Cnidarian-like embryos associated with the first shelly fossils in Siberia

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ABSTRACT

Phosphatized spheroids, ~0.5 mm in diameter, in the Lower Cambrian Manykay Formation at the Bol'shaya Kuonamka River in northern Sakha (Yakutia) are interpreted as cnidarian embryos of late developmental stages. One of the poles has a double cross-like structure, consisting of two sets of four bands each. The bands of the upper set radiate at 90° from each other; those of the lower set also radiate at about right angles from each other, but the set is rotated 45° in respect to the upper set. Although there is a resemblance to the cross-like arrangements of cells in pregastrulation spiralian eggs, in particular those of annelids, the combined evidence favors an interpretation of the bands as incipient tentacles of a cnidarian actinula larva. The embryos occur with one of the first assemblages of shelly fossils in northern Siberia, that of the *Angustiochrea lata* zone. The co-occurring shelly fossils, anabaritids, probably also represent the phylum Cnidaria, but because their tubes have a consistent triradial symmetry, the connection with the tetraradially symmetrical embryos is problematic. The size of the embryos suggests that they are nonplanktotrophic, and the presence of actinula-like features suggests the lack of a free planula stage.

INTRODUCTION

The globular microfossils *Markuelia* Valkov and *Olivooides* Qian from the Early Cambrian are now recognized as phosphatized embryos of metazoans (Bengtson and Yue, 1997). *Markuelia*, from the basal Tommotian of the southern part of the Siberian platform (the Dvortsy section on the River Aldan), is a segmented worm-like animal of problematic affinities (possibly a halkieriid, as suggested by Conway Morris, 1998). *Olivooides*, represented by a nearly complete developmental sequence from early cleavage stages to hatched and grown individuals, is interpreted as a cnidarian similar to the extant coronate scyphozoans (Yue and Bengtson, 1999).

These and other discoveries of phosphatized embryos (see also Zhang and Pratt, 1994) in Cambrian deposits suggested that such fossils have been overlooked because of their nondescript morphology. Following the Cambrian discoveries, embryonic fossils were reported from the late Neoproterozoic Doushantuo Formation in southern China (Li et al., 1998; Xiao et al., 1998). We report here embryos of probable cnidarian affinity associated with the *Anabarites* fauna in northern Siberia, which represents the oldest shelly fossils from the Precambrian-Cambrian transitional strata in that area.

MATERIAL AND METHODS

The material derives from our field work in the summer of 1996 along the Malaya and Bol'shaya Kuonamka Rivers on the northeastern flanks of the Anabar massif, Sakha (Yakutia). The locality, 96K4, is in the Manykay Formation on the left

bank of the Bol'shaya Kuonamka, 1 km upstream of the mouth of the brook Ulakhan Tyulen (Fig. 1). It corresponds to section A-51 of Val'kov (1975, 1987). The globule-containing sample, 96K4-4.0, is from a carbonate packstone that

forms a 10–15-cm-thick layer on top of an erosional surface in a thrombolitic sequence, 3.1 m above the first shelly fossils in the exposed section. It corresponds to the "marker bed with angustiochreids [anabaritids]" of Val'kov (1975,
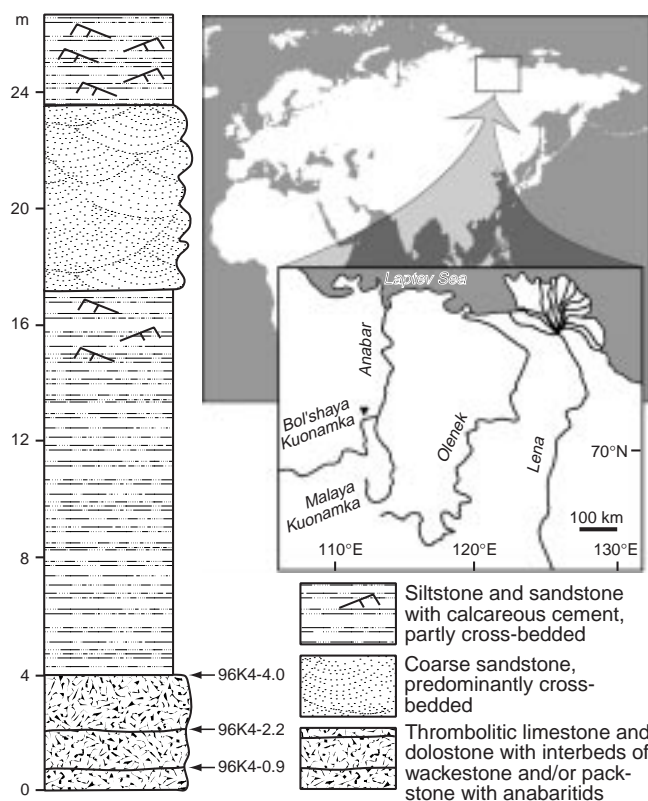

