Metasequoia: An Overview of Its Phylogeny, Reproductive Biology, and Ecotypic Variation

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Dawn redwood *Metasequoia glyptostroboides*

Coast redwood *Sequoia sempervirens*

The discovery of the dawn redwood sparked renewed interest in the relationship between two important families, Cupressaceae (well-known genera include *Chamaecyparis, Cupressus, Juniperus, Thuja, Calocedrus*) and what used to be called Taxodiaceae *(Cryptomeria, Cunninghamia, Glyptostrobus, Metasequoia, Sciadopitys, Sequoia, Sequoiadendron, Taiwania, Taxodium). M. glyptostroboides* is similar to Cupressaceae in the opposite arrangement of the vegetative and floral organs, whereas the pollen and wood anatomy of *M. glyptostroboides* are most similar to members of Taxodiaceae. It was on the basis of these morphological peculiarities that *Metasequoia* was placed in its own family—Metasequoiaceae (Hu and Cheng 1948). However, this placement was never widely accepted; taxonomists have traditionally classified it within Taxodiaceae. Based on recent phylogenetic studies, many now combine Taxodiaceae with Cupressaceae under the latter name.

Initially, many botanists believed *Metasequoia* to be closely allied with four genera, three of which consist of a single species: *Sequoia sempervirens* (California redwood, endemic to the California coast), *Sequoiadendron giganteum* (giant sequoia, endemic to the Sierra Nevada mountains of California), *Glyptostrobus pensilis* (the water pine, endemic to the south coast of China), and *Taxodium* (the bald cypress), which has two species, *T. distichum*, of the southeastern United States, and *T. mucronatum*, which is scattered throughout Mexico.

In a study of the chromosomal and morphological characteristics of these five genera, G. L. Stebbins (1948) concluded that *Glyptostrobus* and *Taxodium* resemble each other more than either resembles *Sequoia, Sequoiadendron,* or

Metasequoia. Among the last three genera, he concluded that if only vegetative characteristics (notably, leaf arrangement and nondeciduousness) are considered, the two North American genera are more closely allied, but that on the basis of number of chromosomes, the giant sequoia is more similar to the dawn redwood than to the coast redwood.

In more recent research—an examination of DNA sequences in the chloroplast *rbc*L gene conducted in 1994 by Brunsfeld and co-authors—all three genera were found to be closely related, but the authors concluded that the closest relationship is between *Sequoia* and *Sequoiadendron*. Their conclusions are supported by other lines of evidence, including the karyotypic similarities found by Schlarbaum and Tsuchiya in 1984; the 1989 immunological analysis of Price and Lowenstein; and cladistic analyses of morphological, anatomical, and chemical traits conducted by Yu in 1996.

