Silicified and phosphatized *Tianzhushania*, spheroidal microfossils of possible animal origin from the Neoproterozoic of South China

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Comparative study of microfossils from two kinds of sediments: chert intercalations (studied in thin section) and phosphorite/phosphatic carbonate (in thin section and maceration), from the upper Neoproterozoic Doushantuo phosphorites in the Weng'an area, Guizhou Province, South China, shows that the phosphatized *Megasphaera ornata* and the chert-preserved *Tianzhushania tuberifera* should be regarded as representing the same taxon preserved by different mineralization processes. In phosphatized specimens the outer wall is often peeled off, exposing the ornamented middle wall. Some phosphatized specimens isolated from the rock matrix and specimens seen in thin sections of phosphorites show a partly preserved outer wall with spines, which can be compared to the thin-sectioned specimens from the chert beds. The small pits usually seen on the surface of the ornamented middle wall of phosphatized specimens correspond to the attachment spots of the spines in the outer wall. The presence of a spiny outer wall is a characteristic of *Tianzhushania* Yin and Li, 1978. *Tianzhushania ornata* (Xiao and Knoll, 2000) comb. nov. is here proposed as the valid name for the species. The proposed resting-egg nature of *T. ornata*, mainly based on the ornament type of the middle wall, cannot be excluded. The presence of a spiny outer wall, however, suggests that it is a pelagic rather than a benthic form.

Key words: Metazoa, *Tianzhushania, Megasphaera*, microfossils, phosphorites, cherts, Doushantuo Formation, Neo-proterozoic, China.

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Introduction

The upper Neoproterozoic Doushantuo Formation in south China provides a clear window on terminal Proterozoic life. In the last two decades, a wealth of fossils, including diverse microfossils preserved as the results of siliceous (L. Yin and Li 1978; Z. Zhang 1981a, b, 1984; Awramik et al. 1985; Z. Zhang 1986; Zhao et al. 1988) and phosphatic (Y. Zhang 1989; Y. Zhang and Yuan 1992; X. Yuan et al. 1993; X. Yuan and Hofmann 1998; Zhang et al. 1998; Zhou et al. 2001) permineralizations, as well as Burgess Shale-type compressions in shale (Chen and Xiao 1991, 1992; Chen et al. 1994; Xiao et al. 2002), have been reported from Doushantuo cherts, phosphorites, and shales. More recently, Xiao and Knoll (2000b) described phosphatized globular fossils with well-preserved tubercular envelope ornamentation as Megasphaera ornata Xiao and Knoll, 2000. They further interpreted M. ornata, as well as M. inornata Chen and Liu, 1986, as eggs enveloped in their egg cases, while the previously described Parapandorina Xue, Tang, Yu, and Zhou, 1995, represents equally and totally cleaving stereoblastulas. They considered Megasphaera to be preserved by phosphatic coating and impregnation. The outer envelope was coated on both sides with larger apatite crystals, and encrusting crystals nucleated on and radiated from both the inner and outer surfaces of the membranous envelope. The coating on the outer surface is less extensive than that on the inner surface, so the original envelope ornament with small tubercles or anastomosing ridges can be well preserved (Xiao and Knoll 2000b).

Palaeontological investigations of the Doushantuo phosphorites commonly focused on one of the two main methods of microfossil studies—thin sections or extractions from the rock matrix. Earlier studies were principally based on petrographic thin sections, and only a few employed acetic-acid digestion (Chen and Liu 1986; L. Yin and Xue 1993; Xue et al. 1995). Because phosphatized fossils in the Doushantuo rocks of the Weng'an area can be easily isolated from their matrix by maceration in acetic acid, more recent research emphasizes the morphological information obtained from phosphatic fossils (Xiao et al. 1998; Xiao and Knoll 1999, 2000b). If the different types of preservation and observation are not taken into account, the same taxon may be described under several different names. In this paper, we report new observations from petrographic thin sections of cherty intercalations and adjacent fossiliferous phosphorites, as well as from phosphatic fossils isolated by acetic-acid digestion from the same geographical area. Comparing the fossils obtained by the two methods, we propose that *Megasphaera ornata* Xiao and Knoll, 2000, and *M. inornata* Chen and Liu, 1986, belong in the genus *Tianzhushania* Yin and Li, 1978 (type species: *T. spinosa* Yin and Li, 1978), and that *T. ornata* is a senior synonym of *T. tuberifera* Yin, Gao, and Xing, 2001. Thus the record of metazoan embryos, or at least egg cases, has been extended from the typical phosphatic taphofacies to the siliceous (cherty) taphofacies of the Doushantuo stage.

