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1.3 Billion years of acritarch history: An empirical morphospace approach

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Abstract

Acritarchs are a group of organic-walled vesicular microfossils interpreted as protists, and are among the first eukaryotes preserved in the fossil record. Taxonomic inconsistencies amongst acritarch workers have made it difficult to address the evolutionary history of this group through more traditional methods (i.e., biodiversity through species counts). We have constructed an empirical morphospace to examine the first 1.3 billion years of acritarch evolution. We show that protist morphologic evolution is broadly correlated with major environmental and biologic revolutions in Earth history such as late Neoproterozoic global glaciations, the first appearance of the Ediacaran metazoans and the Cambrian explosion. Our results also show that protist morphologic expansion precedes their taxonomic diversification; this pattern, similar to that seen in Phanerozoic animal clades, suggests that early morphospace saturation and convergence are common occurrences in eukaryote macroevolution. In addition, our data do not support a monotonic increase in maximum diameter of acritarch vesicles through the Proterozoic; instead, maximum vesicle diameter appears to fluctuate in the Proterozoic before decreasing significantly in the early Cambrian.

Keywords: Proterozoic; Cambrian; Acritarchs; Morphological disparity; Macroevolution

1. Introduction

Acritarchs, a group of decay-resistant organic-walled vesicular microfossils, dominate the fossil record of Proterozoic (2500–542 Ma) and Cambrian (542–488 Ma) protists. Most acritarchs from the Proterozoic and Paleozoic are interpreted as unicelled photosynthetic protists, though some may represent multicellular algae (Mendelson, 1987; Butterfield, 2004), and a few have been tentatively interpreted as fungi (Butterfield, 2005). Acritarchs are among the oldest eukaryotes in the fossil record (Zhang, 1986; Yan, 1991) and offer the earliest adequate data to assess the history of protistan biodiversity (Knoll, 1994; Vidal and Moczydlowska-Vidal, 1997).

Previous estimates of acritarch diversity suggest that the number of acritarch species was low from the first occurrence in the Paleoproterozoic to as late as the early Neoproterozoic (Fig. 1). Acritarch taxonomic diversity began to increase through the Neoproterozoic, but suffered a decline during mid-Neoproterozoic glaciation events. An unprecedented, though short-lived, diversification occurred after these glaciation events, and was then followed by a taxonomic decline, concurrent with the rise of macroscopic Ediacara organisms, some of which clearly were metazoans (Fedonkin and Waggoner, 1997). Acritarch taxonomic diversity subsequently increased in step with animal radiation in the early Cambrian (Knoll, 1994; Vidal and Moczydlowska-Vidal, 1997).

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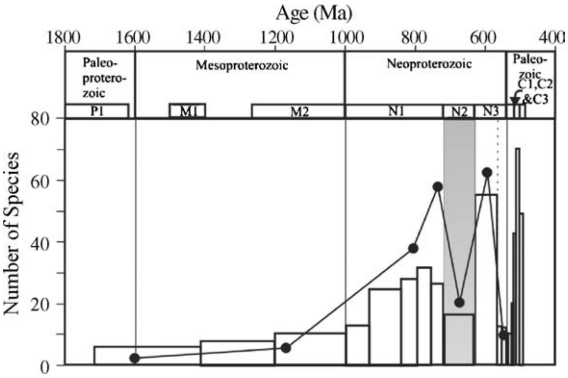

Fig. 1. Estimates of acritarch taxonomic diversity during the Phanerozoic and early Paleozoic. Bars are adapted from Knoll (1994). Black circles adapted from Vidal and Moczydlowska-Vidal (1997). Vertical black lines represent Era boundaries. The dotted vertical line to the left of the Neoproterozoic/Paleozoic boundary represents the first appearance of Ediacara organisms. The gray box represents the Cryogenian Period when multiple global glaciations occurred.

Taxonomic inconsistencies have caused some to question the validity of taxic measures of protistan biodiversity (Butterfield, 2004). The problem is common in paleontology, and can be acute in the study of acritarchs. Evolutionary convergence among simple protists can lead to taxonomic deflation, or an underestimation of diversity; whereas the heteromorphic alternation of generations can lead to taxonomic inflation, or an overestimation of diversity (Butterfield, 2004).

The usefulness of morphometric tools in the analysis of Phanerozoic organisms (Foote and Gould, 1992; Boyce, 2005) encouraged us to use such strategies to independently clarify the morphological history of acritarchs. If acritarch diversity is merely a reflection of form taxa in a uniformly populated morphospace, patterns of morphological disparity and taxonomic diversity should match one another. In contrast, a mismatch would indicate either inconsistent form taxonomy or unevenly populated morphospace. By contrasting diversity and disparity patterns, we can also quantitatively address the issue of morphological constraint and convergence.

Taxonomy aside, quantitative morphological analysis would also allow us to quantitatively address a number of questions related to acritarch evolution, including, among others, the relation between acritarch disparity and major environmental and biotic events. To address these questions, we conducted a literature-based investigation of the first 1.3 billion years of morphological evolution in the Group Acritarcha.

2. Methodology

We used a literature-based morphometric approach to examine the evolutionary history of acritarchs from their first appearance in the Paleoproterozoic through the Cambrian. An extensive (although by no means exhaustive) literature review, utilizing 50 publications (Table 1), produced a database of species descriptions from 47 stratigraphic intervals representing 778 species occurrences (the occurrence of a species in a lithostratigraphic unit), 247 locations and 1766 processed rock samples. The species occurrences were assigned to nine geochronological bins based on our best age estimate of the lithostratigraphic units (Table 2).

Size and morphological data were collected from species descriptions and illustrations published in the literature (Table 1). Vesicle diameter was recorded, when reported, from species descriptions and measured from microphotographs of figured specimens. Thirty-one morphological characters were identified to quantify acritarch morphology (Table 3). Every species occurrence in the database was coded for the presence or absence of all 31 morphological characters based on species descriptions of type specimens found in the literature survey. The resulting database of morphological characters was comprised of binary variables, where a present character was scored as 1 and an absent character was scored as 0 (Table 3).

The characters applied here (Table 3) may at first appear a somewhat redundant representation (alternative states) of only three characters: vesicle morphology, process morphology, and process tip morphology. However, these 31 characters, as classified, are not mutually exclusive. The choice of 31 presence–absence characters, rather than three multi-state characters, makes it possible to accommodate species descriptions that reported multiple morphologies (for example, a single species occurrence might have multiple process tip morphologies). Also, altering our data matrix to combine these morphologic characters would pose analytical problems, because the calculation of dissimilarity coefficients requires binary presence/absence data. Finally, and most importantly, analyses carried out on a non-redundant subset of character states (not shown here) do not differ notably from the results presented below.

2.1. Body size analysis

Maximum vesicle diameters were recorded from species descriptions, when available, for all species occurrences. Figure vesicle diameters were measured from microphotographs of acritarchs. In addition, mean