EARLY CAMBRIAN METAZOAN EGGS, EMBRYOS, AND PHOSPHATIC MICROFOSSILS FROM NORTHWESTERN CANADA

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ABSTRACT—Three-dimensionally phosphatized, spherical fossils, interpreted as metazoan eggs and embryos on the basis of taphonomic features and cleavage patterns, are reported for the first time from the Cambrian of North America. These microfossils occur with a phosphatized biota of skeletonized fossils, including specimens indicative of the earliest Cambrian Anabarites–Protohertzina Zone in the Wernecke Mountains of eastern Yukon Territory, northwestern Canada. They range in size from 0.25 mm to more than 1.0 mm in diameter and can be referred to two genera, Olivooides Qian, 1977 and Archaeooides Qian, 1977. The North American discovery extends the biogeographic range of earliest Cambrian eggs and embryos from coeval successions in China and Siberia, suggesting a wide geographic distribution of these taxa, and emphasizes the crucial role of local environmental and taphonomic conditions in preserving this phosphatic window into the record of early animal evolution. In addition to previously reported taxa, the phosphatized biota also include indeterminate spheroids, fused clusters of Protohertzina siciformis Missarzhevsky, 1973, the enigmatic rodlike fossil Zhejiangorhabdion comptum Yue and Zhao, 1993, phosphatized fossils, including Paradoxiconus typicalis Qian et al., 2001, protoconulid Carinichites sp., and phosphatic tubes assigned to Hyolithellus cf. H. isiticus Missarzhevsky, 1969, cf. Pseudorthotheca sp., and ?Rugatotheca sp.

INTRODUCTION

D I S C O V E R Y OF PHOSPHATIZED ANIMAL EGGS AND EMBRYOS IN CAMBRIAN SEQUENCES

Identification of phosphatized animal embryos in various developmental stages in Cambrian (Zhang and Pratt, 1994; Bengtson and Yue, 1997; Kouchinsky et al., 1999; Yue and Bengtson, 1999; Dong et al., 2004) and Neoproterozoic rocks (Xiao et al., 1998, 2000; Xiao and Knoll, 1999, 2000; Yin et al., 2004) has dramatically advanced knowledge of a previously missing part of the metazoan record. Further exploration of the phosphatization taphonomic window (Brasier, 1990; Dzik, 1994) in the Neoproterozoic–Cambrian transition will provide critical palaeontological data to test various hypotheses about the tempo and mode of early animal evolution (Wray et al., 1996; Ayala et al., 1998; Knoll and Carroll, 1999; Valentine, 2002). New discoveries of these fossils and co-occurring phosphatic microfossils will offer more insights into the morphology, taphonomy, and biogeography of the earliest animals.

All previous reports of phosphatized eggs and embryos of early animals have been from Asia. We report for the first time an earliest Cambrian, Laurentian occurrence of three-dimensionally phosphatized globular microfossils interpreted as animal eggs and embryos from northwestern Canada. In addition, a number of phosphatized shelly microfossils with three-dimensional detail are described. This diverse assemblage adds another view into the evolutionarily dynamic interval of the Proterozoic–Phanerzoic transition.

GEOLOGY AND AGE OF FOSSIL LOCALITY

Carbonate rocks sampled for phosphatic microfossils are from a remote ridge in the Wernecke Mountains, Yukon Territory, northwestern Canada (Fig. 1.1). The upper boundary of the Neoproterozoic Windermere Supergroup in the study area lies at the top of the karsted and massively dolomitized shallow-water carbonate of the Risky Formation (Pyle et al., 2004). Lowermost Cambrian sediments are carbonates of the Inga Formation (Fig. 1.2), specifically thin-bedded, parted to nodular limestones with attributes indicating a mid- to outer-ramp paleoenvironmental setting. This limestone grades up into and is topped by a prominent phosphatic hardground complex, that is in turn overlain by thick, black shale that coarsens upward into hummocky cross-stratified sandstones of the Vampire Formation (Osborne et al., 1986). The phosphatic interval is a rudstone of tabular lime mudstone clasts with all the attributes of storm deposition (cf. Mount and Kidder, 1993), surrounded by a matrix rich in small shelly fossils. These tempestites are capped by a 10–20 cm thick phosphate hardground that forms a rind on top of the clast rosettes and coats pebbles as much as 40 cm below. This phosphatic horizon is interpreted as a maximum flooding surface (cf. Loutit et al., 1988). Material for this study comes from samples collected within the uppermost 70 cm of the Inga Formation (9 m thick total).

Nowlan et al. (1985) described small shelly fossils, including Anabarites trisulcatus Missarzhevsky, 1969 and Protohertzina anabarica Missarzhevsky, 1973, from the phosphitized limestone unit that was referred to as a basal unit of the Vampire Formation before the Inga Formation was named formally. Pyle et al. (2004) reassigned this carbonate unit to the Inga Formation, which lies below the siliciclastic-dominated Vampire Formation in correlative strata of the Mackenzie Mountains. Samples collected from the phosphatic limestone horizon yielded abundant small shelly fossils, including additional specimens of Anabarites Missarzhevsky, 1969 and Protohertzina Missarzhevsky, 1973. This level can be correlated with the oldest shelly fossil zone that marks the base of the basal Cambian Nemakit–Dalniyan Stage in Siberia (Khomentsov and Karlova, 1993) and the Meishucunian Stage in South China (Qian and Bengtson, 1989). Complex trace fossils, including Treptichnus pedum Bahde et al., 1997, Rusophycus aivalonensis Crimes and Anderson, 1985, and Crucifera Sp. d’Orbigny, 1842, indicative of a subtrilobite Cambrian age, occur at the base of the overlying Vampire Formation (Fritz et al., 1983; Nowlan et al., 1985; Narbonne and Atkin, 1995) (Fig. 1.2).