Geological background and age constraints

In late Neoproterozoic times, the Weng'an area was situated near a persistent palaeotopographic high, the Upper Yangtze Oldland (H. Wang 1985). Regionally, the Doushantuo Formation commonly overlies the metamorphic Qingshuijiang Formation of the Banxi Group and may overlie the sporadically distributed Nantuo diamictites. In its stratotype section in the Yangtze Gorges area, the Doushantuo Formation underlies the Dengying dolomites that contain, in their uppermost beds, basal Cambrian skeletal fossils. In the Weng'an area, the Doushantuo succession is subdivided into two members by a subaerial exposure surface in the middle part, each containing a phosphate-rich bed (the lower and upper ore-beds). The lower member consists of a series of manganiferous dolomite, psammitic phosphorite, and dolomite, and represents a shallowing-upward sequence. The upper member is composed of dolorudite phosphorites with matrix phosphate, phosphatic dolomite interbedded with phosphorites, and phosphatic dolomite with phosphorites and cherty beddings, which records a second shallowing-upward sequence.

The fossils illustrated in this paper were collected from the lower part of the upper member, which lithologically consists of black dolorudite phosphorites interbedded with phosphatic dolomite, sporadically intercalated with chert. The upper-member sequence commonly begins with about 5 m of phosphatic grainstone, which consists almost exclusively of phosphatic bioclasts and other intraclasts. These phosphatic grainstones are succeeded by dolomite-bearing intraclastic phosphorites and sporadically distributed cherty intercalations. The sampling spot is the horizon from which rich well-preserved algal thalli and phosphatized spherical fossils were reported (Y. Zhang 1989; Y. Zhang and Yuan 1992; Xiao et al. 1998; X. Yuan and Hofmann 1998; Zhang et al. 1998; Xiao and Knoll 1999, 2000a, b). The spheroids are so abundant that they can be seen in all the collected hand samples, which look like oolitic dolomite.

The Doushantuo Formation is broadly constrained by a 748±12 Ma date for tuffs from the underlying Liantuo Formation (U-Pb on zircon; Lu et al. 1985) and ash beds in the basal Cambrian Zhongyicun Member dated as <539±34 Ma (Compston et al. 1992). Further constraints are still controversial at present. Based principally on correlations of stable carbon isotopes and of diverse acritarchs, the age of the Doushantuo Formation has been suggested to lie between 600 and 550 Ma, with an estimated age of about 570±20 Ma (Xiao et al. 1998; Zhang et al. 1998; Knoll and Xiao 1999; Xiao and Knoll 1999, 2000b). Zhang et al. (1998) and Yin (C. Yin 2001; C. Yin et al. 2001b) pointed out that the presence of large acanthomorphic acritarchs (Tianzhushania and Papillomembrana) in the Doushantuo suggests that they are older than the diverse Ediacaran assemblages. Their age may thus occupy an interval before the early animal diversification marked by Ediacaran biotas, which may indicate that the fossiliferous horizon of the Doushantuo phosphorites probably is nearer to 600 than to 550 Ma (C. Yin 2001; C. Yin et al. 2001b).

Although the results vary, direct isotopic datings of the Doushantuo deposit done in the last two decades are consistent with a pre-Ediacaran age. They include Rb–Sr ages of 700 \pm 5 Ma, 691 \pm 29 Ma, and 727 \pm 9 Ma for illite growth in the siltstone (Compston and Zhang 1983; Ma et al. 1984; Sun 1989) and other Rb–Sr whole-rock datings giving 660 Ma and 669 Ma (in black shale; Hu et al. 1991) as well as 673 \pm 66 Ma and 693 \pm 66 Ma (in black shale; Y. Wang et al. 1980). In addition, a phosphorite sample in the Doushantuo formation gave a Sm–Nd isochron age of 645.4 \pm 23.6 Ma (Yang et al. 1994). Recently, Barfod et al. (2002) obtained dates of 584 \pm 26 Ma (Lu–Hf) and 599.3 \pm 4.2 Ma (Pb–Pb) from the Doushantuo phosphorites.

