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Alternative interpretations of some earliest Ediacaran fossils from China

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In a letter to *Nature* (February, 2011), Xunlai Yuan and collaborators recorded carbon compression fossils from black shales of the Lantian Formation (Ediacaran), southern Anhui Province, South China. The new fossils, described under five morphological types (Types A to E), exhibit degrees of morphological differentiation suggesting that they were multicellular eukaryotes. Some of the Lantian macrofossils were interpreted as algae, but others are of unknown affinities. For reasons noted in this discussion, Type A fossils attracted our particular attention, and we suggest an alternative interpretation of their affinities. According to our view, some of them (at least those with three faces and no globose holdfast at their base) may represent conulariid cnidarians or close medusozoan relatives. The undistorted organism probably was a three-sided cone in life. We believe that our suggested alternative interpretations of the anatomy and affinities of the fossils in question can be useful in guiding future research on the oldest currently known fossil assemblage of multicellular organisms.

Introduction

In a recent letter to Nature Yuan et al. (2011) documented new carbon compression fossils from the Lantian Formation (Ediacaran) of South China. The Lantian Formation is correlated with the Doushantuo Formation (635-551 Myr), one of the most famous Konservat Lagerstätte of the Ediacaran Period, which hosts fossils of acritarchs, multicellular algae, and embryos of the earliest animals (for references see Narbonne 2011). The new Lantian fossils were collected from a 35 m thick interval of finely laminated black shales cropping out in southern Anhui Province (Yuan et al. 2011). Based on stratigraphic and sedimentologic evidence (fine lamination plus absence of grading, cross-stratification or other wave- or current-influenced structures), the black shales were interpreted as suspension deposits that settled out of quiet, shallow marine waters below storm wave base (Yuan et al. 2011). The Lantian fossils are exceptionally well preserved, suggesting that they were buried in situ (Yuan et al. 2011).

Institutional abbreviations.—NIGPAS, Nanjing Institute of Geology and Palaeontology Chinese Academy of Sciences, Nanjing, China.

Historical background

The Lantian fossils provide a unique window on the early evolution of multicellular life (Narbonne 2011), constituting the earliest known assemblage of macroscopic and morphologically complex organisms. Many of the Lantian fossils described by Yuan et al. (2011) were interpreted as algae, but the affinities of others were considered uncertain, raising the possibility that at least some of the fossils were only distantly related to extant groups. Yuan et al. (2011) classified the Lantian fossils into five morphological types, of which Type A attracted our particular attention. As described by these authors (p. 391), Type A fossils "are 16-40 mm in length and characterized by a fan-shaped structure consisting of a globose holdfast at its base, a lower stalk, and an upper crown." The stalk was thought to be originally conical in shape, consisting of a splay of packed filaments and a truncated or slanted upper end. The crown was interpreted to consist of more than ten tentacle-like, non-branching ribbons of unequal to subequal length (2-13 mm) and tending to have a rounded distal end. Interestingly, a globose holdfast is not apparent in the specimen figured by Yuan et al. (2011: fig. 3E), which however appears to be broken at its narrow end. Herein we suggest that at least some Type A specimens, particularly the specimen shown in fig. 3E of Yuan et al. (2011: 392), may represent cnidarians. More specifically, we propose that they may in fact represent conulariids or close medusozoan relatives of this taxon. Conulariids (?Ediacaran to the Late Triassic) are an extinct group of marine forms possibly related to scyphozoans and characterized by a steeply pyramidal, generally four-sided theca composed of calcium phosphate, though some conulariids may be partly preserved as carbonaceous films (Simões et al. 2003; Van Iten et al. 2005; Leme et al. 2008). The corners of the theca are usually sulcate, and the apertural end of each side (face) commonly forms a subtriangular lappet.