MATERIALS AND METHODS

The fossil locality is Section 8E of Nowlan et al. (1985), reexamined as Section D1 by Pyle et al. (2004). Specimens were extracted from archived reconnaissance samples collected for small shelly fossils in 1982 and 1984 and from more detailed collections made during 2002. Samples of the phosphatized limestone were re-examined from a 70 cm interval in a unit assigned to the Inga Formation (Fig. 1.2). After dissolution of samples in 10% acetic acid, phosphatized specimens were manually isolated from the insoluble residue and sorted under a binocular microscope. Samples yielded a total of more than 5,000 globular specimens and thousands of small shelly fossils from all standard sieve fractions.
ranging from less than 150 μm to more than 850 μm. Images were captured using a JEOL 6301F Field Emission Scanning Electron Microscope. Illustrated specimens are housed in the National Type Repository in the Geological Survey of Canada (GSC), Ottawa, Ontario.

SYSTEMATIC PALEONTOLOGY

Identification of spherical microfossils as spawned eggs and early developmental stages of animal embryos is based on the nature of surficial and internal features preserved by three-dimensional phosphatization, particularly taphonomic evidence that the spheres were hollow with a pliable, organic membrane (see discussions within each taxa). Systematics of spherical fossils have been both clarified and complicated by the discovery of internal details of some fossils such as the stellate embryos of *Olivooides* Qian, 1977 (Bengtson and Yue, 1997) and germ band formation in *Pseudooides* Qian, 1977 (Steiner et al., 2004a). Preservational differences among reported occurrences of globular fossils have obscured structural and functional interpretations of spheres that lack distinct embryonic features and have also hampered systematics of these genera. In this present study, where few internal details were evident, form taxonomy is used. Smooth specimens are comparable to *Olivooides* and those with pustulose ornamentation are assigned to the genus *Archaeooides* Qian, 1977. Li and Qian (1999) reviewed the research history of spheroidal fossils. The following describes the phosphatized biota grouped into spherical microfossils, anabaritids and protoconodonts, rodlike fossils, pyramidal, conical, and bulbous fossils, carinachitids, and tubes and plates.

Spherical Microfossils

**Genus OLIVOOIDES Qian, 1977**

*Type species.*—*Olivooides multisulcatus* Qian, 1977.

*Original diagnosis.*—Spheroidal, egglike, wide-elliptical or spindelike shell, 0.33–1.7 mm in diameter, with a hollow interior. Shell thickness uneven, organic. Shell surface smooth, with depressions and furrows (translated from Qian, 1977).

*Occurrence.*—Lower Cambrian, China (Qian, 1977; review of stratigraphic distribution by Xing et al., 1984), India (Bhatt et al., 1985; Brasier and Singh, 1987; Kumar et al., 1987), and Siberia (Yue and Bengtson, 1999).

**OLIVOOIDES sp.**

*Figures 2, 3*

*Description.*—Phosphatized, spherical to elliptical globules ranging from less than 0.4 mm to greater than 1.0 mm in diameter. Specimens have smooth, spherical envelope (Fig. 2.1) or indented, buckled, collapsed, or deflated envelopes (Fig. 2.2–2.5, 2.9, 2.10). Distinct size groupings represented by spheres approximately 0.6–0.7 mm wide (Fig. 2.1–2.4, 2.6, 2.9, 2.10), and 0.4 mm wide (Fig. 2.7, 2.8). Largest specimens are greater than 1 mm long and are elliptical (Fig. 2.5). Envelope typically 5 μm thick (Fig. 2.9) but can be thicker due to infilling by phosphate (Fig. 2.11) and phosphatic encrustation (Fig. 2.12, 2.15, 2.16). Two completely exposed specimens each have two hemispherical internal bodies (Fig. 2.9, arrows). Regular patterning of indentations occurs on smooth envelopes (Fig. 2.2, 2.3, 2.10). Hollow specimens (Fig. 2.12, 2.15, 2.16) show variable degrees of wall thickening, are partially infilled with phosphate, and some contain filaments coated by spherulitic botryoidal apatite (Fig. 2.13). Filaments in cross section have a core 10 μm in diameter, thickened to 22 μm in diameter by spherulitic coating (Fig. 2.14). Large sphere (Fig. 2.15) is 0.9 mm in diameter, of which interior space has diameter of 580 μm and walls thickened.

**FIGURE 1**—Map of northwestern Canada showing generalized stratigraphy, location of phosphatized embryos in the Inga Formation, and detail of the Inga Formation.
to 180 μm by isopachous apatite. One shrunken internal body is 185 μm across and hollow, coated and suspended by phophatic filaments (Fig. 2.15). Second large, hollow sphere is 895 μm in diameter (Fig. 2.16), with walls thickened to about 30 μm in 5 layers (Fig. 2.17, 2.18), the innermost layer formed by botryoidal phosphate. Inner body in this specimen may simply be a body of botryoidal phosphate that irregularly coats the interior of the sphere. Several specimens bear centrally located sulcus on one side (Fig. 3.1, 3.2). In cross-sectional view (Fig. 3.3), specimens are hollow and infilled by radial fibrous apatite crystals (Fig. 3.3, arrow, 3.4).