Material and methods

All figured specimens except the one in Fig. 3B are from the upper member of the Doushantuo Formation in the Wangjiayuan section, Weng'an County, Guizhou Province. The location corresponds exactly to the Wangjiayuan East section of Xiao (see Xiao and Knoll 2000b). The sampling level

Fig. 1. *Tianzhushania ornata* (Xiao and Knoll, 2000) comb. nov. from thin sections of chert in the Doushantuo phosphorites, Weng'an area. A. MESIG \rightarrow 10005 (37.8/92.9); A₁, general view showing the tubercles with thin processes (arrows); A₂, enlarged view of A₁, showing thin processes arising from the tubercular envelope (arrows), penetrating a lightly pigmented layer; A₃, further magnified view of A₂, showing details of the polygonal ornament and processes penetrating the lightly pigmented layer to support an external membrane (arrows). **B**. MESIG 10004 (37.3/87); B₁, whole view, showing the structure of the wall (arrow shows position of B₂); B₂, enlarged view of B₁, showing processes supporting an external membrane (arrows) and a shrunken internal body with dark included materials; B₃, enlarged view of B₂, showing details of the structure of the vesicle (upper arrow points to tube-like process; middle arrow to the middle wall, and lower arrow to the inner membrane).



is the horizon where abundant and well-preserved algal thalli and phosphatized spherical fossils have been discovered, and the lithology is characterized by black dolorudite phosphorites interbedded with phosphatic dolomite, sporadically intercalated with cherty partings. Most of the collected hand samples were thin-sectioned as well as macerated in acetic acid. Thin sections are usually less than 50 μ m thick and cut vertically to the bedding plane. They were photographed under plain light using a Nikon optical microscope.

The phosphatic dolomite samples were broken into small pieces and treated in 5-10% acetic acid to resolve the carbonate matrix rocks. When adding new acid, about 20% of the reacted acid was kept as a buffer to protect the sandy residue. The residues were dried in room temperature to avoid heat damage to the fossils. They were then picked manually under a binocular microscope, and several thousands of phosphatized globular fossils were obtained.

Well-preserved specimens of *Tianzhushania* were obtained from thin sections in cherty intercalations and phosphatic dolomite as well as from digestion residues. The figured specimens and thin sections are deposited in the Museum of Earth Science, Institute of Geology, Chinese Academy of Geological Sciences, Beijing (MESIG). For Figs. 1–5, coordinates are given for each photomicrograph.

Results

General nature of Tianzhushania.— Tianzhushania has been considered one of the most distinctive acanthomorphic acritarchs in the Doushantuo or any other Neoproterozoic formation. It is characterized by large diameter $(350-750 \,\mu m)$ and processes that penetrate a multilamellate wall layer to support an external membrane (Zhang et al. 1998). Previous palaeontological research on the genus has been based mainly on petrographic thin sections made from chert nodules or bandings in the Doushantuo Formation at the Yangtze Gorges, Hubei Province, and Weng'an, Guizhou province (C. Yin et al. 2001b). The genus was first found at Tianzhushan Mountain near Changyang County and was reported as bearing vesicles that were poorly defined as a result of partial degradation (L. Yin and Li 1978). C. Yin and Liu (1988) restudied the Doushantuo chert in the same area and reported the detailed structure of the outer covering of Tianzhushania.

So far, two morphospecies of *Tianzhushania* have been reported, both from cherty intercalations in the Doushantuo

Formation (Figs. 1–3). The type species, *T. spinosa* (Yin and Li, 1978) (Fig. 3B), was first found in the Yangtze Gorges area (L. Yin and Li 1978; C. Yin and Liu 1988) and later in the Weng'an area (C. Yin et al. 2001b). At Weng'an, *T. spinosa* is usually preserved as spheroids with a distinctive multilamellar outer covering (Fig. 2A). The morphological characters are quite similar to those found in the specimens from the eastern Yangtze Gorges. The other species is *T. tuberifera* Yin, Gao, and Xing, 2001, found in the same horizon in the Doushantuo phosphorites of the Weng'an area. This species differs from the ones described as *T. spinosa* in having a distinct dense and robust middle wall with clearly demarcated tubercles or arches (Fig. 1).

