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Notes

Ediacarian sponge spicule clusters from southwestern Mongolia and the origins of the Cambrian fauna

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ABSTRACT

Carbon and strontium isotopic data are used to show that the earliest sponge spicule clusters and associated phosphatic sediments (with *Anabarites*) from southwestern Mongolia are of Ediacarian age. Spicule morphologies include bundles of oxeas arranged in three-dimensional quadrules, linked together at junctions by tetracts, pentacts, hexacts, or polyactines. All are referred to the Phylum Porifera, Class Hexactinellida. These sponge spicules provide the oldest remains that can be assigned without question to an extant phylum, and also the first firm evidence for filter feeding and metazoan silica biomineralization in the fossil record. It is suggested that siliceous and phosphatic members of the “Cambrian fauna” may have had their origins in eutrophic and outer shelf facies of the Late Proterozoic.

INTRODUCTION

Sponges are the most primitive of metazoan clades and their presence in the Proterozoic is hinted at by both molecular (rRNA) and morphological phylogenies (Conway Morris, 1994). Although Late Proterozoic rocks contain high concentrations of the sponge biomarker 24-isopropylcholestane (Moldowan et al., 1994), this evidence may not be wholly diagnostic, and even the fossil evidence for Ediacarian sponges has remained controversial. Isolated spicule-like structures in cherts from the lower part of the Doushantuo Formation of southern China (Tang et al., 1978; Ding et al., 1988) are poorly illustrated and remain questionable (Steiner et al., 1993). Spicule-like structures from the younger, Dengying Formation of southern China (Steiner et al., 1993) are poorly preserved and illustrations appear to

include casts or molds of filamentous cyanobacteria or algae. Some medusa-form impressions from South Australia have also been interpreted as of sponge grade (Gehling and Rigby, 1996), though the latter authors accept that this interpretation must be controversial. Until now, the oldest convincing hexactinellid sponge spicules have been simple tetracts of mid-Nemakit-Daldynian to Tommotian age (Rozanov and Zhuravlev, 1992; Steiner et al., 1993; Brasier, 1992; Brasier et al., 1993) and more diverse spicules of Atdabanian-Botomian age (Bengtson et al., 1990; Zhang and Pratt, 1994).

The exceptionally well preserved sponge spicule assemblages in Figure 1 come from the lowest skeletal fossil horizon in southwestern Mongolia, in limestones just above a phosphorite–chert–black shale marker bed in