Occurrence.—Lower Cambrian, Wernecke Mountains, Yukon Territory, Canada.

Discussion.—Several ontogenetic stages of stellate and striate embryos described by Bengtson and Yue (1997) suggest cnidarian affinities for *Olivooides multisulcatus*. The present material does not have the stellate and striate structures of *O. multisulcatus*, but it does resemble smooth spheres described by Qian (1977) as *Olivooides*. Identification at species level requires postembryonic features that were not preserved in the present material. Developmental stages beyond the two-celled stage were not present, thus the Wernecke material is referred to as *Olivooides* sp. Among the thousands of globular specimens recovered, spheres have several size groupings which suggest that more than one taxon may be represented. External features indicate an original flexibility to the membrane which supports the biological nature of these spheres and indicates that postmortem infoldings formed prior to phosphatic replacement and encrustation. Buckling of the envelope is a feature exhibited in other *Olivooides* material (e.g., Yue and Bengtson, 1999, figs. 4, 5), in smooth vesicles of the Duoshanto material (e.g., Xiao and Knoll, 1999, fig. 6e), and in collapsed egg envelopes of Recent copepod eggs (van Waveren, 1993). Regularity of the buckling patterning of the envelope may mirror underlying internal bodies and is similar to a polygonal pattern observed by Kouchinsky et al. (1999) that was interpreted as a hollow blastula stage embryo. Specimens interpreted as two-celled embryos bear a cleavage furrow that approximately divides the sphere into two hemispherical bodies that are interpreted as blastomeres separated by a unipolar furrow (Fig. 2.6, 2.8). Deep sulci on specimens (Fig. 3) could simply be due to compression while the outer membrane was still pliable.

The spherical microfossils, like the co-occurring small shelly components of the biota, were preserved by phosphatization. Calcium phosphate within the spheres and within their envelopes was indicated by qualitative elemental analysis using energy-dispersive X-ray spectrometry. The pliable nature of the envelope indicates secondary, diagenetic phosphatization whereby phosphate replaced soft tissue and/or encrusted the envelope, thus thickening it. The hollow specimens filled with filaments are similar to those illustrated in other phosphatized embryos (e.g., Kouchinsky et al., 1999, fig. 3d; Yue and Bengtson, 1999, fig. 9) and Early Cambrian small shelly fossils (e.g., Conway Morris and Chen, 1992, fig. 7.10). Filaments differ from unbranched tunnels identified as microbial endolithic borings (e.g., fig. 10 in Bengtson et al., 1990). Filaments may instead be a diagenetic feature representing decomposed soft tissue where a filamentous organic structure such as bacteria or fungal hyphae were encrusted by phosphate (Yue and Bengtson, 1999; Xiao and Knoll, 2000). In the Duoshanto material examined by one of us (SX), where microspherules and filaments are present in abundance, cellular preservation tends to be compromised. This may account for the paucity of preserved blastomere patterns.

**Genus Archaeooides** Qian, 1977

**Type species.**—*Archaeooides granulatus* Qian, 1977.

**Original diagnosis.**—Spheroidal, oblate or elliptical spheroidal shell, 0.5–2.5 mm in diameter. Shell wall thin, composed of chitin or phosphate. Shell has hollow interior space. Shell surface ornamented by regularly distributed nodes, closely spaced, some of which contain a tiny hole. Surface of some specimens bears depressions and foldings (translated from Qian, 1977).

**Occurrence.**—Lower Cambrian, Australia (Conway Morris in Bengtson et al., 1990 and discussion of synonymy therein), China (Qian, 1977; Qian and Bengtson, 1989 and references therein), Mongolia (Voronzin et al., 1982), Siberia (Sokolov and Zhuralev, 1983; Volkov, 1987), Kazakhstan (=?*Goparella porosa* Missarzhevsky in Missarzhevsky and Mametov, 1981), and India (?=Maikhanella sp. Bhatt et al., 1985, although this species is a cap-shaped fossil rather than a sphere and the Tal specimen may be a fragment of *Archaeooides*).

**Archaeooides** sp.

**Figure 4**

**Description.**—Phosphatized, subspherical to spherical globules ranging from less than 0.4 mm to greater than 1.5 mm in diameter. Spheres with pustulose surficial ornamentation on outer envelope bear well-developed, regular pattern of protuberances over entire sphere (Fig. 4.1–4.12, 4.16–4.18) or subtle, more irregular pattern (Fig. 4.13–4.15). Similar size range and groupings to smooth spheres, but typically larger specimens (greater than 600 μm in diameter) have most pronounced ornamentation. Specimens are spherical (Fig. 4.1) to subspherical (Fig. 4.9, 4.10) and many have buckled and deflated envelopes (Fig. 4.2, 4.3, 4.5, 4.6, 4.11, 4.18). Broken specimen (Fig. 4.6) reveals a thin, ornate wall (less than 10 μm, Fig. 4.8) enclosing the partially hollow sphere.

