Protist

PROTIST NEWS

Dating Algal Origin Using Molecular Clock Methods

Algae and plants are the dominant primary producers on our planet and define an evolutionarily diverse group of taxa (Graham and Wilcox 2000). Despite their importance, dating algal origin is frustrated by a limited fossil record (Knoll 1992). Recent molecular phylogenetic trees place algae near the

base of the eukaryotic tree of life (e.g., Baldauf et al. 2000, 2003; Nozaki et al. 2003). This suggests that endosymbiosis, the process that gave rise to algal plastids (Bhattacharya and Medlin 1995), was an ancient and fundamental force in eukaryotic evolution. To estimate the date of the cyanobacterial primary



4500 Age of Earth (earliest limit for clock calculations)

Figure 1. Schematic representation of plastid relationships and divergence times for the red, green, glaucophyte, and chromist algae. These photosynthetic groups are outgroup-rooted with the Opisthokonta that putatively ancestrally lack a plastid. The branches on which the cyanobacterial primary and red algal chromist secondary endosymbioses occurred are shown.

endosymbiosis that gave rise to the Plantae (i.e., red, green, and glaucophyte algae and land plants [Cavalier-Smith 1998]) and to date other important splits in the algal tree of life, we constructed a multigene phylogeny using six plastid genes from red, green, and chromist algae. These organellar genes were used as surrogate host markers because of strong evidence that the red and green algae share a monophyletic origin (e.g., Moreira et al. 2000). The origin of chromists that contain a plastid of secondary endosymbiotic origin was also studied under this framework because recent data are consistent with the single origin of the chlorophyll c-containing secondary plastid in chromists (Yoon et al. 2002; Harper and Keeling 2003), supporting the monophyly of these host cells. The plastid gene tree had robust bootstrap support and significant Bayesian posterior probabilities at all the critical nodes. Maximum likelihood methods, using the r8s program (Sanderson 2003), were used to estimate algal divergence times on the "best" tree and the credible tree set identified by Bayesian inference. This strategy incorporated uncertainty about the evolutionary model parameter estimates and the resulting branch lengths in the dating procedure. Our data (summarized schematically in Fig. 1) strongly support an ancient origin of photosynthetic eukaryotes with the split of red and green algae occurring about 1500 million years ago (Ma), the origin of the chromists about 1300 Ma, and the charophyte algae appearing by 800 Ma. The plastid primary endosymbiosis occurred at least 1600 Ma, before the split of the glaucophyte from the red plus green algae (Yoon et al. 2004). These dates are consistent with the Paleoproterozoic model of eukaryotic origin and provide a timeline for understanding algal evolution.

unit ribosomal RNA coding regions. J Phycol **31**: 489–498

Cavalier-Smith T (1998) A revised six-kingdom system of life. Biol Rev Camb Philos Soc 73: 203–266

Graham LD, Wilcox LW (2000) Algae. Prentice-Hall, Upper Saddle River, NJ

Harper JT, Keeling PJ (2003) Nucleus-encoded, plastid-targeted glyceraldehyde-3-phosphate dehydrogenase (GAPDH) indicates a single origin for chromalveolate plastids. Mol Biol Evol **20**: 1730–1735

Knoll AH (1992) The early evolution of eukaryotes: a geological perspective. Science **256**: 622–627

Moreira D, Le Guyader H, Philippe H (2000) The origin of red algae and the evolution of chloroplasts. Nature **405**: 69–72

Nozaki H, Matsuzaki M, Takahara M, Misumi O, Kuroiwa H, Hasegawa M, Shin IT, Kohara Y, Ogasawara N, Kuroiwa T (2003) The phylogenetic position of red algae revealed by multiple nuclear genes from mitochondria-containing eukaryotes and an alternative hypothesis on the origin of plastids. J Mol Evol 56: 485–497

Sanderson MJ (2003) r8s: Inferring absolute rates of molecular evolution and divergence times in the absence of a molecular clock. Bioinformatics 19: 301–302

Yoon HS, Hackett JD, Pinto G, Bhattacharya D (2002) The single ancient origin of chromist plastids. Proc Natl Acad Sci USA **99**: 15507–15512

Yoon HS, Hackett J, Ciniglia C, Pinto G, Bhattacharya D (2004) A molecular timeline for the origin of photosynthetic eukaryotes. Mol Biol Evol 21: in press

References

Baldauf SL (2003) The deep roots of eukaryotes. Science 300: 1703–1706

Baldauf SL, Roger AJ, Wenk-Siefert I, Doolittle WF (2000) A kingdom-level phylogeny of eukaryotes based on combined protein data. Science **290**: 972–977

Bhattacharya D, Medlin L (1995) The phylogeny of plastids: A review based on comparisons of small-sub-

Debashish Bhattacharya^{a,1} and Linda K. Medlin^b

^a Department of Biological Sciences and Center for Comparative Genomics, University of Iowa, 210 Biology Building, Iowa City, IA 52242-1324, USA ^b Alfred Wegener Institute, Am Handelshafen 12, D-27570 Bremerhaven, Germany

> ¹ Corresponding author; fax 1 319 335-1069 e-mail dbhattac@blue.weeg.uiowa.edu