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the **TIMETREE** *of* **LIFE**

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foreword by James D. Watson

Gymnosperms

Susanne Renner

Department of Biology, Menzingerstr. 67, University of Munich, Munich, Germany (renner@lrz.uni-muenchen.de)

Abstract

Gymnosperms (~1010 sp.) are grouped into four taxa: Coniferophyta, Cycadophyta, Ginkgophyta, and Gnetophyta. Most molecular phylogenetic analyses support the monophyly of extant gymnosperms, although relationships of the groups are not resolved. Some analyses place the root of gymnosperms between cycads and the remaining groups, while others place it between a cycad-Ginkgo clade and a conifer-gnetophyte clade. A nesting of gnetophytes inside conifers, closest to Pinaceae, is supported by some molecular analyses, but contradicted by others and morphological data. Most major gymnosperm lineages are extinct, and the abundant fossil record has not yet been well-integrated with molecular time estimates.

Gymnosperms, also called Acrogymnospermae (*1*), are a group of seed-bearing plants (spermatophytes) with ovules on the edge or blade of an open sporophyll or ovuliferous scale (Fig. 1). Their closest extant relatives are the angiosperms, which have ovules enclosed in a carpel. Gymnospermae is a problematic name because, when fossils are included as is usually the case, the name is widely understood to apply to a paraphyletic group of seed plants from which the angiosperms also arose (*1*). There are just over a 1000 living species of gymnosperms in the taxa Cycadophyta, Ginkgophyta, Coniferophyta, and Gnetophyta. Here, the relationships and divergence times of families in these phyla are reviewed.

The conifers, Coniferophyta, include ~630 species in seven families of which Pinaceae is by far the largest and most widespread (12 genera, 225 species) (*2*). Araucariaceae (three genera, about 35 species) mostly occur in the tropics and subtropics, and are absent from Africa. Cephalotaxaceae (two genera, 10–12 species) are confined to Asia; Cupressaceae (including Taxodiaceae, 31 genera, 173 species) occur in mesic habitats worldwide; Podocarpaceae (including Phyllocladaceae and Nageiaceae, 17–19 genera, 180 species) occur mostly in the Southern Hemisphere; Sciadopityaceae comprise a single

species in the mountains of Japan; and Taxaceae (4–5 genera, 20–25 species) are again widespread, although nowhere abundant. The cycads, Cycadophyta, contain c. 300 species in the Families Cycadaceae (one genus, 97 species), Stangeriaceae (two genera, three species), and Zamiaceae (eight genera, 200 species) (*3*). Ginkgophyta contain only *Ginkgo biloba*, while Gnetophyta comprise three genera with together 80 species, *Ephedra* (50 species), *Gnetum* (30–35 species), and *Welwitschia* (one species).

Molecular phylogenetic evidence for the close relationship between gymnosperms and angiosperms is strong. A study of seven genes (from the chloroplast, mitochondrial, and nuclear genome), with a sampling of 18 gymnosperms, 19 angiosperms, and numerous other landplants (192 species total), yielded maximum likelihood (ML) bootstrap values of 87% and 100%, respectively, for the monophyly of gymnosperms and angiosperms (*4*). With



Fig. 1 Female strobili of a gymnosperm (*Pinus sylvestris*) Credit: R. B. Zimmer.

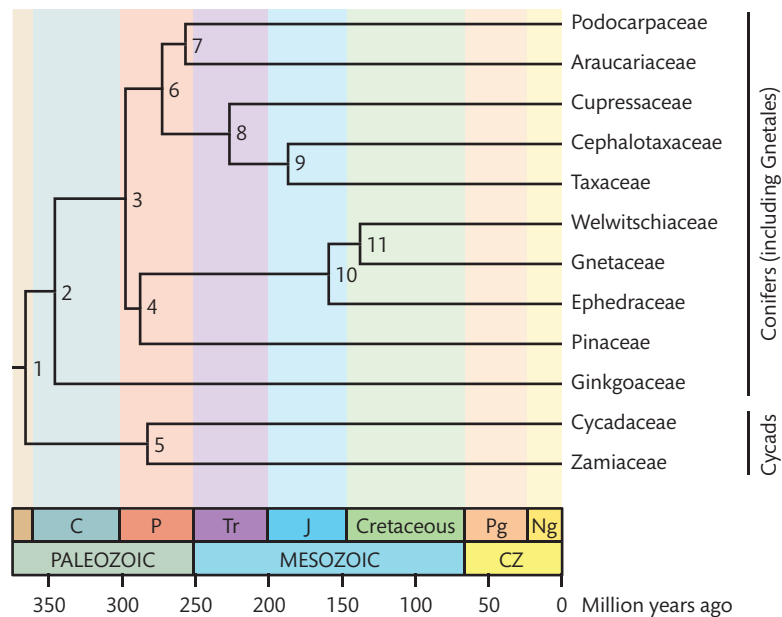


Fig. 2 A timetree of gymnosperms. Divergence times are shown in Table 1. *Abbreviations:* C (Carboniferous), CZ (Cenozoic), J (Jurassic), Ng (Neogene), P (Permian), Pg (Paleogene), and Tr (Triassic).