Figure 1. Schematic section of Manykai Formation at locality 96K4, Bol'shaya Kuonamka.

p. 8), which belongs to the *Angustiochrea lata* zone of the Manykaian stage. The sample was dissolved in 10% acetic acid, and the specimens, preserved as calcium phosphate, were isolated from the insoluble residue. Four globules of 430–550 μm size (Figs. 2 and 3, A and D) and more than 100 smaller globules (Fig. 3, B and C) were found, in association with an assemblage of anabaritids (Fig. 4). The specimens are housed in the Swedish Museum of Natural History, Stockholm, Sweden.

DESCRIPTION OF THE SPECIMENS

Of the globules investigated (Figs. 2 and 3) only two show structures that permit any specific morphological conclusions (Fig. 2). The first specimen (Fig. 2, A–C) is a slightly irregular oblate spheroid, 520–550 μm in diameter and 500 μm in axial length, displaying at one pole a pattern of tetraradial symmetry. This pattern consists of 50-mm-wide and 100-mm-long bands that have diffuse outer ends and meet at 90° in the center; at 45° angle to these bands

there are similar bands that appear to be beneath the first bands and to meet at slightly oblique angles, apparently as a result of the slight elongation of the spheroid in the direction of one of the radii (Fig. 2B). Most of the remaining surface has the appearance of a somewhat buckled membrane (Fig. 2A).

The second fossil (Fig. 2, D–F) is a somewhat smaller, prolate spheroid, with a diameter of 430 μm and an axial length of 460 μm. Most of the surface is covered with filaments (2–5 μm wide). At one of the poles, the filaments are radially arranged, and in the central part they are covered by a phosphatic crust (Fig. 2E), similar in appearance to that of the first specimen. Toward the edges of this radial zone, there are radial folds in which the filaments converge to form a chevron pattern (Fig. 2, E, G–I); eight such folds appear to be present. Beyond the radial zone, the arrangement of the filaments is somewhat more disorderly, but broadly they seem to define a concentric pattern that is perpendicular to the radial pattern (Fig. 2F).

Other globular specimens vary from 265 μm to 510 μm in diameter. They are either smooth (Fig. 3C) or have a buckled or collapsed surface (Fig. 3, A, B, and D). Whereas the smooth forms may represent nonbiogenic structures, particularly ooids, the buckled specimens clearly represent an outer, flexible membrane covering a partly collapsed interior, strongly suggesting a biological nature. The polygonal pattern of buckling in some specimens (Fig. 3, A and B) may reflect an underlying cellular pattern. Another specimen (Fig. 3D) has a broken outer membrane, and the interior part shows botryoidal apatite covering thread-like structures. This is a common diagenetic structure inside phosphatized fossils, apparently reflecting the presence of degraded soft tissue (e.g., Bate, 1972, Plate 67:1; Bengtson, 1976, Fig. 3, D and E; Conway Morris and Chen, 1992, Fig. 7; Yue and Bengtson, 1999, Fig. 10).

INTERPRETATIONS OF EMBRYONAL STRUCTURES

The two specimens in Figure 2 are interpreted as animal embryos, on the basis of a distinct polarity, the presence of a thin, smooth outer membrane, and the morphological similarity with the late embryonal stages of *Olivooides*. Although the two specimens are different in appearance, that both express an octaradiate or tetraradiate pattern, are of similar size, and occur together suggest that they belong to the same taxon, the difference between them being due to a difference in preservation or developmental stage.