Thin sections of Tianzhushania ornata reveal tube-like, cylindrical (occasionally narrowing distally), very thin and irregularly distributed processes arising from the top of tubercles and penetrating a lightly pigmented layer (in some specimens, this layer is lamellated) to support an external membrane (Figs. 1, 2B, C). In many cases, the outer coverings and processes have been obscured by degradation, leaving faintly visible structures between the envelope and the external membrane (Figs. 2B, C, 5B, C, 6A, B), or have completely disappeared, leaving a tubercular ornamented envelope (Figs. 4, 6C-I). Strongly degraded specimens of T. spinosa are commonly preserved without the outer covering, leaving a smooth envelope (see parts of Figs. 2A₁ and 5D). Within the middle wall of both species, there is an internal membrane surrounding the internal cavity (Figs. 1B, $2C_1$, 3B, 6C), and sometimes this membrane and the cavity are slightly shrunk, leaving a space between the envelope and the internal membrane (Fig 1B). As a consequence, the ornamented envelopes in some specimens seem to be easily peeled off from the membrane-enclosed body (Figs. 2C, 6D). Thus it is not clear whether the smooth phosphatized globular fossils originally had ornamented envelopes. It is worth noting that a specimen of Tianzhushania sp. in our collection has a well-preserved outer covering enclosing two internal bodies (Fig. 3A). This may indicate a cleavage embryo at the two-cell stage as seen in phosphatized fossils obtained from maceration (Fig. 7B).

Comparisons of *Tianzhushania* from thin sections of cherts *versus* phosphorites.—In thin sections of silicified specimens, detailed membrane structure and wall processes are usually exquisitely preserved. Ellipsoidal specimens have the outer, multilamellar parts of the wall preserved around the poles of the long axis, whereas the wall in the more equatorial regions appears more strongly abraded (Fig.

Fig. 2. *Tianzhushania spinosa* Yin and Li, 1978 (A) and *Tianzhushania ornata* (Xiao and Knoll, 2000) comb. nov. (B, C) in thin-sections of chert in the \rightarrow Weng'an area. A. *Tianzhushania spinosa*, MESIG 10003 (35/95.9); A₁, whole view, showing the well-preserved outer covering at the two poles of the longer axis (arrows a and b); A₂, enlarged view of section indicated by arrow a, showing thin processes penetrating a lightly pigmented multilamellar layer and supporting an external membrane (arrow); A₃, further magnified view of A₂, showing details of the multilamellar layer structure (arrow points to bundle of tube-like processes). B. *Tianzhushania ornata*, MESIG 10001 (33.1/85.9); B₁, whole view, showing the unique envelope ornamentation of tubercles with thin processes (arrow shows position of B₂); B₂, enlarged view of B₁, showing details of the structure of the wall (arrow points to external membrane). C. *Tianzhushania ornata*, MESIG 10002 (55.5/89.3); C₁, whole view, showing the outer part of the wall having separated from the naked internal body (arrow shows position of C₂). C₂, enlarged view of C₁, showing details of the envelope ornamentation (arrow points to external membrane).



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Fig. 3. **A**. *Tianzhushania* sp. with possible two-cell stage cleavage from thin sections of chert in the Weng'an area, MESIG 10003 (44/89.6); A_1 , general view, showing the wall and internal structures; note that the internal body is cleaved into two; arrow shows position of A_2 ; A_2 , enlarged view of A_1 , showing details of the structure of the envelope. **B**. Typical *Tianzhushania spinosa* Yin and Li, 1978, found in a chert nodule from eastern Yangtze Gorges, MESIG 10006 (40.1/94.2); B_1 , general view, for comparison with the specimen (Fig. 2A) found in the Weng'an area (arrow shows position of B_2); B_2 , enlarged view of B_1 , showing details of the structure of the structure of the wall (arrow points to external membrane between two bundles of processes).

2A). Spheroidal specimens commonly lack the outer parts altogether. The outer parts of the wall are usually lighter in colour when observed in thin sections. This may indicate a difference in original density which may facilitate the peelingoff or decomposition of this layer.