12 genes (from all three genomes) and 23 exemplars (10 of them gymnosperms), and with nine genes (from the three genomes) and 12 exemplars (nine of them gymnosperms), the mutual monophyly of gymnosperms and angiosperms had 100% ML bootstrap support (5, 6). A parsimony analysis of 42 genes (from the three genomes) plus morphological data for seven land plants (four of them gymnosperms) yielded a support of, respectively, 97% and 100% for gymnosperms and angiosperms (7), and a Bayesian analysis of 56 chloroplast genes from 36 exemplars (five of them gymnosperms) yielded posterior probabilities of 1.0 for mutual monophyly angiosperms and gymnosperms (8).

While extant gymnosperms thus appear monophyletic, the relative positions of cycads, *Ginkgo*, and gnetophytes remain unresolved. Most recent analyses place the deepest split between cycads and all remaining clades (4–7), but the 56-gene study placed cycads as closest to *Ginkgo* (8). The placement of gnetophytes as closest to Pinaceae and thus embedded in conifers is still weakly supported (4–6, 8).

Morphological cladistic analyses (e.g., of 102 informative characters for 48 taxa, 25 extinct and 23 partly extant; 10) usually yield the so-called anthophyte topology (cycads (*Ginkgo* (conifers (gnetophytes, angiosperms)))), in contradiction to the DNA-based studies (for reviews of the contradictory results, see 5, 10, 11). Contradictions

probably arise from the inclusion of fossil taxa in morphological studies; there are many more extinct gymnosperm lineages than living ones. With fossils included, gnetophytes often group with Bennettitales, *Pentoxylon*, *Caytonia*, and angiosperms (10–16). However, trees that are a few steps longer place gnetophytes in conifers (11) or in a clade with living and extinct conifers and *Ginkgo* (10, 16).

The absence of a solid gymnosperm phylogeny almost certainly is the reason that no study has focused on deep divergence times in this clade, in spite of the generally good fossil record of woods and cones that might be used for calibration. Whether the true topology is (cycads (*Ginkgo* (conifers including gnetophytes)), ((cycads, *Ginkgo*)(conifers, gnetophytes)), or the anthophyte topology will affect molecular dating to a larger or smaller degree depending on the node of interest. For example, in a study focusing on divergence times in the gnetophyte genus *Gnetum* (17) estimates for the ingroup barely differed with either of four alternative seed plant topologies (the approach used was a Bayesian relaxed molecular clock approach with ancestor-descendent correlated rates).

Table 1 summarizes molecular divergence time estimates among gymnosperms and Fig. 2 presents a timetree. The age of the root node, that is, the split between extant angiosperms and gymnosperms has not been the

Table 1. Divergence times (Ma) and their confidence/credibility intervals (CI) among gymnosperms, from ref (17).

Node	Timetree	
	Time	CI
1	366	382–344
2	346	369–319
3	298	324–270
4	288	316–258
5	283	307–271
6	273	303–243
7	257	287–228
8	227	265–189
9	187	231–144
10	159	196–132
11	138	175–112

Note: Time estimates are based on *rbcl* and *matK* genetic distances analyzed with a Bayesian autocorrelated rates approach. The matrix included angiosperms and was rooted on the fern *Psilotum*. The unconstrained topology resulting from ML analysis of these data shows gnetophytes as the closest relative of all remaining seed plants. A conifer family not represented here, Sciadopityaceae, branches off below Cupressaceae + Taxaceae (4).

focus of any study. The oldest seed precursors are 385 Ma (18). These early seeds, which have lobed integuments that are thought to reflect their origin from fused sterile telomes, are quite different from the seeds of “modern” seed plants. Modern seeds with completely fused integuments are not known until the late Mississippian (~325 Ma; J. Doyle, personal communication, July 2005). Modern seed plants thus arose 385–325 Ma.

Divergence time estimates for the deepest splits in extant conifers require much larger gene and taxon sampling than currently available. Conifers are documented from the middle Pennsylvanian (~310 Ma), and Cordaitales, which are probably basal stem relatives of conifers that existed in the earliest Pennsylvanian (~318 Ma). The deepest split among extant cycadophytes, should be at least 270 Ma, based on *Crossozamia* from the early Permian, which is similar to modern cycads (19). The *rbcl*-based estimate of 92.5 Ma for the split between Cycadaceae and Zamiaceae (20) is almost certainly an underestimate.

The oldest Pinaceae-type cones are 225 Ma (21), and early Tertiary fossils are often assigned to extant genera of Pinaceae (22). Very young divergence time estimates within Pinaceae (23, 24) are probably unreliable because of miscalibration (25).

The split between Araucariaceae and Podocarpaceae may be at least 160 Ma based on Middle Jurassic Araucariaceae cones from Argentina; probable stem relatives of Podocarpaceae (*Rissikia*) date to the Triassic (J. Doyle, personal communication, July 2005). The oldest fossils of modern Araucariaceae are Albian (112–100 Ma) pollen grains that resemble those of *Wollemia* (26), the closest relative of *Agathis*. An age of 89 Ma from slightly younger pollen was used as the root constraint in a study of within-*Agathis* divergence times (27). The divergence between Cupressaceae and the Taxaceae/Cephalotaxaceae clade has been dated to 227 Ma (Table 1) and that between Taxaceae and Cephalotaxaceae to 187 (Table 1) or 230–192 Ma (28). The divergence of extant Ephedraceae from the remaining gnetophytes is estimated at 159 Ma old; the oldest *Ephedra* seeds are Barremian–Albian (29, 30). The split between extant Welwitschiaceae and Gnetaceae may date back to 138 Ma ago (Table 1); the earliest fossils of *Welwitschia* are 110 Ma old (31).

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