Giant redwood *Sequoiadendron giganteum*

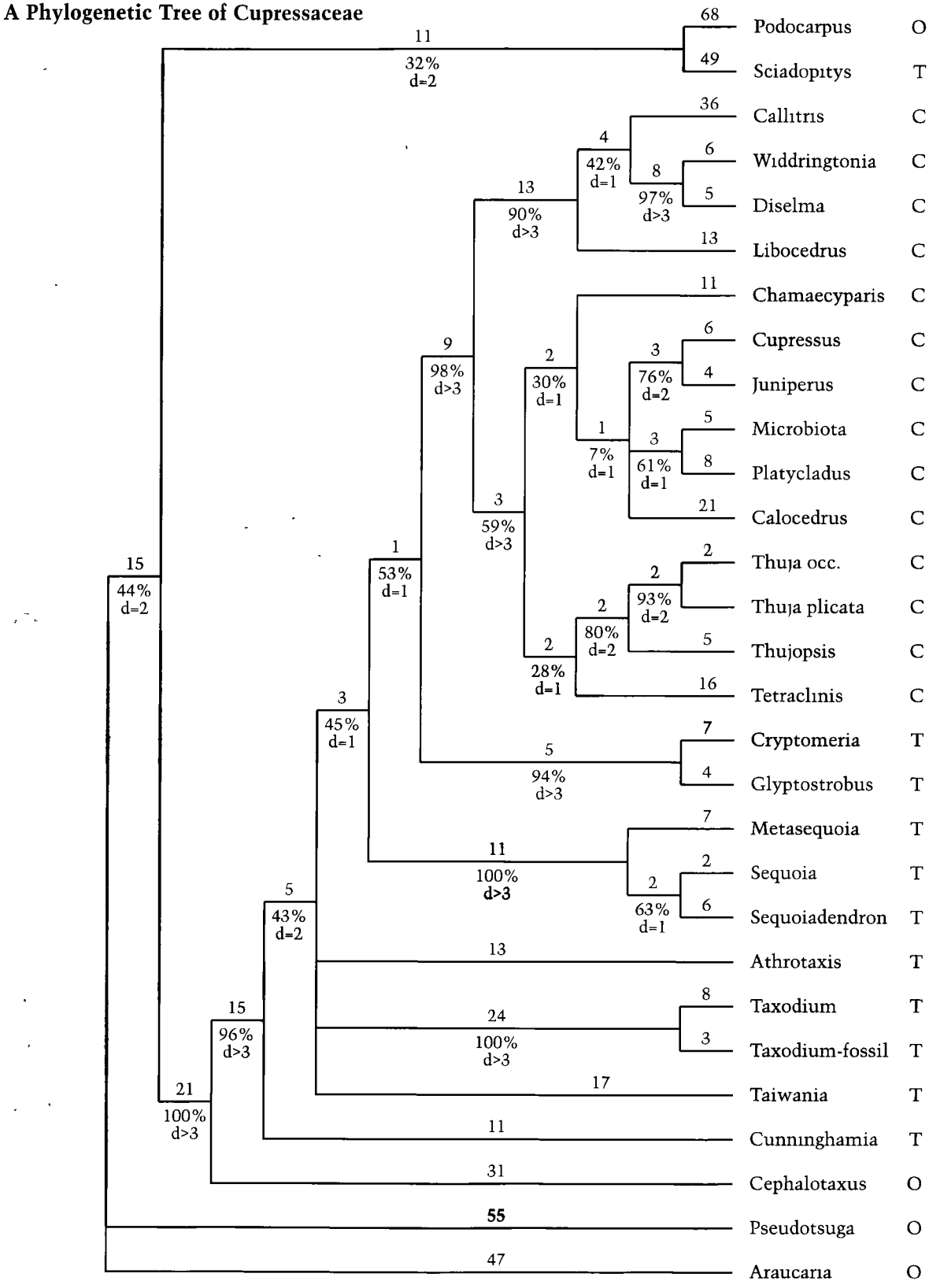
Reproductive Biology

Metasequoia is monoecious (with both female and male cones on the same plant). The male cones appear in mid-June, the female in early July.

Table 1. Comparison of Some Morphological Characters

	Metasequoia	*Sequoia*	*Sequoiadendron*
Deciduousness	yes	no	no
Leaf arrangement	opposite or decussate	alternate or spiral	alternate or spiral
Leaf shape	linear	needle and scale	scale
Number of microsporangia	3	3	3
Ovule orientation	anatropous	anatropous	anatropous
Seed wing	lateral	lateral	lateral
Seed scale	wide	wide	wide
Cotyledon number	2	2	6
Chromosome number (2n)	22	66	22

A Phylogenetic Tree of Cupressaceae



Pollen forms in November and is carried to the female cone by the wind in early spring of the following year. Fertilization occurs in June; the embryo matures in October or November.

Seed production is low, for several reasons. In the wild, a dawn redwood tree does not produce

Developing cones of Metasequoia glyptostroboides. *Left, female cones; male cone at right.*

A branch of Metasequoia *with young female cones*

Female Metasequoia *cones*

This cladogram, or phylogenetic tree, is taken from Brunsfeld and co-authors (1994); it represents their interpretation of the phylogenetic relationships within a plant family. "T" denotes genera traditionally placed in Taxodiaceae and"C," Cupressaceae, "O" stands for outgroup, genera outside the family that are close relatives of the ingroup and which are included in order to "root" the tree.

The numbers above the branches on the tree indicate the numbers of changes in nucleotide—the building blocks of DNA—composition in the gene that Brunsfeld and his co-workers studied. These changes occurred during the evolution of the now-extinct ancestors that are represented by the branch, the lower the number, the closer the relationship.