Micro ornament varies from distinct, regularly distributed, raised protuberances that bear a central pore (Fig. 4.1–4.7) to more subtle, nodular ornament (Fig. 4.9–4.18). Protuberances are as high as 15 μm and about 40 μm across (Fig. 4.4, 4.7). Protuberances are preserved as irregular or distinct pustules that range from 15 to 80 μm in diameter. Preservation of ornament varies where pores of pustules are degraded (Fig. 4.1) or may be coated with phosphate where pores are not evident (Fig. 4.9–4.18). Degradation of outer layer containing pores occurs whereby pustules are preserved only within deflated surfaces (Fig. 4.5).

External features include regular patterns of deflation with one (Fig. 4.3) to two concavities (Fig. 4.5, 4.11, 4.18). One specimen bears an X-shaped furrow on one pole that divides the sphere into at least four bodies (Fig. 4.17). Some smaller specimens (Fig. 4.13–4.15) exhibit coarser, more subdued, irregular surfaces.

**Occurrence.**—Lower Cambrian, Wernecke Mountains, Yukon Territory, Canada.

**Discussion.**—Qian and Bengtson (1989) synonymized several species within *Archaeooides granulatus* and a wide species concept has been applied to this genus. Specimens resembling *Archaeooides* in bearing a regular pustulose surface were assigned to *Aetholicopalla adnata* Conway Morris in Bengtson et al., 1990 (full synonymy by Demidenko in Gravestock et al., 2001). These genera seem to be distinct with the latter bearing a double-walled sphere with a central cavity filled with tubules, reticulation of the inner wall, and flattened surfaces of the sphere related to an encrusting habit (full synonymy by Demidenko in Gravestock et al., 2001). Some forms of *Aetholicopalla* Conway Morris in Bengtson et al., 1990 superficially resemble *Archaeooides*, but are distinguished by flattened surfaces and tubular pillars that connect the walls of the sphere. *Aetholicopalla* resembles *Archaeooides* when the external wall is not preserved (Wrona, 2004). *Aetholicopalla* is known from Australia (Conway Morris in Bengtson et al., 1990) and Germany (Elicki, 1998), and likely includes specimens previously assigned to *Archaeooides* such as those illustrated by Kerber (1988).

There is a wide variety of surficial features among specimens.
These globular specimens have one side that is broadly convex, spines preserved in the pores (Fig. 5.3). Some mushroom-shaped ''stem'' of the mushroom. One globular fossil (Fig. 5.5, 5.6) has the need to have additional internal features such as described for Aetholicopalla to begin differentiating morphotypes. Some forms referred to Archaeooides may appear to preserve excystment (e.g., Chen, 1984), although these specimens may better be classified as Olivooides as they do not have tubercular ornaments. Forms such as Bacatisphaera Zhou, Brasier, and Xue, 2001 from the Duoshantuo Formation are spheroids with a pustulose surface sculpture that varies from loose to regular arrangement. These were interpreted as acritarchs.

**Indeterminate Spheroids**

**Figure 5**

**Discussion.**—A number of spherical fossils have morphological features that are different from those of Olivooides and Archaeooides. Two specimens are 425 μm in diameter with a finely porous envelope (Fig. 5.1–5.3) and are similar to porous spheroids from the Lower Cambrian of China were called Blastospongia polytreta Conway Morris and Chen, 1990. Pores are 10–15 μm wide (Fig. 5.1) and as small as 3 μm wide, possibly with fine fines preserved in the pores (Fig. 5.3). Some mushroom-shaped specimens were recovered that have smooth surfaces (Fig. 5.4). These globular specimens have one side that is broadly convex, a maximum diameter of 620 μm forming the ''cap'' of the mushroom, and one narrower (380 μm), flattened side forming the ''stem'' of the mushroom. One globular fossil (Fig. 5.5, 5.6) has triradial symmetry in which three equal-sized lobes are each 214 μm across and separated by broad sulci. The spheroid is as high as its maximum width. It is possible that this is an internal mold of Anabarites, but the preservation is unlike corroded molds that are dull in luster. A variety of elliptical spheroids were recovered, ranging in size from 540 μm long (Fig. 5.7) to 1,195 mm long (Fig. 5.8). Some forms are smooth and rounded at both ends (Fig. 5.7), while one has an open-ended stalklike structure, 100 μm long, at one end (Fig. 5.8). Similar ovate forms have been illustrated as Nephrooides speciosus Qian, 1977 (pl. 2, fig. 27) and Archaeooides by Ding and Qian (1988, pl. 4, fig. 14) and invite comparison with invertebrate eggs.

**Anabaritids and Protoconodonts**

**Genus ANABARITES Missarzhevsky, 1969**

**Type species.**—Anabarites trisulcatus Missarzhevsky, 1969.


**ANABARITES TRISULCATUS Missarzhevsky, 1969**

**Figure 6.1–6.4**

**Synonyms.**—See Qian and Bengtson (1989).

**Material examined.**—GSC 124010–124012, 123013.

**Discussion.**—Anabarites trisulcatus is the most abundant component of the fauna as noted by Nowlan et al. (1985). Many forms are similar to the type material, but wide preservational variation exists. Fragments are less than 1 mm long to almost 4 mm long, and range from less than 100 μm to more than 800 μm in width. Ends are either open or intilled with phosphate and no structure is preserved at either end. Shapes vary between straight, tapered, sinuous, and curved. Cross sections vary among specimens from circular to triradiate (Fig. 6.1–6.3). Specimens with thin outer layers bear regularly spaced annulations perpendicular to the long axis (Fig. 6.4), but more commonly, the internal molds are preserved. Details of anabaritid wall structure described by Kouchinsky and Bengtson (2002) suggested an original aragonitic composition of the tube and possibly serpulid affinities.