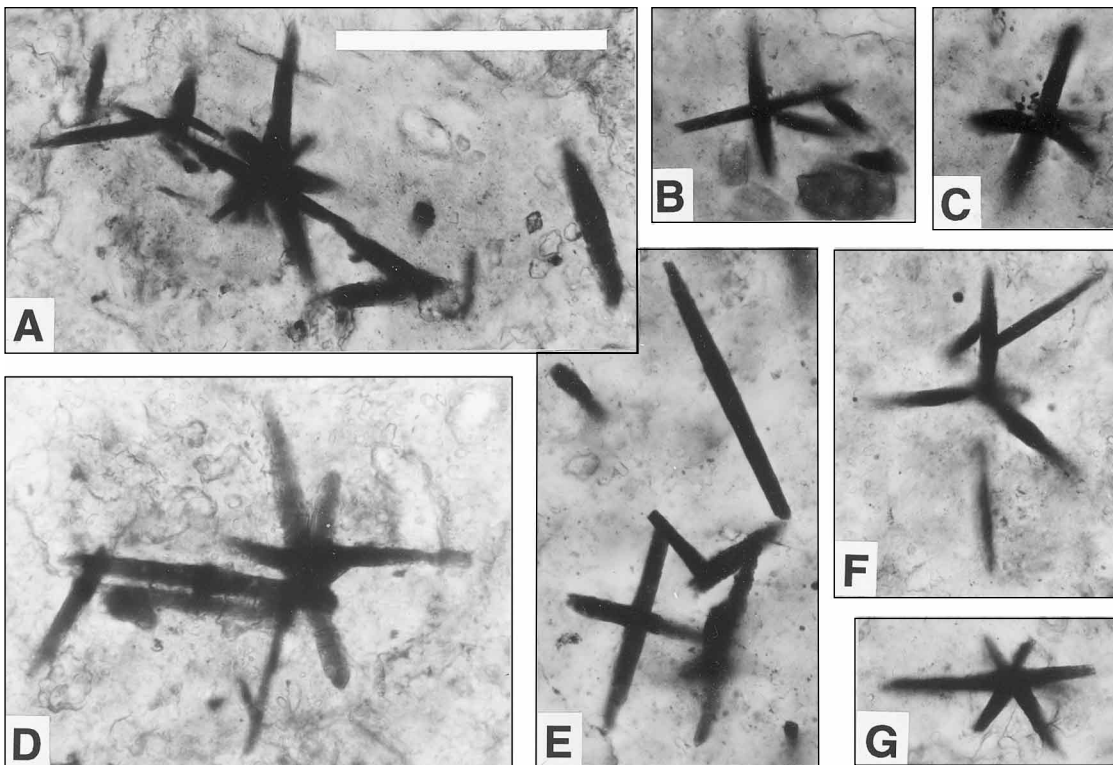


Figure 1. Clusters of Ediacarian hexactinellid sponge spicules from southwestern Mongolia, preserved in iron oxide within early diagenetic chert concretions. Spicule morphologies include monaxons (oxeas, A, D, and E; Oxford University Museum specimens A/Y. 35 to 37); triaxons (tetracts, B; pentactines, C; triactines, F; hexactines, G; specimens A/Y. 38 to 41), each with rays in various planes; also flowerlike polyactines (focusing at different planes shows these to be modified hexactines with one or more extra rays, i.e., not accidentally overlapping spicules; A at center). Clusters can preserve original skeletal architecture, such as bundles of monaxons with reticulate lattices arranged in three-dimensional quadrules or triaxons (A and D). Scale bar = 0.1 mm.

