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**USING PHYLOGENY TO INVESTIGATE THE HISTORY OF MORPHOLOGICAL  
EVOLUTION IN HETEROSPOROUS FERNS**

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**ABSTRACT:** Throughout the evolutionary history of plants on land there have been repeated re-invasions of aquatic environments by terrestrial plants from distantly related groups. In order to survive these very different physical conditions, these plants have had to dramatically modify their vegetative, reproductive, and dispersal systems. Few living ferns are aquatic, most are terrestrial and homosporous. The exceptions are heterosporous ferns, with morphologically distinct spores producing unisexual gametophytes. Heterosporous ferns are monophyletic and comprise two extant families, the semi-aquatic Marsileaceae and the aquatic Salviniaceae. Except for very recent interest in the relationships among the five extant heterosporous genera, these ferns have been largely ignored in systematic studies and infrageneric relationships are virtually unknown. Similarly, our knowledge of the history of the morphological character evolution that accompanied the transition of these ferns to their aquatic environments is limited. Heterosporous ferns are relative newcomers that diversified during the Cretaceous, at the same time as flowering plants, and the fossil record has preserved a rich history of these ferns, mostly in the form of microfossils with a remarkable diversity of ornamented spores. Together we are reconstructing a comprehensive phylogeny for the heterosporous aquatic ferns. Our study will be among the first to include both living and fossil members of a group, incorporating data from multiple genes, morphology, and developmental studies for the living taxa, and integrating ultrastructural morphological data from fossil taxa. Understanding the history of character evolution in these ferns requires integration of fossil taxa, necessarily using morphology pertinent to the spores. Understanding the development and structure of the spore wall, primarily through electron microscopy, is critical to this project because the character-rich spore wall is well preserved in fossils and will permit fossil taxa to be integrated into the phylogeny. We hope to understand better the morphological character state transitions associated with the ecological specialization of these ferns to aquatic habitats.

**RATE HETEROGENEITY AMONG LINEAGES OF TRACHEOPHYTES:  
INTEGRATION OF MOLECULAR AND FOSSIL DATA AND EVIDENCE FOR  
MOLECULAR LIVING FOSSILS**

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**ABSTRACT:** Many efforts to date evolutionary divergences using a molecular clock have yielded age estimates that are grossly inconsistent with the paleontological evidence. Such discrepancies are often attributed to the inadequacy of the fossil record, but many potential sources of error can affect molecular-based estimates. In this study, we minimize the potential error due to inaccurate topology and uncertain calibration times by using a well-supported tree, multiple genes, and multiple well-substantiated dates to explore the correspondence between the

fossil record and molecular-based age estimates for major clades of tracheophytes. Age estimates varied due to gene effects, codon position, lineage effects, method of inferring branch lengths, and whether or not rate constancy was assumed. However, even methods designed to ameliorate the effects of rate heterogeneity among lineages could not accommodate the substantially slower rates observed in *Marattia* + *Angiopteris* and in the tree ferns. Both of these clades of ferns have undergone dramatic decelerations in their rates of molecular evolution and are "molecular living fossils", consistent with their relative morphological stasis for the past 165-200 million years. Similar discrepancies between the fossil record and molecular-based age estimates noted in other studies may also be explained in part by violations of rate constancy among lineages.

## **THE ROOT OF THE ANGIOSPERMS REVISITED**

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**ABSTRACT:** Most recent phylogenetic analyses of basal angiosperms have converged upon the placement of Amborella as sister to all other extant angiosperms. However, certain recent studies suggested that Amborella and Nymphaeales (water lilies) form a clade sister to all remaining angiosperms or that Nymphaeales alone are the sister to the remaining angiosperms. We report here (i) maximum parsimony, maximum likelihood, and Bayesian phylogenetic analyses of 11 genes (> 15,000bp/taxon) for 16 taxa, (ii) maximum parsimony analysis for a subset of these genes for 104 taxa, and (iii) tests of alternative rootings using the non-parametric bootstrap and the likelihood ratio test using the parametric bootstrap. In addition, we use simulation analyses to examine the amount of bias that may be present in our methods of phylogeny estimation. Amborella continues to receive strong bootstrap support as the sister to all other extant angiosperms, and three of four tests reject alternative hypotheses of the angiosperm root. Although we cannot conclusively choose between Amborella vs. Amborella + Nymphaeales as sister to all other angiosperms, most analyses favor the former rooting.

## **COMBINING FAST EVOLVING CHLOROPLAST DNA SEQUENCES FOR PHYLOGENETIC ANALYSIS IN BASAL ANGIOSPERMS**

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**ABSTRACT:** Our understanding of flowering plant phylogeny has been enhanced considerably by recent information from gene sequences. A number of plastid, nuclear and mitochondrial genes have been used in deep level phylogenetic reconstruction. Emphasis has been placed on using slow evolving genes with the notion that levels of homoplasy will be kept at a minimum. We have been exploring the potential contribution of the plastid *matK* gene and the noncoding parts of the *trnT-F*-region, both evolving at higher rates than other genes used in angiosperm phylogenetic reconstruction. These two regions provide robust phylogenies for basal angiosperms that are congruent with each other and with recent angiosperm phylogenies based on combined data of gene sequences from the plastid and nuclear or from all three genomes (Soltis et al., 2000, Qiu et al., 1999, 2000). Analysis of the combined *matK* and *trnT-F* data sets resulted in a single most parsimonious tree. Statistical support for the majority of nodes

substantially increased compared to previous analyses. The results of the present study point to the effectiveness of fast evolving DNA regions in providing strong historical signals that can recover a reliable and robust phylogeny for angiosperms.