**Genus PROTOHERTZINA Missarzhevsky, 1973**

**Type species.**—Protohertzina anabarica Missarzhevsky, 1973.

**Occurrence.**—China (Qian and Bengtson, 1989 and references therein), Siberian Platform and Kazakhstan (Missarzhevsky, 1973), India (Brasier and Singh, 1987), Australia (Bengtson et al., 1990), and North America (Conway Morris and Fritz, 1980; Nowlan et al., 1985; McIlroy and Szaniawski, 2000).

**Discussion.**—Protohertzina represents a genus that is in need of revision. Several species have been erected and distinguished using their cross sections (Missarzhevsky, 1977, fig. 1) and dimensions of the cone (curvature, length, width). Qian and Bengtson (1989) included several species of both slender and robust forms in the synonymy list of P. anabarica. Different species may represent different morphotypes of the same apparatus (Nowlan et al., 1985) in which variation of elements is suggested to form

**Figure 2**—Scanning electron microscope (SEM) photomicrographs of fossil eggs and embryos referred to Olivooides sp. 1–4. Spheres with smooth outer membranes showing similar size of specimens and nature of indented and buckled surfaces. Sample 1680-1, GSC 123973, 123974, 123975, 123976; 5, large specimen showing collapse features and folding of membrane, Sample 1680-2, GSC No. 123977; 6, two-cell stage lacking smooth outer membrane, Sample 99127, GSC 123978; 7, 8, smaller spheres showing smooth membrane with polar indentation (on right side, 7) and two-cell stage lacking smooth outer membrane, 1680-2 and 1680-1/3, GSC 123979, 123980; 9, broken specimen showing thin egg envelope and possible blastomere boundary at arrows, Sample 1680-2, GSC 123981; 10, 11, broken specimen showing thin envelope at arrow in 10 (enlarged in 11), Sample 1680-2, GSC 123982; 12–14, hollow specimen filled with filaments that internally thicken the outer envelope, 13 shows spherulitic texture, 14 shows cross section and internal detail of diagnostically phosphatized filament. Sample 1680-1, GSC 123983; 15, hollow specimen showing thickening of outer envelope, internal filaments, and partially degraded inner body, Sample 99127, GSC 123984; 16–18, hollow specimen showing thickening of envelope (at arrows, detail in 17 and 18) by several layers of phosphate and internal coating of botryoidal phosphate. Sample 1680-2, GSC 123985.
a *P. anabarica*-unguliformis plexus (Brasier and Singh, 1987). Although the task of revising *Protohertzina* is not addressed here, the present collection contains several morphotypes. As with the spherical fossils and *Anabarites*, preservation by phosphatization plays a role in systematics. *Protohertzina* specimens are long, delicate structures that are easily broken and many illustrated specimens in the literature do not show the nature of the base.

**Protohertzina anabarica** Missarzhevsky, 1973

*Figure 6.5–6.8*

**Synonyms**—See Qian and Bengtson (1989).

**Material examined.—**GSC 124014–124017.

**Discussion.**—Among the present collection, there are both compressed (anabariform) elements (Fig. 6.5) and more rounded (unguliform) elements (Fig. 6.6, 6.7). Phosphatic coatings of some specimens give them a smooth exterior, yet broken specimens reveal a fibrous cone internally (Fig. 6.7). Large forms (Fig. 6.8) with rounded bases comparable to *P. robusta* Qian, 1977 (synonymized with *P. anabarica* by Qian and Bengtson, 1989) are rare among the present collection and may represent a different species.

**Protohertzina siciformis** Missarzhevsky, 1973

*Figure 6.9–6.14*

*Protohertzina siciformis* Missarzhevsky, 1973, p. 56, text-fig. 6. pl. 9, fig. 5; 1977, fig. 1.8; Azmi and Pancholi, 1983, pl. 1, fig. 8; Azmi, 1983, pl. 5, figs. 5–7, 9; Bhattacharyya, Mamgain, and Misra, 1985, pl. 1, fig. 14; Ding and Qian, 1988, pl. 1, fig. 6.

*Protohertzina* cf. *siciformis* Missarzhevsky, Qian and Bengtson, 1989, p. 71–72, fig. 43; Bengtson, Conway Morris, Cooper, Jell, and Runnegar, 1990, p. 330–331, fig. 209.


**Description.**—Elements small (0.7–0.9 mm long), gently tapered, with long slender cusp, compressed posterior or postero-lateral margin that forms keel at posterobasal corner and extends as long carina to cusp tip. Lateral ridges weak. Basal cavity deep. Base small with rounded to teardrop-shaped outline depending on development of carina. Laterally compressed element has rounded anterior margin, strong posterobasal keel and sharp posterior margin or carina, and weak lateral ridges (Fig. 6.9). More rounded elements have round basal outline and variable development of posterior carina (Fig. 6.10–6.14). Two fused clusters each containing two elements show variation in symmetry based on position of carina (Fig. 6.11, 6.12).