Alternative interpretations of the fossils include unicellular eukaryotes, such as acritarchs, or propagules and/or cysts of algae. However, we are not aware of any structure similar to the double cross in such organisms; the function of the cross would be unexplained in such an inter-

Figure 2. Fossil embryos from sample 96K4-4.0. A–C: Specimen SMNH X 2345. 100× magnification. A: Aboral view, showing smooth buckling of outer membrane. B: Oral view, showing tetraradial structure interpreted as eight incipient tentacles arranged in one oral and one suboral circlet (o1, o2: two oral tentacles; so1, so2: two suboral tentacles). C: Side view (notation as in B). D–I: Specimen SMNH X 2346. D: Aboral view, showing concentric filaments. E: Oral-lateral view, showing concentric (cf) and radial (rf) filaments and radial folds (arrows, shown in G–I), and incomplete outer membrane (m). F: Side view, showing concentric (cf) and radial (rf) filaments and membrane (m). D–F: 115× magnification. G–I: Radial folds at oral pole, 600× magnification.
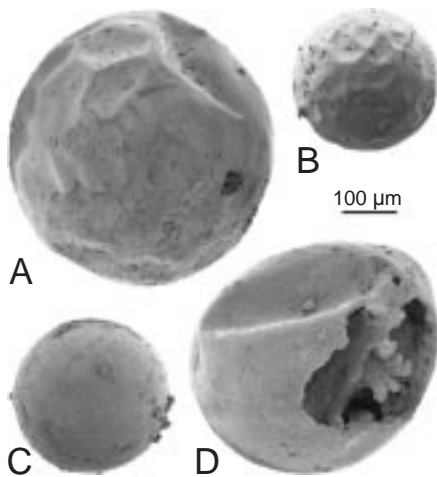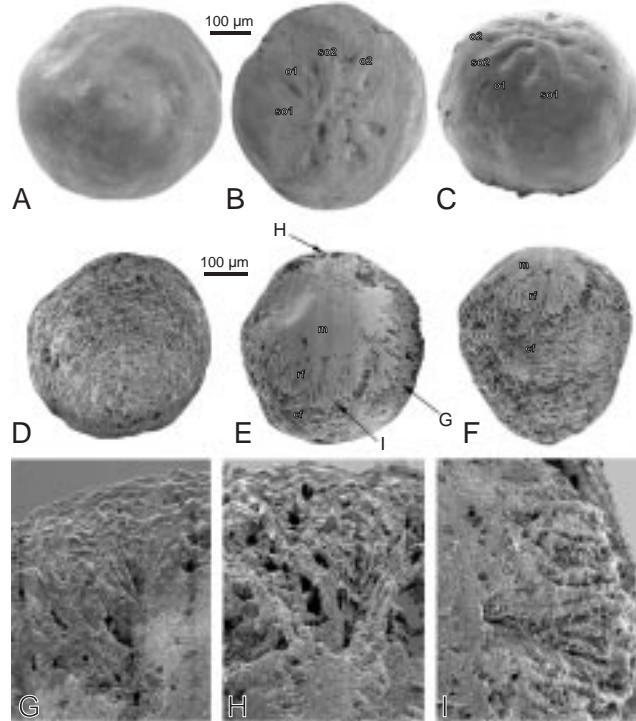
Figure 3. Fossil eggs (A, B, D) and egg-like object of possible nonbiogenic origin (D) from sample 96K4-4.0. A: Specimen SMNH X 2347. B: Specimen SMNH X 2348. C: Specimen SMNH X 2349. D: Specimen SMNH X 2350.
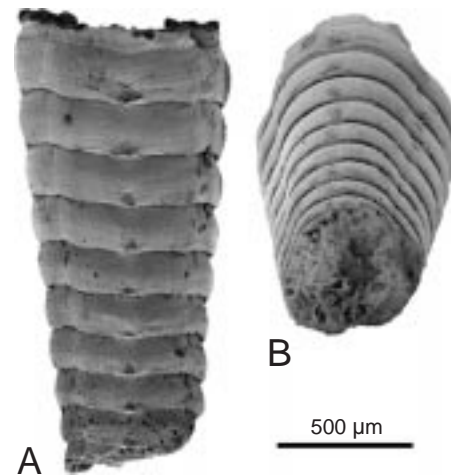
Figure 4. Anabaritid *Aculeochrea ornata* Val'kov and Sysoev, 1970, from sample 96K4-4.0. Internal mold. Specimen SMNH X 2351. A: Lateral view. B: Apical-lateral view.

pretation. In addition, the co-occurrence of forms with suggestions of collapsed cells under a membrane (Fig. 3, A and B) is a further indication that embryos are present in this fossil material.

Embryos of one taxon tend to be similar in size, and during the early cleavage stages they typically do not grow, as the total cytoplasm remains approximately the same. The specimens in Figure 3, A and D, are of the same size as the embryos in Figure 2 and may represent the same taxon. The one illustrated in Figure 3B is only about half as wide as the other ones and probably represents another taxon or life stage. The specimen shown in Figure 3C is of the same size as that in Figure 3B, but its biogenic origin is uncertain.