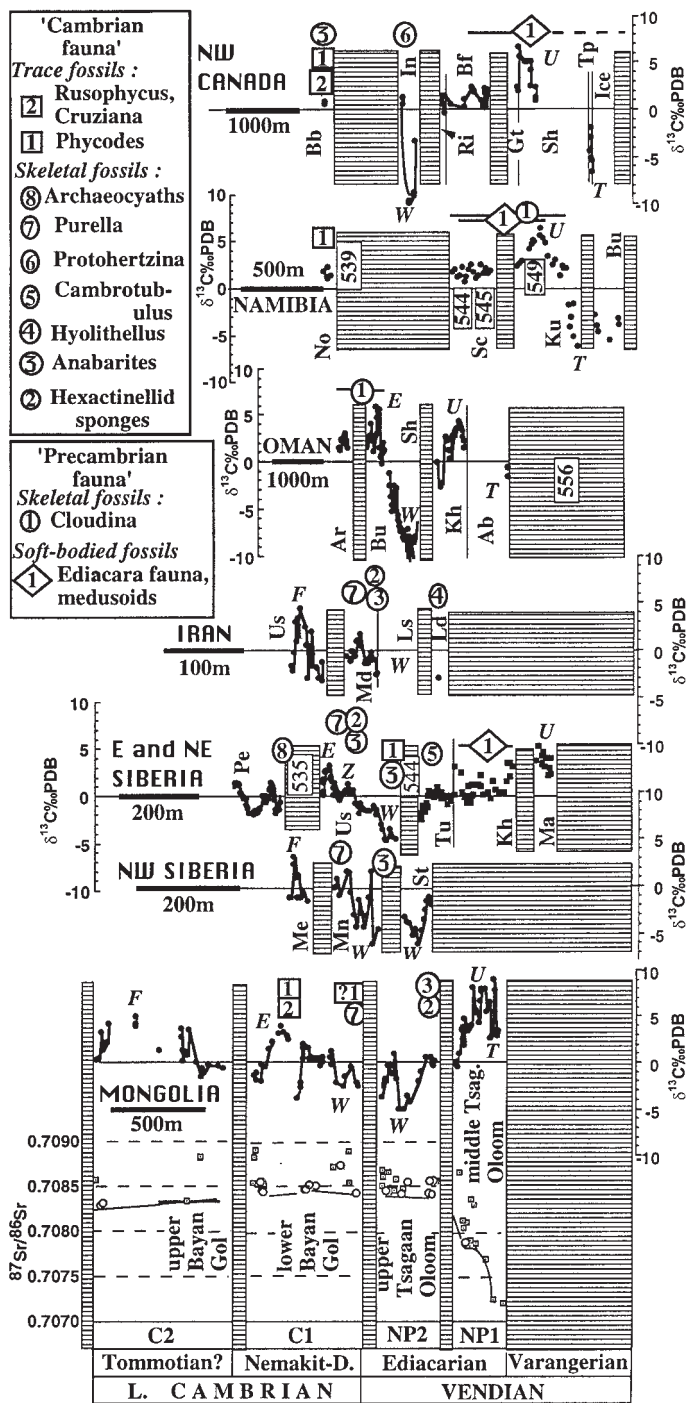


Figure 2. Calibration of Precambrian and Cambrian fauna against $^{87}\text{Sr}/^{86}\text{Sr}$ and $\delta^{13}\text{C}$ stratigraphy from Mongolia and other key sections. Interval with parallel lines are presumed gaps in record. Radiogenic dates in square boxes after cited sources. Carbon isotopic features T, U, W, E, and F after Brasier et al. (1996). Southwestern Mongolia (white circles = least-altered $^{87}\text{Sr}/^{86}\text{Sr}$ data; Brasier et al., 1996); northwest Siberia (Pokrovsky and Missarzhevsky, 1993; Knoll et al., 1995a; Kaufman et al., 1996; St = Staraya Rechka, Mn = Manykay, Me = Medvezhin); eastern Siberia (Brasier et al., 1994; Us = Ust-Yudoma, Pe = Pestrotsvet); northeastern Siberia (Bowering et al., 1993; Knoll et al., 1995b; Pelechaty et al., 1996; Ma = Mastakh, Kh = Khatyspyt, Tu = Turkut); Iran (Brasier et al., 1990; Ld = lower dolomite; Ls = lower shale; Md = middle dolomite; Us = upper shale); Oman (Burns and Matter, 1993; Ab = Abu Mahara, Kh = Khufai, Sh = Shuram; Bu = Buah, Ar = Ara); Namibia (Kaufman et al., 1991; Grotzinger et al., 1995; Bu = Buschmanns, Ku = Kuibis, Sc = Schwarzrand, No = Nomtsas); northwestern Canada (Narbonne et al., 1994; Ice = Icebrook, Tp = Teepee; Sh = Sheepbed, Gt = Gametrail, Bf = Blueflower, Ri = Risky, In = Ingta, Bb = Backbone Ranges).

flowerlike polyactines occur (Fig. 1A). Bundles of oxeas are arranged in three-dimensional quadrules, linked together at the junctions with triaxons or polyactines (Fig. 1, A and D). All spicules can be referred to the Cambrian-recent glass sponges (Class Hexactinellida). Because the metazoan affinities of the Ediacara fauna, *Cloudina*, and supposed worm tubes are still disputed or unknown (e.g., Retallack, 1994; Steiner, 1994), these remains provide the earliest clear evidence for organisms that can be assigned without question to an extant metazoan phylum, and the first firm evidence for filter feeding and metazoan silica biomineralization in the fossil record.

CHEMOSTRATIGRAPHY

The Proterozoic age of this Mongolian sponge assemblage can be demonstrated by means of carbon and strontium isotope stratigraphy on associated carbonates (Fig. 2). Globally proven temporal fluctuations in $\delta^{13}\text{C}$ are thought to reflect global changes in ocean chemistry, in response to shifts in the rate of photosynthesis and/or carbon burial (Kaufman and Knoll, 1995). Variations in least-altered $^{87}\text{Sr}/^{86}\text{Sr}$ are thought to indicate gradual changes in the erosion rate of older, radiogenic continental crust relative to the formation rates of new oceanic crust (Derry et al., 1992; Nicholas, 1996).