**Material examined.—**GSC 124018–124023.

**Discussion.**—Specimens are assigned to *Protohertzina siciformis* based on the most compressed element (Fig. 6.9) that resembles the type material in having a strongly compressed posterior edge and teardrop-shaped basal outline. Elements figured by Qian and Bengtson (1989) and Bengtson et al. (1990) resemble each other, but are questionably included in the present synonymy due to the shape of their bases, which are expanded and form an angle with the cusp. Brasier and Singh (1987) placed *P. siciformis* in synonymy with *P. anabarica* and described elements as “siciform,” but based on the present collection, two species are differentiated. The discovery of fused clusters herein assigned to *P. siciformis* suggests a complex protoconodont apparatus (Fig. 6.9–6.14). Other reports of natural assemblages of protoconodonts include an “unassigned conodont cluster” from Iran (Hamdi, 1989), a pyritized cluster from Newfoundland described as *Protohertzina? canadia* McIlroy and Szaniawski, 2000, and clusters of *P. robusta* Qian, 1977 (Azmi and Paul, 2004). The apparatus described below invites comparison to the apparatus of the Late Cambrian protoconodont *Phakelodus* Miller, 1984 which has been

**Figure 4.—**SEM photomicrographs of spheres referred to *Archaeooides* sp. 1, Spherical form, Sample 99139, GSC 123989; 2, deflated sphere, Sample 99127, GSC 123990; 3, 4, sphere with deflated surface and detail of protuberances, Sample 1680-2, GSC 123991; 5, highly deflated sphere showing preservation of protuberances in deflated surfaces, Sample 99127, GSC 123992; 6–8, deflated hollow sphere with detail of protuberances (7) and detail of thin wall (at arrow in 6) and internal filament with spherulitic texture (at arrow in 8), Sample 99139, GSC 123993; 9, 10, regularly ornamented spheres, Sample 1680-2, GSC 123994, 123995; 11, deeply deflated, ornamented sphere, Sample 99127, GSC 123996; 12–15, small spheres, Samples 1680-3, 1680-2, 1680-2, 1680-1/3; GSC 123997, 123998, 123999, 124000; 16, large sphere, Sample 1680-2, GSC 124001; 17, ornamented sphere with polar “X,” Sample 1680-3, GSC 124002; 18, coarsely ornamented sphere, Sample 1680-2, GSC 124003.
TABLE 1—Ratio of maximum sphere diameter to protuberance diameter.

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<th>Protuberance diameter (µm)</th>
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<td>Fig. 4.13</td>
<td>375</td>
<td>25</td>
<td>15:1</td>
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<td>Fig. 4.14</td>
<td>398</td>
<td>50</td>
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<td>Fig. 4.15</td>
<td>400</td>
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<td>Fig. 4.16</td>
<td>1,644</td>
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<td>Fig. 4.17</td>
<td>816</td>
<td>60</td>
<td>14:1</td>
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<td>Fig. 4.18</td>
<td>800</td>
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**Description.**—Cylindrical and tapering rodlike fossil with regular pattern of spherical depressions or hollows flanked by spiny projections along length of rod. Hollows packed along length of rod forming pattern like a honeycomb or egg carton. Flanking projections range from subdued nodes to well-developed, flattened, slightly tapering square-tipped spines. Rods range in length from greater than 2 mm (Fig. 7.1) to fragments 0.7 mm and shorter. Rods taper from wider, basal end to more slender, apical end. Range in width from 100 µm basally to 65 µm apically (slender form, Fig. 7.1), to more robust forms that taper subtly from 170 µm to 125 µm (Fig. 7.2). Some rods have well-preserved spines (Figs. 7.3–7.6) that have a maximum length of about 60 µm. Ends appear broken, but one specimen tapers to an almost hexagonal apical termination 80 µm across (Fig. 7.5). In lateral view, spines are rectangular with squared ends (Fig. 7.5). In plane view of tapered end of one specimen (Fig. 7.6, 7.7), they are more rounded nodes (possibly weathered), that arise from six points of a hexagon framing a hollow. Two spines of each segment of hexagon are shared by neighboring hollow (Fig. 7.7). On less-tapered, basal end of this specimen (Fig. 7.6, 7.8), spines are rectangular. Hollows are fairly regular along a rod, and range in size from 35 µm to 110 µm among various sizes of rods. Hollow spheres found preserved in hollows of some specimens (Figs. 7.6, 7.11). Hollow spheres that fill hollows range in size from about 30 µm across on a smaller rod (Fig. 7.11) to about 100 µm across on a larger rod (Fig. 7.8–7.10). On the larger rod, only one sphere is preserved. It is hollow, with outer layer or envelope and two concave discs on either side that may be envelopes of neighboring spheres. On the smaller rod, many spheres fill hollows (Fig. 7.11) and fewer spines are present. Spheres contact one another and are hollow, with outer envelope preserved between some spheres.
(Fig. 7.12, arrow). Small discs adhere to some spheres, with their concave sides facing adjoining hollow (Fig. 7.13–7.15). Discs are about 25 μm in diameter, some with a concave center that may open into sphere (compare to discs of Fig. 7.8, 7.10), and have thickened, rounded edges that are segmented along periphery (Fig. 7.14, 7.15, arrows). Smaller discs (14 μm in diameter) lie on some smaller spheres (Fig. 7.16, arrow).

