



Proterozoic microfossils revealing the time of algal divergences

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Morphological and reproductive features and cell wall ultrastructure and biochemistry of Proterozoic acritarchs are used to determine their affinity to modern algae. The first appearance datum of these microbiota is traced to infer a minimum age of the divergence of the algal classes to which they may belong. The chronological appearance of microfossils that represent phycoma-like and zygotic cysts and vegetative cells and/or aplanospores, respectively interpreted as prasinophyceen and chlorophyceen microalgae, is related to the Viridiplantae phylogeny. These divergence times differ from molecular clock estimates, and the palaeontological evidence suggests that they are older.

The best examples of unicellular, organic-walled microfossils (acritarchs) from the Mesoproterozoic to Early Ordovician are reviewed to demonstrate features, which are indicative of their affinity to photosynthetic microalgae. The first indication that a microfossil may be algal is a decay- and acid-resistant cell wall, which reflects its biochemistry and ultrastructure, and probably indicates the ability to protect a resting/reproductive cyst. The biopolymers synthesized in the cell walls of algae and in land plants ("plant cells"), such as sporopollenin/algaeenan, are diagnostic for photosynthetic taxa and were inherited from early unicellular ancestors. These preservable cell walls are resistant to acetolysis, hydrolysis and acids, and show diagnostic ultrastructures such as the trilaminar sheath structure (TLS). "Plant cell" walls differ in terms of chemical compounds, which give high preservation potential, from fungal and animal cell walls. Fungal and animal cells are fossilized only by syngenetic permineralization, whereas "plant cells" are fossilized as body fossils more ubiquitously and without mineralization.

Microalgae radiated quickly in the Cambrian and Ordovician; however, several morphotypes with features related to the reproductive cycle occur in the Proterozoic, although they are not always recognized as such. The assignment of Proterozoic unicellular microfossils with resistant cell walls to specific eukaryotic groups is tentative. However, we argue that the new interpretations of their functional morphology, combined with cell wall ultrastructure and biochemistry, allow their assignment to microalgal classes. Microfossils with advanced ornamentation and ontogenetically formed excystment structures or endocysts, which prove that they are cysts in a complex life cycle with sexual reproduction, are related to the basal lineage of the Chlorophytes and the class Chlorophyceae. A cell wall ultrastructure with a TLS supports the affinity of some spheroidal taxa to the Chlorophytes.

The phylogeny of the Chlorophytes shows a sequence of branching nodes from a stem-group of the Viridiplantae that leads to the classes Prasinophyceae and Chlorophyceae, and then the Ulvophyceae. Based on a modern interpretation of the record, the timing of these nodes is deduced to be prior to c. 1650 Ma for the Prasinophyceae, c. 1450 Ma for the Chlorophyceae, and c. 950 Ma for the Ulvophyceae. The origin of the Chlorophytes, and in general the Viridiplantae, predates 1.8 Ga. These ages, based on microfossils, are earlier than the estimates based on molecular clocks.