In Mongolia, it is convenient to distinguish four time intervals characterized by distinctive isotopes and biota (Brasier et al., 1996) and separated by breaks in sedimentation (Fig. 2; Lindsay et al., 1996b). Interval NP1 (beneath the sponge assemblage) has a pronounced carbon isotope excursion (feature U), reaching values of $<8.0\text{‰}$, calibrated by a sharp rise in $^{87}\text{Sr}/^{86}\text{Sr}$ values from 0.7072 to 0.7079. These values allow correlation with the middle range of the Ediacara fauna in northwestern Canada, and the lower range of the Ediacara fauna and *Cloudina* tubes in Namibia (Fig. 2), dated as ca. 548.8 ± 1 Ma (Grotzinger et al., 1995). Glacial deposits beneath this cycle in Namibia are generally regarded as Varangerian, and dated at ca. 600 Ma (Grotzinger et al., 1995) but glaciations in Algeria, and possibly in Oman, appear to be younger than ca. 556 Ma (Betrand-Sarfati et al., 1995; Burns et al., 1994).

Interval NP2 begins with phosphorite–chert–black shale, followed by limestones with sponge cherts. At Tsagaan Gol, $\delta^{13}\text{C}$ values begin at $+0.2$ to $+0.5$ and then drop sharply to -5.5 (negative anomaly W), while $^{87}\text{Sr}/^{86}\text{Sr}$ values remain at around 0.7084 (Brasier et al., 1996). Phosphatized cnidarian(?) skeletons of *Anabarites trisulcatus* and *Cambrotubulus decurvatus* appear at a similar level to the sponges in Orolchayn Gol (Khomentovsky and Gibsher, 1996). Although comparable carbon and strontium isotope values occur with the latest Ediacara fauna of northwestern Canada (Narbonne et al., 1994), it is notable that the supposedly prolonged interval with $\delta^{13}\text{C}$ values of 1‰ – 2‰ , known from Canada, Namibia, and Siberia, is not recognizable in Mongolia (Fig. 2). It is within this interval, dated at 545.1 ± 1 and 543.3 ± 1 Ma (Grotzinger et al., 1995) that the most diverse assem-

the upper Tsagaan Gol Formation (Fig. 2). The fossil horizon lies above a succession that includes Sturtian-age diamictites, post-Sturtian limestones, and Ediacarian dolostones with the stromatolite *Boxonia grumulosa*, and beneath limestones, sandstones, and shales yielding increasingly diverse Nemakit-Daldynian to Tommotian-type skeletal faunas (Lindsay et al., 1996a; Khomentovsky and Gibsher, 1996; Brasier et al., 1996). The spicules are small (<0.1 mm long and <0.02 mm thick) and abundantly preserved in translucent brown iron oxides within layers of small spongiform cherts, each a few millimetres thick. Absence from associated peloidal wackestones indicates that spicule preservation required early diagenetic mineralization of the axial canal and spongin fibers, followed by preservation within diagenetically mobilized opaline silica, presumably from the spicule walls.

The morphology of the spicules is surprisingly diverse. Monaxons predominate, but triaxons are common (including spicules with rays $>90^\circ$) and

blages of Ediacarian fossils have been found. Phosphorite facies at this level in Mongolia, however, indicate that the lower part of interval NP2 is likely to be condensed. Recent radiometric dating also shows that the prolonged interval of stable $\delta^{13}\text{C}$ in Namibia cannot have lasted more than a few million years (Grotzinger et al., 1995). This implies that the earliest sponge fauna in Mongolia may well have been coeval with the acme of the Ediacara fauna elsewhere.

The base of the Cambrian in northeastern Siberia may be taken at the first appearance of *Phycodes* sp. in the Kessyuse Formation (Bowering et al., 1993). Carbon isotopes suggest correlation of this level with one of the troughs of negative anomaly W in Mongolia (Fig. 2), which occur on either side of a major sedimentary break. It may be significant that major sedimentary breaks occur close to anomaly W across the globe (Fig. 2). Whereas these breaks may well be diachronous, they could also indicate a synchronous regression, during which the first troughs of negative anomaly W, at the end of NP2, were locally removed by erosion. The latter certainly appears to be the case across northeastern Siberia (Pelechaty et al., 1996). Because the trough of anomaly W is unlikely to be much younger than 543.9 ± 1 Ma (Bowering et al., 1993), and the sponge assemblage described above clearly lies below anomaly W, then the sponges are likely to be older than ca. 544 Ma. This draws us again toward the conclusion that the sponge fauna is likely to be coeval with the diverse Ediacara fauna of Namibia, dated at ca. 543–549 Ma (Fig. 2; Grotzinger et al., 1995).