Structures similar to the cross on the best-preserved specimen (Fig. 2, B and C) occur at the blastula stages in bilaterally symmetrical metazoans with spiral cleavage. This is the so called "annelid cross," typical of annelids and echiurans, and the "molluscan cross," typical of molluscs and sipunculans. These structures are formed by radial rows of cells arranged around the animal pole of the embryo. The arms of the annelid cross project at angles of 45° to the cells of the apical rosette (Pilger, 1997, Fig. 10.17), whereas those of the mollusc cross are situated in the radii of the apical rosette (Pilger, 1997, Fig. 10.8).

Although the similarity of these crosses, especially that of the annelid type, to our fossil is intriguing, we think that the combined evidence from the two fossil specimens suggests that we are dealing with a taxon that shows tetraradial symmetry during a prolonged phase of its late embryology, perhaps also as a larva or adult. Furthermore, the band-like structures on the best-preserved specimen (Fig. 2, B and C) do not show any cellular pattern.

Tetraradial symmetry is characteristic of several groups of cnidarians, particularly hydrozoans and scyphozoans, but also octocoral anthozoans. Octocoral planulae metamorphose into small polyps with eight tentacles (Tardent, 1978). In some hydrozoans, the planula larva metamorphoses into an actinula larva typically bearing eight tentacles; this metamorphosis may take place within the parental gonophore (Martin, 1997; Tardent, 1978), thus technically at the embryonal stage. In the meiofaunal hydrozoan order Actinulida, the embryo develops directly into an actinula-like juvenile; further ontogeny essentially consists of modifications of the actinula pattern (Swedmark and Teissier, 1966).

The crossed bands seen in Figure 2 (B and C) might represent eight incipient tentacles of a cnidarian embryo developing into an actinula. The two levels of bands at 45° angles to each other are suggestive of the two circles of tentacles typically present in actinula larvae (e.g., Swedmark and Teissier, 1966; Vyver, 1968, Fig. 3). Because the pole opposite that with the crossed bands shows no sign of an opening (Fig. 2A), we interpret this pole as aboral, the tentacles thus occupying an oral position. Larvae such as those of the Actinulida in Figure 5 would, if developing within spherical egg membranes, probably be very similar to the fossil specimen in Figure 2, A–C. These particular recent larvae, however, have their tentacles near the aboral, not the oral, pole.

The presence of radiating structures at one pole resembles the condition in late embryos of *Olivooides*. The latter is probably a scyphozoan, judging from the similarities between the conical hatchlings of *Olivooides* and the sheaths of the sedentary polyps in certain modern scyphozoans (Bengtson and Yue, 1997; Yue and Bengtson, 1999). *Olivooides* has a pentaradial symmetry, visible in the apical part of the hatched cones (and possibly in the aboral pole of at least some embryos; cf. Yang et al., 1983, Plate IV:3c). The tetraradial structure of the Kuonamka embryos thus sets them apart from *Olivooides*, but is consistent with a cnidarian affinity. Judging from the size and from the presence of actinula-like features, the new embryos appear to have been nonplanktotrophic direct developers without a free planula stage. In this, they also resemble *Olivooides* (Bengtson and Yue, 1997; Conway Morris, 1998; Yue and Bengtson, 1999).

The presence of an embryo with tetrameral symmetry and what may be interpreted as eight incipient tentacles suggests that these fossils are cnidarian embryos. (The filaments in Fig. 2, D–I, may represent cilia or microvilli thickened by diagenetic incrustation of apatite.) The only fossils of adult animals cooccurring with these embryos are anabaritids, the tubes of which are unusual because they are characterized by *triradial* symmetry. Whereas it is quite possible that the Kuonamka embryos derive from co-occurring animals that failed to be fossilized, the possibility that the embryos represent anabaritids needs also to be considered.

