanthoxeas resemble oxeas but are covered with fine spines, and hexactine forms bear four short rays (Fig. 3A).

2. Some smooth spicules resemble tylostyles—long, thin rhabdomes with a globular swelling at one end—but have a cladome of three to nine slightly curved clads at the other end (Fig. 3, B–D). Triaenes with three clads (Fig. 3C) are common in the fossil sponge record. A second type in this group bears a series of cladlike but short spines arranged in rings along the end of the rhabdome opposite the terminal knob (Fig. 3D).

3. A series of smooth spicules has a primary ray and four to nine rays radiating in a common plane from a central focus, forming orthopolyaenes (Fig. 3E). Some have rays that are slightly curved in an irregular manner (Fig. 3F).

4. Triactines have three smooth rays diverging from a central focus (Fig. 3G).

5. Oxyasters bear many rays that also diverge from a central focus (Fig. 3, H and I).

6. Two kinds of smooth spicules exhibiting forked rays are particularly common in this assemblage. Dichopentactines have four straight rays with one short projection orthogonal to them (Fig. 3J); dichostauractines lack the short ray, and the forked rays are both straight and curved (Fig. 3K). Rays may have one to four degrees of splitting independent of size and, therefore, probably independent of spicule growth.

7. Many spicules are ornamented with short spines. Acanthopentactines have five rays (Fig. 3, L and M) and, although variable, may be roughly subdivided into two kinds: one bearing a short rhabdome and four rays approximately equal in size but curved and extending irregularly (Fig. 3L), the other with short rays

on one plane and a very long rhabdome (Fig. 3M). Acanthohexactines have six rays, but the primary one is markedly thicker (Fig. 3N).

DISCUSSION

The seven spicule groups belong to the Hexactinellidae and Lithistidae. Some of them seem to be unique and probably represent new taxa. The high degree of diversity and size variation of these sponge spicules confirms Bengtson's (1990) suggestion that some taxa were structurally advanced, with spicules arranged into inner and outer walls. Varying spicule size in the skeletal framework can be attributed in part to progressive growth.

The Shaanxi spicule fauna bears some similarities to a coeval assemblage from South Australia (Bengtson, 1990) but lacks representatives of the Calcarea, presumably because the Shaanxi fauna lived in a deeper water setting. Our tylostyles resemble *Nabaviella* from South Australia and from the Upper Cambrian of Iran (Mostler and Mosleh-Yazdi, 1976), but the Australian one lacks the terminal swelling present on the primary rays; clavules from the Upper Ordovician of New South Wales are also similar (Webby and Totter, 1993, Figs. 3.11 and 3.12). Our orthopolyaene form may correspondingly belong to *Heterostella* from approximately coeval strata in Siberia (Fedorov, 1987) and questionably from South Australia. It is also similar to *Taraxaculum*, but in this taxon the tip of the primary ray may be pointed or split into short processes (Bengtson, 1990). Our curved-ray hexactine may belong, or be related, to *Inflexiostella*, also from Siberia. Our acanthopentactines and acanthohexactines are similar to forms from the Upper Cambrian of Queensland (Bengtson, 1986), the Upper Silurian of Arctic Canada (de Freitas, 1991), and the Upper Triassic of Austria (Mostler, 1986), although in the South Australia Lower Cambrian fauna only hexactinellid spicules developed acanthose surfaces (Bengtson, 1990, Fig. 15). Our dichopentactines and dichotetractines appear to be new.

CONCLUSIONS

Hexactinellid sponges made their first appearance in the Tommotian as isolated stauractines in Siberia (Rozanov and Zhuravlev, 1992) and as hexactines and pentactines in South China (Ding and Qian, 1988), and possibly appeared even earlier (Brasier, 1992, Fig. 4). By the Atdabanian, siliceous sponges seem to have become fairly widespread in low-energy, offshore marine environments in China, Australia, and Siberia. This supports Webby's (1984) suspicion of a deep-water origin for these sponge groups, but more sampling is needed. Laurentian strata, for example, have yielded no such assemblages.

The Shaanxi sponge-spicule assemblage is complex and strikingly modern in appearance, and therefore suggests not only a rapid diversification of the siliceous sponges during the Cambrian "explosion," but that they achieved quickly an architecture that remained stable during their subsequent evolutionary history.

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