**Material examined.**—GSC 124024–124033.

**Occurrence.**—Lower Cambrian, East China, North America (this study).

**Discussion.**—Material from the present study (more than 100 specimens) shows more variation in features than those described in the original diagnosis. The main difference in the ornament is due to preservation, whereby the Chinese material may have been more eroded to give the spines a nodose appearance. Yue and Zhao (1993) speculated on the affinities of this peculiar microfossil, comparing it to sponge and echinoid spines. The nature of the hollows and features of the spheres that fill them suggests the spheres can be biologically shed from the spiny rod and may represent some sort of reproductive structures. Discs that lie upon
and between spheres vary in size with the smaller ones bearing segmentation. Some larger discs could possibly form the outer envelope between neighboring spheres. It is difficult to tell if the center of the small discs bears a hole, which may be infilled, or if the hollow center is due to erosion of the disc.

Pyramidal, Conical, and Bulbous Fossils

Figures 7.21, 8.1–8.3

Discussion.—A pyramidal fossil (Fig. 7.21) is deeply hollow with a tapering shell that may curve slightly apically. Basal outline is broadly triangular, with a wide flat side, narrow flat side, and a gently outwardly convex side. A rounded keel forms the apex of the triangular base. Maximum width of base is 444 µm, tapering to apex that is 84 µm wide. Outline of the apex is oval. Walls are thin and outer surface lacks ornament. The specimen is somewhat similar to Tianzhusania described by Qian et al. (1979, pl. 2, figs. 17, 18, 25) but the cross section is not irregularly pentagonal, nor is there any longitudinal and transverse ornament.

Two types of ornamented conical fossils were recovered that resemble Paradoxiconus typicalis Qian et al., 2001. One has a smooth conical apex and broad, tall, ornamented base that occupies two-thirds of the total height of the cone (1.13 mm) (Fig. 8.1). The apex is slightly concave on one (inner) side and convex (outer, figured side in Fig. 8.1) on the other. The tip of the apex is rounded and its cross section is oval. The entire base is ornamented by longitudinal, rounded ribs separated by grooves. The ornament is less pronounced about halfway along the cone and ribs are crenulated near the base of the cone. Many ribs have a bifurcating branching pattern. The base is buckled in a similar way to spheres and tubes within the biota (convex side, Fig. 8.1). Cone is infilled but the base was likely deeply hollow. A second form (Fig. 8.2) also has an oval cross section apically but is broken to reveal an infilled base. The base similarly has longitudinal ribs separated by grooves, but is broader. Where the cone is broken, this rib ornamentation gives a convolute oval outline. The ribs are ornamented by small nodes and some also exhibit a branched pattern (Fig. 8.2). The second form is closest to Type III of Paradoxiconus typicalis illustrated by Qian et al. (2001, pl. 1, fig. 8). These conical fossils may also be compared in outline to Acanthocassis He and Xie (1989), but the latter bears more prominent spines but less prominent “longitudinal radial lines” (He and Xie, 1989, plate 3, figs. 1–9). In addition, Steiner et al. (2004b) show that complete specimens of Acanthocass has have multiple spine-bearing arms and a subtending stem, which is very different from Paradoxiconus typicalis.

One shelly fossil (Fig. 8.3) with a bulbous, netlike “base” (650 µm long) and slightly curved, ovate “stem” (500 µm long) was recovered. It appears broken at the bulbous end, which has a regular pattern of an open lattice with longitudinal and transverse ribs enclosing subquadrate depressions.

Carinachitids

Figure 8.4, 8.5

Discussion.—One tetraradially symmetrical tube (Fig. 8.4–8.5), 370 µm high, with four broad, transversely ribbed faces separated by longitudinal furrows is assigned to Carinachites Qian, 1977, based on the emended diagnosis for the genus by Conway Morris and Chen (1992). The nature of the subdued ornamentation suggests some affinity to C. tetrusculus (Jiang in Luo et al., 1982), but the degree of tapering is much stronger in the latter species. Compaction flattened and imparted slight asymmetry to the fossil. Ridges on the faces have rounded crests.

Tubes and Plates

Figures 7.18–7.20, 8.6–8.19

Discussion.—Phosphatized tubes and plates are abundant components in the present collection and are among the largest fragments, together with Anabarites (millimeter scale). Nowlan et al. (1985) described several of these fossils, but some additional forms are described briefly here to summarize the range of morphology within the biota. Several forms of hollow tubes occur. A hollow cylinder, 560 µm in diameter with walls 100–140 µm thick lacks any internal or external features and may be a coating of a tubular microfossil (Fig. 7.18). Another hollow cylindrical tube (Fig. 7.19) with one closed and one open end is 620 µm long and 322 µm across. It has thin walls, about 10 µm across, and lacks internal and external structure. Other similar-sized and shaped tubes that show tapering (Fig. 7.20) and are probably internal molds.