In phosphorite thin sections, most specimens have no outer wall preserved. Some preserve the outer wall, but the spiny structure can hardly be seen (Fig. 5B). Generally, the phosphatized specimens are less well-preserved than the silicified ones. This may indicate that phosphatization occurred at a relatively later stage, or that later geological processes like the activity of ground water have altered the preserved structure of the phosphorite/carbonate. Different degrees of degradation have also been observed (Figs. 4, 5A, B). During degradation, the spines in the outer covering may have become decomposed, leaving a slightly pigmented material between the external membrane and inner wall, which may be the degradation residue of the outer covering (Fig. 5B). Some specimens have a partially preserved outer wall with some faint radiating lines, which may be vestiges of spines (Fig. 5D).

Synonymy of *Megasphaera ornata* and *Tianzhushania tuberifera.*—*Megasphaera ornata* was named by Xiao and Knoll (2000b) based on Weng'an specimens from macerated phosphorite/ carbonate and in thin sections of phosphorite/ carbonate. Five kinds of surface ornaments were recognized. In thin sections, the surface ornaments were seen as contours of relief (Xiao and Knoll 2000b: fig. 3.12–13).

Our collection, besides confirming the ornaments described by Xiao and Knoll (2000b), shows in some specimens an outer layer with a thickness of about 25–90 μ m encrusting the ornamented surface (Fig. 6A, B). Most specimens do not have this layer preserved, however (Fig. 6C–I). The interpretation of this layer as part of the original biological structure rather than a secondary phosphatic coating is supported by the fact that the thickness is rather stable and proportional to the diameter of the cell in different speci-

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Fig. 4. *Tianzhushania* in thin-section of phosphorites from the Weng'an area. **A**. *Tianzhushania ornata* (Xiao and Knoll, 2000) comb. nov., MESIG 10008 (42.1/98.2), cross-section view of specimen lacking the surrounding multilamellar outer covering (arrow in A₁ shows position of A₂); A₂, close-up of A₁, showing contour of prominences. **B**. *Tianzhushania* sp., MESIG 10008 (59.7/96.2), cross-section view of surface tubercles. **C**. *Tianzhushania* sp., MESIG 10007 (19.1/84.3), equatorial view of the tubercular wall.

mens. It does not show the typical fibro-normal structure characteristic of most diagenetic apatite crusts (e.g., Yue and Bengtson 1999, fig. 9). It has the same thickness as the outer layer of *Tianzhushania* in both chert (Figs. 1A₃, B₂, 2B, C) and phosphorite (Fig. 5B–D) thin sections.

Tianzhushania tuberifera, based on specimens studied in thin sections from chert intercalations (C. Yin et al. 2001b), and Megasphaera ornata, based mainly on isolated specimens from phosphatic carbonate (Xiao and Knoll 2000b), are thus both derived from the Doushantuo Formation at Weng'an, composed mainly of phosphorite/phosphatic carbonate with chert intercalations. The two taxa have the same overall outline, i.e., round or somewhat elliptical, and the same size, i.e., from 400 to 1100 µm, most around 500-600 µm (Xiao and Knoll 2000b; C. Yin et al. 2001b; and the present paper). Megasphaera ornata has different types of envelope ornamentation (Xiao and Knoll 2000b: fig. 4.3–12), which seem to correspond to the types of projections on the inner wall of T. tuberifera found in chert thin sections (Figs. 1, 2B, C). If the whole outer wall is peeled off, T. tuberifera looks identical to M. ornata (compare Fig. 5C1 herein with Xiao and Knoll 2000b: fig. 3.12) in phosphorite thin sections. The polygonal ornament shown on the surface of the phosphatized *M. ornata* can also be seen in thin sections of the silicified *T. tuberifera* (Fig. 1A). On isolated *M. ornata*, small pits are seen scattered on the whole surface (Xiao and Knoll 2000b, fig. 4.10; Fig. $6A_2$, F_2 , H_2 herein). These may correspond to the attachment points of the thin spines in the outer layer. The possibility that the outer covering on phosphatic specimens (Fig. 6A, B) is formed by secondary phosphatic coating seems not conceivable for the reasons discussed above.