ANABARITIDS

The anabaritids (Fig. 4) are a group of animals with tubular to conical shells, apparently confined to the latest Proterozoic and earliest Cambrian. They are particularly characteristic of the Precambrian-Cambrian boundary beds of the Siberian platform and of the Palaeotethys phosphorite belt. Although anabaritids were described as early as 1919 from the Cambrian of Sweden (Rosén, 1919), taxonomic work did not start until 50 years later with the erection of the genus *Anabarites* Missarzhevsky (Voronova and Missarzhevsky, 1969). The distinctive feature of anabaritids is the triradial symmetry, usually expressed as three, occasionally six, longitudinal grooves. The morphology is quite variable, and some forms have the triradial symmetry only weakly expressed or not at all. The walls were probably aragonitic, grow-
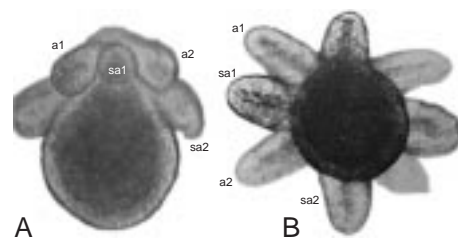
Figure 5. Actinula larvae of extant actinulid *Halammohydra schulzei* Remane, showing two sets of tentacles (a1, a2: two aboral tentacles; sa1, sa2: two subaboral tentacles). A: Lateral view. B: Oral view. From Swedmark and Teissier (1966, Fig. 3, J and K; no magnification given).

ing by internal and apertural accretion, with a fibrous microstructure (Bengtson et al., 1990; Conway Morris and Chen, 1989).

Originally regarded as polychaetes (Glaessner, 1976; Voronova and Missarzhevsky, 1969), the anabaritids were later reinterpreted as cnidarians (Missarzhevsky, 1974), probably closely related to scyphozoans (Bengtson et al., 1990; Val'kov, 1982). The main basis for this interpretation is the radial symmetry and morphological similarities with the Paleozoic conulariids and with strobilating polyps of modern scyphozoans. Val'kov (1982) referred them to a scyphozoan subclass Angustimedusae Val'kov, 1982, stressing that the triradial symmetry would distinguish them from other scyphozoans. Fedonkin (1986) drew attention to the presence of Vendian disk-like fossils (e.g., *Tribrachidium*, *Albumares*) with triradial symmetry, implying a possible phylogenetic relationship with the anabaritids.

The notion that the tetraradial embryos recorded from the Kuonamka section may have given rise to triradial anabaritid adults may seem farfetched, but it is not inconsistent with cnidarian biology. Tetraradial symmetry is a widespread feature in cnidarians, and secondary derivation of other symmetry forms has been documented. For the scyphozoans, Gershwin (1999) worked with clonemates of five species and found variation in symmetry to be prevalent. It is not unusual for a scyphistoma of one symmetry to give rise to larvae of numerous different symmetries. The symmetry of the adult is fixed in the larval stage; thus, nontetramerous larvae grow into nontetramerous adults.

In the scyphozoan *Aurelia*, not only is symmetry plastic, but it appears to be correctable over time. Gershwin (1999) found that an initially highly variable (88.9% nontetramerous individuals) population of *A. labiata* showed a significant decrease in variability (to 29%) after 4.5 months of laboratory breeding. These findings suggest that, at least in *Aurelia*, symmetry variation is due to developmental disturbances rather than to genetic variability. In several extant taxa of hydrozoan medusae, symmetry number re-

mains flexible throughout ontogeny; that is, the medusa adds parameres as it grows (Mayer, 1901). In others, however, the deviation from tetramerous symmetry seems genetically fixed. For example, Mayer (1901) and Burkenroad (1931) reported apparently stable populations of pentamerous hydromedusae. Furthermore, there are at least six species characterized by hexamerous symmetry, and several more that are octamerous (Mayer, 1901). Thus, while symmetry is highly variable, it is capable of fixation.

Whereas triradial medusae are not uncommon as members of symmetrically variable populations (e.g., Browne, 1901; Hargitt, 1901, 1905; Romanes, 1877, Plate 16:4), stable populations of trimerous individuals are not known in modern cnidarians. The Actinulida, which show the closest similarities with the embryos described here, may have a propensity for triradial symmetry: Swedmark and Teissier (1966, p. 120) reported that about 90% of the specimens of *Halammohydra vermiformis* examined had three tentacles in the aboral girdle, only 10% having four. This does not represent total triradial body symmetry, however, as all specimens had four subaboral tentacles and four statocysts.

The anabaritids might conceivably represent a case of a triradially symmetrical cnidarian retaining traces of tetraradial symmetry in the embryo, and perhaps in the larva. However, unless specimens (embryonal or postembryonal) can be found that combine the two forms of symmetry, this idea must be regarded as speculative.

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