However, quantity does not always convert to quality, and the percentages given below the branches indicate the results of a test applied to the data to see just how strongly the evidence supports each branch of the tree. The closer the figure is to 100 percent, the better supported a branch is; figures much below 70 percent suggest at most only moderate support.

Branches in phylogenetic trees are usually paired. Sometimes, however, as with Taiwania, Taxodium, *and* Athrotaxis, *several branches arise together, and that probably means that the particular gene studied did not provide enough data to convert this part of the cladogram into its normal bifurcating condition.*

If we read the tree from the "root" up, within Cupressaceae (defined as including Taxodiaceae), Cunninghamia *is the "basal offshoot"; the other genera (excepting* Sciadopitys, *which many taxonomists place in its own family) are all part of a "clade," or lineage, that comprises the rest of the family. Within this large clade,* Metasequoia *and the even more closely related* Sequoia *and* Sequoiadendron *form a small clade (the Metasequoia clade), as do* Glyptostrobus *and* Cryptomeria *(the Glyptostrobus clade). The Glytostrobus clade and the clade of traditional Cupressaceae (C) share a common ancestor (the node connecting the two clades); thus, they are more closely related to each other than either is to the Metasequoia clade The phylogenetic tree, therefore, suggests that traditional Cupressaceae originated within Taxodiaceae.*

The authors also point out that because Metasequoia *is closely allied to the nondeciduous* Sequoia *and* Sequoiadendron *and because the three deciduous genera—*Metasequoia, Glyptostrobus, *and* Taxodium*—lack close affinities, the deciduous habit may have evolved as many as three separate times in the Taxodiaceae.*

fertile male cones—nor, therefore, viable seeds—for twenty-five or thirty years. The extreme humidity and high rainfall in the habitat of the native *Metasequoia* during the pollination period may affect pollen transport and/or prevent the female cones from opening to accept the pollen. As a consequence, on plantations artificial pollination is often used to increase seed production.

Ecotypic Variation

The largest natural populations of the dawn redwood are limited to small valleys within an area of about 600 square kilometers (235 square miles) in western Hubei Province. Albeit small, these valleys include a variety of microhabitats, in which dawn redwoods of different types have developed. Local researchers, after years of intensive observation, have recognized three

Table 2. Traits of the Three Ecotypic Variations of Dawn Redwood

Ecological type	*Large cone*	*Medium cone*	*Small cone*
Cone size (cm)	2.2 x 2.0	2.0 x 1.8	1.5 x 1.4
Number of seeds per 500 grams	128	161	280
Number of seeds per cone	106	85	62
Seed size (cm)	0.6 x 0.5	0.53 x 0.48	0.48 x 0.42
Weight per 1,000 seeds (grams)	2.96	2.84	2.4
Seed germination rate (%)	**15**	**21**	**18**
Branch angle	>90	medium	<50
Branch distribution	sparse	medium	dense
Branch canopy	wide	medium	narrow
Leaf density	low	medium	high
Leaf color	yellowish green	green	dark green
Stem furrows	distinct	very distinct	indistinct
Bark color	gray	brownish gray	brown
Bark thickness	thick	medium	**thin**
Ecological preference	mountain slope drought-tolerant	wide; medium drought-tolerant	ditch or creek drought-intolerant
Growth rate	fast	medium	slow

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variations based on the size of their cones, large, medium, and small. The large-cone type tends to grow on mountain slopes. Compared to the other types, it resists drought better and develops a broader canopy, making it the preferred choice for use as a street tree. It also surpasses the others in seed production, a quality useful for plantations. At the other end of the spectrum, the small-cone type grows along streambanks. It tolerates drought less well, but develops a more uniform trunk and is therefore the type of choice for construction timber.

The delineation of these variations is based solely on morphological observations; further study is needed to determine whether they are genetically different. Assessment of the correlation between genetic and ecotypic variations should provide a basis for horticultural and economic selections. Allozyme research has revealed genetic variation in wild dawn redwoods, but studies have not addressed genetic structure associated with ecotypic variations.

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Acknowledgments

The author is grateful to Karen Madsen for her great efforts in making the article more readable and to Dr. Peter Del Tredici for constructive suggestions.

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