## **FAGALES OVERVIEW**

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## **PHYLOGENETIC ANALYSES OF FAGALES BASED ON MULTIPLE DNA SEQUENCES FROM THREE GENOMES**

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**ABSTRACT:** Nucleotide sequences of five genes and one DNA region from three genomes were used to analyze the inter- and infra-familial relationships of Fagales. All 31 genera (excluding *Ceuthostoma*) were sampled representing eight families of the order. The parsimonious analyses of combined data set strongly supported the three major clades in the Fagales, i.e., *Nothofagus*, Fagaceae and core "higher" hamamelids as recognized by Manos and Steele (1997). *Nothofagus* is sister to all the other Fagales, and Fagaceae is sister to the core "higher" hamamelids. Two main subclades were resolved in the core "higher" hamamelids by the combined analysis, one being Myricaceae (Rhoipteleaceae (Juglandaceae)), the other Casuarinaceae (Ticodendraceae (Betulaceae)). The latter subclade is strongly supported, while the former is moderately supported although the positions of Myricaceae are quite different in each single-gene trees. Fagaceae, Betulaceae and Juglandaceae form their own clade with 100% bootstrap support, respectively.

Keywords: Fagales, "higher" hamamelids, Myricaceae, phylogeny, combined analysis

## **ESTIMATING TIME DIVERGENCE IN THE BIRCH FAMILY (BETULACEAE): RATE HETEROGENEITY, MULTIPLE CALIBRATION POINTS AND STEM LINEAGE-CROWN GROUP INTERVAL**

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**ABSTRACT:** We present a phylogenetic analysis of the Betulaceae including at least one species of each subgeneric division (26 taxa) of the six genera (*Betula*, *Alnus*, *Carpinus*, *Corylus*, *Ostrya*, *Ostryopsis*). Parsimony analyses based on ribosomal DNA sequences of 5S gene spacers and ITS supported the monophyly of the subfamilies and all genera. Likelihood ratio tests showed rate heterogeneity across lineages, therefore we made the phylogenetic trees ultra-metric by transforming ML and MP branch lengths (HKY85 + gamma model of DNA evolution) using the non-parametric rate smoothing method of Sanderson. We estimated divergence times within the family using one of the six most parsimonious trees and eight calibration points from the extensive fossil record of Betulaceae. To assess the problem of using dates for stem lineages or crown groups in the calibration procedure, we calculated age estimates by placing each fossil on the stem lineage node and crown group node, creating an interval. The median value of those estimates was determined for each node. According to these results, the ages of the crown groups

of the Betulaceae and subfamilies Coryloideae and Betuloideae are 97.7 Ma, 57.6 Ma and 89.8 Ma respectively. Taking into account the error estimates, these ages are similar to those inferred from the fossil record. Deceleration of rates of molecular evolution is observed in certain clades of the Betulaceae.

## **FUNCTIONAL FIELD ECOLOGY OF AMBORELLA AND ITA PLANTS**

Taylor Feild

## **PALEOBOTANICAL DATA AND THE PALEOBIOLOGY DATABASE INITIATIVE**

Hallie J. Sims

**ABSTRACT:** The Paleobotany Working Group (part of the Paleobiology Database; see <http://www.paleodb.org/>) has begun a project to compile locality-based occurrence data for Phanerozoic land plant localities, using a web-based, relational database. The database is structured around four tables: references, collections, occurrences, and taxa. Each collection record has the geographic coordinates and geologic age of the site, lithologic and paleoenvironmental context, and taphonomic modification of the remains. This is linked with a list or lists of taxon occurrences (and abundance data where available), including which plant parts are present. Taxonomic names are being linked to tables that allow taxonomic usage to be updated and plant parts to be associated, recording the opinions of different workers. Data are drawn from the primary literature, museum collections, and unpublished field work, and every datum entered is associated with a reference and an enterer. As a group of specialists (currently fifteen members), we are updating stratigraphic information and building a table of valid species, genera, and their synonyms. By making the data publicly available as a web-searchable database, the paleobotanical community will be invited (and perhaps incited?) to identify omissions and errors. The group has several scientific goals, including producing a sampling standardized plant diversity curve, assessing changes in within-community diversity over time, and exploring trends in morphological evolution. However, the lists of valid taxa and occurrence lists from well-constrained localities, vetted by specialists, can form building blocks for a wide range of research projects. We hope that this initiative will gain momentum within the community to maintain and contribute to a public repository of high-quality paleobotanical data.

## **MORPHOBANK**

Maureen O'Leary