Reinterpretation of some "Type A" fossils of Yuan and collaborators

We suggest that the specimen (NIGPAS-LT-295) shown in Yuan et al. (2011: fig. 3E), and possibly other specimens as well, can be interpreted as consisting of a tapered theca exhibiting two or three faces, with each face bearing a subtriangular apertural lappet at its

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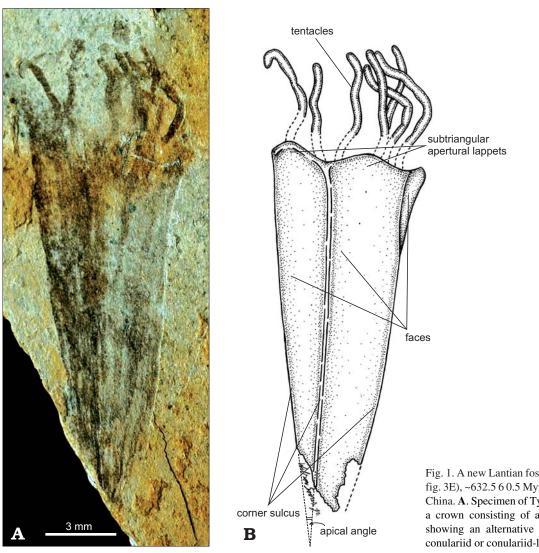


Fig. 1. A new Lantian fossil illustrated by Yuan et al. (2011: fig. 3E), ~632.5 6 0.5 Myr, southern Anhui, Province, South China. **A**. Specimen of Type A (NIGPAS-LT-295) showing a crown consisting of a single ribbon. **B**. Line drawing showing an alternative interpretation of this fossil as a conulariid or conulariid-like cnidarian.

wide end (Fig. 1). A broken apical end and at least one corner sulcus that extends discontinuously from the apical end to the possible aperture are also discernible. The undistorted theca may have had three or four faces, and we may note here that three-, five-, and six-fold symmetries turn up multiple times in conulariid evolution (Van Iten et al. 2005, 2006). Projecting from the possible aperture are relatively dark elongate features that may represent tentacles or similar soft-part structures. Somewhat similar, narrow strap-like bands extending through the "theca" are more difficult to interpret under our model, but they may represent endodermal canals (Paulyn Cartwright personal communication, 2011). Although we cannot discern transverse or longitudinal ornament clearly comparable to the transverse ribs and nodes of conulariids, this apparent absence may be an artifact of preservation.

Conulariids and the "slow burn" scenario of metazoan evolution

As noted by Seilacher et al. (1998), there are currently two alternative scenarios concerning the early evolution of metazoans: the "Cambrian explosion" hypothesis and the "slow burn" hypothesis. According to the first hypothesis, animal phyla originated rather suddenly during the Proterozoic-Phanerozoic transition (ca. 540 Myr), though several lines of evidence have extended the paleontological record of animals to at least 580 Myr (see references below). The second hypothesis is that Metazoa developed over a much longer period of time, more than 1 billion years ago (see Fedonkin 2003). New carbon-isotope data indicate that the Lantian biota is 635 million to 577 million years old (Narbonne 2011; Yuan et al. 2011). Hence, in terms of the evolution of major taxa, the most significant information to come out of some of the Lantian fossils may be the possible gross anatomical evidence for Early-Middle Ediacaran animal phyla (cnidarians or close relatives). Phylogenetically, our suggested alternative interpretations are reasonable, as all stem group medusozoans, including both polyps and medusae, are well documented from the Cambrian (Van Iten et al. 2005; Cartwright et al. 2007). If corroborated by future discoveries, the alternative anatomical interpretations here presented would confirm that some animal groups had a relatively deep Precambrian history (the "slow burn" scenario), a view now supported by

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both paleontological (Hofmann 1994; Fedonkin and Waggoner 1997; Seilacher et al. 1998; Fedonkin 2003; Budd 2008) and molecular data (Ayala and Rzhetsky 1998; Cartwright and Collins 2007; Peterson et al. 2008).

Finally, our reinterpretation has implications for our understanding of conulariids in particular and medusozoans in general, setting the origin of this clade back several million years. In addition, the preservation of possible soft parts, such as the tentacles in association with the conulariid shaped theca, is a remarkable fossil find.

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