Annulated rods are represented by the genera Hyolithellus Mis- sarzhevsky, 1969, cf. Pseudorthotheca Cobbold, 1935, and ‘Rugatotheca’ Cobbold and Pocock, 1934. Species of the genus Hyolithellus are distinguished by the nature and spacing of their transverse ribs. Specimens from the present collection are closest to Hyolithellus cf. H. isicus Misarzhevsky, 1969 as illustrated by Nowlan et al. (1985, fig. 7) and similar to forms illustrated by Brasier and Singh (1987, fig. 8.3–8.5). Buckled and crumpled forms (Fig. 8.6, 8.7) show that the tubes distorted without fracturing, which may suggest they were flexible. Fragments range in length from a few millimeters to less than 0.5 mm. A similar form of annulated tube comparable to Pseudorthotheca has a small hole (Fig. 8.8, 8.9). Nowlan et al. (1985, fig. 10) also noted these borings that are similar to predatorial borings illustrated in Cambrian tubular fossils by Conway Morris and Bengtson (1994). Another form of annulated tube is also crumpled, and ornamented with transverse ribs separated by wrinkled longitudinal striae (Fig. 8.10). This tube is comparable to Rugatotheca but has broader spacing of ribs and better-developed striae than in forms illustrated by Yue and He (1989). It is also comparable to postembryonic stages of Olivooides referred to as the Punctatus/Pyrigitestype body fossils illustrated by Yue and Bengtson (1999, fig. 2), although no apical portions nor stellate surface sculpture were observed among the present collection.

A wide variety of tuberculate and reticulate plates occur as millimeter-scale fragments (Fig. 8.11–8.19). These represent a range of forms bearing regularly distributed, subequal, rounded, moundlike tubercles (Fig. 8.11–8.13) and more defined, raised, and projecting tubercles (Fig. 8.14, 8.15). Of these forms, many are planar fragments, but some have a rounded shape, with tubercles covering all surfaces. The most complete example (Fig. 8.13) is ovate, with one closed, rounded end and one open end with a rounded outline. One plate has a reticulate structure with...
parallel, meandroid ribs alternating with rows of small depressions, 25 μm wide. The pattern becomes less defined toward one end of the plate (Fig. 8.16). A variety of large fragments have less distinct tubercles. One specimen has irregularly arranged, poorly defined, subspherical tubercles, up to 110 μm across, some of which have a centrally located slit (Fig. 8.17). A second form (Fig. 8.18) similarly has poorly defined tubercles (80 μm across) and a wrinkled surface upon which tubercles seem to lie in rows but may have been disturbed by crumpling of the specimen. A third form (Fig. 8.19) has a more regular ornament of small, indistinct tubercles, 50 μm across, and is irregularly incised by grooves.

**GLOBAL COMPARISONS AND IMPLICATIONS**

Initial reports of terminal Neoproterozoic and earliest Cambrian fossils were geographically scattered, triggering explanations for
their distributions that focused on biogeography (McMenamin, 1982; Donovan, 1987). Fossil discoveries in western North America, such as Ediacaran dickinsonoids (Narbonne, 1994) and swaptipondits (Hagadorn and Wagggoner, 2000), calcified Neoproterozoic metazoans including Cloudina Germs, 1972 and Namacalathus Grozinger, Watters, and Knoll, 2000 (Hofmann and Montjoy, 2001), small shelly fossils from northwestern Canada (Conway Morris and Fritz, 1980; Nowlan et al., 1985), and now earliest Cambrian phosphatized eggs and microfossils (this report), are clarifying the originally cosmopolitan nature of these biotas. Cambrian paleogeographic configurations, although varied, suggest that Siberia and Laurentia may have remained in close proximity in an equatorial position until the Cambrian (Pelechay, 1996; Sears and Price, 2000), while the South China Block was possibly part of East Gondwana in low latitudes during the Cambrian (Huang et al., 2000). The presence of strikingly similar animal eggs and embryos in similar Early Cambrian facies on three disparate continents emphasizes that these organisms were widespread biogeographically. Paleocoenographic conditions, perhaps linked to the carbonate ramp/platform settings and associated climate of these three longitudinally separated regions, favored rapid phosphogenesis that preserved embryonic fossils.

Reports of animal embryos augment the hidden or “missing” record of early animal evolution and some studies permit detailed embryonic reconstruction (e.g., Dong et al., 2004). Exceptionally preserved microfossils in North America reported here further fill an apparent gap in the seemingly stepwise fossil record of early animal evolution from the Neoproterozoic to the Cambrian, and emphasize the role of local environment and taphonomy in preserving these important microscopic remains. Taphonomic processes associated with rapid mineralization of metazoan eggs is becoming better understood through experimental work (Briggs and Wilby, 1996; Martin et al., 2003). Early Cambrian phosphorites and phosphatic limestones were widespread and volumetrically significant (Cook and Shergold, 1984), and reflect rapid phosphatization over large areas. As with the eggs and embryos described in this paper, many small shelly fossil assemblages were preserved through secondary phosphatization, and these are also widespread in Lower Cambrian strata, declining at the end of the Botomian Stage of the Early Cambrian synchronous with a decrease in the abundance of phosphatized facies (Porter, 2004).

Braisier and Lindsay (2001) suggested explosive phases of evolutionary diversity are illusory, related to special preservational conditions controlled by the sedimentary record. It is through these phosphatization taphonomic windows that we are able to glimpse the record of an unexpectedly widespread biota, including the early record of animals with no calcified hard parts that would otherwise be destroyed by taphonomic processes or simply not preserved if the ocean chemistry was not suitable. The occurrence of phosphatized eggs and embryos in the Early Cambrian of North America is an example of exceptional mineralization associated with a phosphatization event. It is likely that investigation of similar environmental and taphonomic windows containing these “rare” assemblages will lead to additional significant discoveries in North America and elsewhere.

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