Eukaryotic Organisms in Proterozoic Oceans

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I. Introduction

A. In combination, molecular phylogenies and fossils of early animals indicate the Eukarya (of which animals are a subclade) must have existed in Proterozoic oceans. Comparative biological estimates of how deep that eukaryotic history might be range from extremely shallow (e.g., Cavalier Smith) to very deep (Pace). In recent years, most molecular clock estimates for eukaryotic divergence have split the difference (note the stem vs. crown group issue):

Soon et al. 2004
Bapteeste et al. 2004
Hedges et al.
Doolittle et al. ????
Others?

B. Such estimates obviously carry predictions for what paloentologists should see in investigations of Proterozoic sedimentary rocks. In this paper, we review the early the fossil record of eukaryotic organisms, as currently understood, and then use this record to make inferences about the functional evolution of nucleated organisms in Proterozoic oceans.

II. How can we tell that a fossil was made by a eukaryote?

A. Best to start with an example: *Shuiyousphaeridium macroreticulatum*

1. Attributes:

a. Size
b. Surface in polygonal fields -- TEM images show that wall is multilayered: homogeneous layer of organic plates lies between an outer layer of debris and sectioned processes and a thin electron-tenuous layer that lines the inner side of the plates
c. Regularly arranged processes
d. Preservable organic composition

2. Interpretation: Prokaryotes can be large, they can have processes, and they can have preservable walls. But no prokaryote currently known has all three at once. And none exhibits the complexity of form from TEM, SEM, and light microscopy observed in *Shuiyuosphaeridium*. Many eukaryotes do. Therefore, we believe the most parsimonious interpretation of this population is that it was made by a eukaryotic organism, indeed a eukaryote with a sophisticated cytoskeleton. Age is greater than 1000

Ma; likely greater than 1250 Ma. Finer systematic attribution not possible. Could be stem or crown.

B. A second example: *Bangiomorpha*

1. Attributes

a. Multicelluar structure
b. Cell differentiation – differentiated holdfast.
c. Orientation, erect filament swayed in water column.
d. Intercalary division of vegetative cells in filament; pie-like division of reproductive cells
e. Taphonomic details

2 Intepretation: Once again, prokaryotes, especially cyanobacteria, exhibit individual characters found in *Bangiomorph*a; but if this fossil is prokaryotic, it contains a number of features not otherwise known in cyanobacteria or any other prokaryotic group: differentiated holdfast, radial cell division without intervening growth; taphonomy. In contrast, these features occur together in modern rhodophyte *Bangia*. Thus, either this population is a cyanobacterium with features convergent on *Bangia* and otherwise unknown for the clade – or the simpler explanation is correct: it is a red alga. Age is only indirectly known – thought to be ca. 1200 ma (give details)

III. Paleontological estimates of eukaryotic antiquity

A. The foregoing examples suggest that eukaryotes existed in mid-Proterozoic oceans. Other fossils support this interpretation:

1. Tappania
2. Satka
3. Valeria
4. Grypania/Horodyskia
5. Steranes

If eukaryotes diverged only 700-800 Ma (Cavalier Smith), then all of these interpretations must be in error, and numerous mid-Proterozoic prokaryotes possessed attributes that were subsequently lost and reevolved convergently by eukaryotes. If any one of them is correct, then eukaryotes existed in mid-Proterozoic oceans. We strongly support this second alternative.

B. Other fossils in > 1200 Ma rocks are less clear – large leiosphaerids, chuarids, and compressions.

C. Little fossil record of older eukaryotes; steranes (tread lightly here)

D. More evidence of eukaryotic divergence in younger Proterozoic rocks:

1. Xanthophytes > 1000 Ma
2. Lobose and filose amoebae in 750 Ma rocks
3. Green algae in 700-800 ma rocks.
4. Fungi in Proterozoic rocks?
   Discussion of Shaler "Tappania"and its relationship to older Tappania (I think it is weak)
   Tests -- microchemistry
5. Steranes
6. Oldest evidence of animals – 575-580 Ma; evidence of complex seaweeds in rocks of comparable age. Peterson and Butterfield ecology argument; complementary argument from biogeochemistry (redox conditions in ocean)

E. REDO ACRITARCH DIVERSITY CURVE and discuss succinctly.
F. Summarize systematic and ecological record

IV. A functional approach to the record (a la Hewitt)

A. Forget systematics for the nonce and concentrate on form, function, behavior, and development

i. Oldest evidence for cytoskeleton – Tappania?
ii. " " " multicellularity – Grypania?
iii. " " " behavior – Eosaccharomyces
iv. " " " cell fusion – "Tappania"
v. " " " tissues – Doushantuo reds and Ediacarans
vi. Other attributes

B. Discussion

V. Summary and conclusions

Figures:

1. Shuiyousphaeridium and attributes
2. Bangiomorpha and attributes
3. A plate of >1000 Ma eukaryotes: Tappania, Satka SEM, Valeria light (1640 Ma) and SEM, TEM on fossils, Grypania, Horodyskia, Eosaccharomyces, Trachyhystrichosphaeridium
4. A plate of Neoproterozoic fossils: Butterfield “Tappania”, Grand Canyon testate amoebae, Doushantuo acritarchs, red algal permineralizations, and compressions
5. History diagram showing time, main events/fossils, and acritrach diversity