Thus we propose that *Tianzhushania tuberifera* and *Megasphaera ornata* represent the same species preserved by different mineralization processes. The finding of the outer wall, a diagnostic feature of *Tianzhushania*, on *M. ornata* suggests that it belongs to the former genus. The name *M. ornata* has priority over *T. tuberifera*, and therefore *Tianzhushania ornata* (Xiao and Knoll, 2000) comb. nov. is proposed as the valid name for the taxon.

The nature of *Tianzhushania spinosa* is currently uncertain. A specimen from a phosphorite thin section (Fig. 5D) shows great similarity to one of *T. ornata* from the same lithology (Fig. 5C₁). Both have partially preserved outer wall, the only difference between them being in the projections from the middle wall. The *T. spinosa* specimen (Fig. 5D) has



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Fig. 6. Phosphatized *Tianzhushania ornata* (Xiao and Knoll, 2000) comb. nov. in Doushantuo phosphorites at Weng'an. **A**. MESIG 21042; A_2 , detail of A_1 , showing a part of outer covering surrounding the envelope with tubercles. **B**. MESIG 21045, specimen preserving part of outer covering. **C**. MESIG 21064; note the internal membrane. **D**. MESIG 20303, showing shrunken internal body with membrane and secondary overgrowth on internal body. **E**. MESIG 20190, polygons with fractal branching; note numerous dimples at top. **F**. MESIG 21076; F_2 , detail of F_1 , showing details of irregularly distributed dimples. **G**. MESIG 21078, polygonal envelope ornamentation; note that dimples also occur on arches. **H**. MESIG 21009; H_2 , detail of H_1 , showing deflated envelope and details of envelope ornamentation. **I**. MESIG 21026, deflated envelope with envelope ornamentation.

in its outer wall faint outward-radiating spines, while this structure is not visible in the *T. ornata* specimen (Fig. $5C_1$). Considering the state of preservation of other *T. ornata* specimens (Fig. 4A, B) and the fragility of the spines/outer wall, the lack of the spines in the partially preserved outer wall may indicate that the spines were obscured during phosphatization rather than being primarily absent.

Biology, taphonomy, and preservation

Xiao et al. (1998) first interpreted *Megasphaera* as an animal resting egg. Later, Xiao, and Knoll (2000b: fig. 12) compared the ornament with that of branchiopods in supporting

 [←] Fig. 5. *Tianzhushania ornata* (Xiao and Knoll, 2000) comb. nov. (A–C) and *Tianzhushania spinosa* Yin and Li, 1978 (D) in thin-sections of phosphorites/carbonate in the Weng'an area. A. MESIG 10004 (32.1/90), poorly preserved *Tianzhushania ornata* with incomplete processes and outer covering (arrow in A₁ shows position of A₂); A₂, enlarged view of A₁; note inner wall with broad tubercles, incomplete processes and unclear external membrane (arrows). B. MESIG 10009 (38.2/88.1), phosphatized *Tianzhushania ornata*, strongly degraded, showing the degraded outer layer without processes on top of tubercles (arrow in B₁ shows position of B₂); B₂, enlarged view of B₁, showing details of tubercular structure and outer covering (arrows). C. MESIG 10007 (53.1/102.2), specimen of *Tianzhushania ornata* with well-preserved ornamented middle wall and a part of the outer covering; C₂, enlarged view of the area marked with an arrow in C₁, showing details of the tubercular structure with an outer covering (arrow). D. MESIG 10010 (28/95.2), *Tianzhushania spinosa*; note partial preservation of outer covering and indistinct radiating lines (arrow).

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Fig. 7. Phosphatized globular fossils from Doushantuo phosphorites in the Weng'an area. A. MESIG 21070, *Tianzhushania ornata* (Xiao and Knoll, 2000) comb. nov. with enclosed smooth internal body. **B–J**. *Parapandorina raphospissa* Xue et al. 1995. **B**. MESIG 20296, two-cell stage. **C**. MESIG 21027, four-cell stage. **D**. MESIG 20304. **E**. MESIG 21031. **F**. MESIG 21033, eight-cell stage. **G**. MESIG 21037. **H**. MESIG 20252. **I**. MESIG 20258. **J**. MESIG 21129, possible later stages. **K**, **L**. Globular fossils with smooth envelope. **K**. MESIG 20211. **L**. MESIG 21122.