Interval C1 in Mongolia is marked by a distinctive, oscillatory rise in $\delta^{13}\text{C}$ from -3.6 to $+4.3$, and by least-altered $^{87}\text{Sr}/^{86}\text{Sr}$ values that vary little from 0.7084 (Fig. 2; Brasier et al., 1996). In Mongolia, this suite contains the first appearance of Cambrian-type ichnofossils and *Purella* zone skeletal fossils (Goldring and Jensen, 1996; Khomentovsky and Gibsher, 1996; Brasier et al., 1996). If the break at the base of C1 is assumed to be synchronous, then it could be correlated with the break at the base of the Manykay, Kessyuse and Ust-Yudoma formations reported across Siberia by Khomentovsky and Karlova (1993).

These data indicate that the first appearance of Cambrian-type skeletal fossils was diachronous. In most parts of the world, the Cambrian fauna appears above negative anomaly W. In southwestern Mongolia, however, the first skeletal fossils appear below this anomaly, at a level similar to that of the anabaritid tube *Cambrotubulus* in northeastern Siberia (Karlova, 1987; Knoll et al., 1995b) and the latest Ediacara fauna in Namibia (Grotzinger et al., 1995). Our carbon isotopic correlation between Iran and Oman (Fig. 2) is consistent with previous correlations made on the basis of basin history and lithofacies and indicates that the Nemakit-Daldynian (i.e., Cambrian) fauna and the Ediacarian skeletal fossil *Cloudina* coexisted in separate environments. This Nemakit-Daldynian fauna (including siliceous sponges, anabaritids, siphononuchitids and protoconodonts) is typically found on platform margins subjected to phosphogenesis, whereas *Cloudina* may have preferred less-oceanic conditions. We suspect that members of the “Cambrian” and “Ediacara” faunas partially overlapped but seldom coincided, perhaps because of adaptation to water masses of differing chemistry.

DISCUSSION

Our discovery that the earliest known hexactinellid spicules occur in assemblages of relatively advanced form (Fig. 1), including flowerlike spicules hitherto unknown below the Upper Cambrian (Dong and Knoll 1996), implies that hexactinellid sponges had achieved skeletal diversity by the latest Precambrian, earlier than previously demonstrated (Steiner, 1994; Zhang and Pratt, 1994; Gehling and Rigby, 1996). Together with molecular evidence, this implies that sponges had a largely unpreserved history prior to their entry into the skeletal fossil record. It is valid, therefore, to look for environmental factors that may have enhanced the taphonomic preservation of sponge spicules and other early skeletal fossils at this point in Earth history.

In Mongolia, the first sponge cherts and phosphatized anabaritids appear above phosphorite–chert–black shale facies, which in turn overlie ex-

tensive dolomites. This succession may be taken to indicate the drowning of a peritidal carbonate platform by cooler, eutrophic, oxygen-depleted waters (cf. Muchey and Jones, 1992; Brasier, 1992, 1995a). This drowning event also punctuates a rise in the rate of sediment accumulation (Lindsay et al., 1996b) so that the entire facies shift may be explained in terms of increasing rates of crustal subsidence during the Late Proterozoic–Cambrian rift-to-drift transition (e.g., Bond et al., 1988; Brasier, 1995b). This implies that the delayed appearance of well-developed sponge spicules and biogenic cherts in the fossil record was related not only to biological evolution (cf. Maliva et al., 1989), but also to the delayed and tectonically controlled appearance of suitable biofacies and taphofacies.

Our data confirm that siliceous biomineralization preceded calcareous biomineralization in sponges (e.g., archaeocyaths, Fig. 2) by more than 10 m.y. Because the former are mainly found in eutrophic settings and the latter in more interior, oligotrophic ones (cf. Brasier, 1992), it seems likely that the biomineral secreted within a given clade was closely related to localized Si, P, or Ca enrichment of the water column. Furthermore, the biomineral revolution that ushered in the so-called Cambrian fauna may have begun in eutrophic and outer shelf facies of the late Neoproterozoic and spread shoreward with the Cambrian transgression.

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