this interpretation. At the same time, they emended the diagnosis of *Megasphaera* as large microfossils with only one internal body enclosed by a thin envelope, which can be smooth (*M. inornata*) or ornamented (*M. ornata*), with diameters varying between 400 and 1100 μ m. It is notable that the envelopes of the latter bear tubercles or polygons with fractal branching, and that most projections have distinct dimples on the top. The discovery of the outer wall does not exclude Xiao and Knoll's interpretation. The spiny outer wall, however, similar to that of planktic copepod eggs (Van Waveren et al. 1993), seems to indicate that *Tianzhushania* is a pelagic rather than a benthic form.

Doushantuo microfossils are preserved principally as permineralizations in early diagenetic cherty intercalations and phosphorites in the Weng'an area. The state of preservation is good in both lithologies and can be exceptional in some cherty intercalations, which contain a unique record of exquisite envelope ornamentation of globular fossils. Based on our new observations, most silicified fossils occur in pockets of chert within bedded collophane precipitated in interbedded, or locally derived, collophane grain- and gravelstones. The grainstones are poorly sorted, and clasts consist predominantly of collophane with local patches of chert, where organic constituents commonly are light brown and well preserved. It is obvious that the pervasive oxidation of fossils in phosphorites post-dates silicification. The silicification in the Weng'an area occurred early in diagenesis prior to significant burial compaction. Consistent with this observation, globular fossils and acritarchs in Doushantuo chert are generally preserved uncompressed.

Comparing the silicified *Tianzhushania* from the Yangtze Gorges with those discovered in the Weng'an area, the obvious difference is that the former is mostly preserved compressed (L. Yin and Li 1978; C. Yin and Liu 1988; Zhang et al. 1998; C. Yin 1999), only a few uncompressed forms having been found among thousands of specimens collected by us (Fig. 3B). In contrast, most specimens of the genus in the Weng'an area are fully preserved in three dimensions. Phosphatization seems penecontemporaneous with deposition (Zhang et al. 1998; C. Yin et al. 2001b), but was evidently later than silicification. Globular microfossils were probably phosphatized soon after a partial decay of the organic structures, but prior to burial compaction. Local storms can rework the silicified or phosphatized pavements, to be transported along with other intraclasts for a short distance and then redeposited to be cemented in place by carbonate, phosphate or silica (Zhang et al. 1998). Against this background, a range of preservational variations can be discriminated, and relatively straightforward morphological interpretations can be carried out.

Conclusions

Morphological and taphonomic studies of permineralized fossils in cherts and phosphorites of the Doushantuo phosphorites in the Weng'an area (Guizhou Province, South China) indicate that specimens assigned to Megasphaera ornata Xiao and Knoll, 2000, are preservational variants of Tianzhushania tuberifera Yin, Gao, and Xing, 2001, which have lost the original outer coverings, leaving dimples on the top of tubercles in the underlying wall. Consequently, the two species are considered synonymous and are referred to as Tianzhushania ornata (Xiao and Knoll, 2000) comb. nov. Tianzhushania spinosa (Yin and Li, 1978) may be a senior synonym of T. ornata, but this is as yet undecided. In cherts, silicified specimens of Tianzhushania usually show exceptionally preserved processes and distinctive wall structure, but phosphatized specimens in phosphorites or phosphatic dolomite commonly lose the outermost covering structure.

The preservational variation between silicification and phosphatization in Doushantuo phosphorites at Weng'an suggests that silicification took place a little earlier than phosphatization, but both happened in early diagenesis, prior to compaction. Because substantial evidence on detailed morphology supports the interpretation of *Tianzhushania* as animal resting eggs and embryos (Xiao and Knoll 2000b), the new discovery extends the record of metazoan embryos from the typical phosphatic taphofacies to the siliceous (cherty) taphofacies of the Doushantuo stage.

The discovery of *Tianzhushania* both in the Weng'an area and in the Yangtze Gorges provides not only new data for studying spheroidal microfossils in phosphorite but also a way to correlate the silicified assemblages with phosphatized ones. The fossiliferous horizons at Weng'an and in the Yangtze Gorges are coeval (Zhang et al. 1998; C. Yin et al. 2001b).

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