

## *h2* Angiosperms appear < no affinity to gymnosperms >

“Are you going to tell me,” said Arthur, “that I shouldn’t have green salad?”

“Well,” said the animal, “I know many vegetables that are very clear on that point. Which is why it was eventually decided to cut through the whole tangled problem and breed an animal that actually wanted to be eaten and was capable of saying so clearly and distinctly. And here I am.”

It managed a very slight bow.

—Douglas Adams, *The Restaurant at the end of the Universe*.<sup>1</sup>

Flowering plants, Division Anthophyta (Gk. *anthe*, flower; *phyto*, plant) (Magnoliophyta or Angiospermae), characteristically have seeds enclosed within a fruit of some sort. Their spectacular (pun intended) diversity (about 250,000 species are extant) is inferred to be due to a mindless, sometimes collaborative, sometimes antagonistic, coevolution with animals. As to this, they evolve chemicals which variously attract pollinators and repel pests. Virginia Walcott cites “6000 species of hispine leaf beetles [that] feed on the ginger family alone.” Armanda Tromans gives the example of maize that “releases a cocktail of volatile indole and terpenoid compounds when attacked by the beet armyworm caterpillar (*Spodoptera exigua*). These compounds attract a parasitic wasp, which deposits its eggs in the caterpillar; the wasp larvae then devour the caterpillar.”

Familiar staple food crops as wheat, rice, and maize, and valuable horticultural plants as daffodils, orchids, and lilies, are monocots. Molecular and morphological analyses indicate that monocots (class Liliopsida, with seeds, each with one cotyledon, meaning “embryonic leaf”), are an ancient offshoot from primitive dicots (class Magnoliopsida, with seeds, each with two cotyledons), familiar as peas, beans, peanuts, tomatoes, daisies, apples, and magnolia. These “obvious” leaf distinctions shown by sprouts were made circa 370 BC in a first systematic botany by Aristotle’s pupil Theophrastus, then by John Ray in *Methodus Plantarum Nova*, 1682, (terms “petal” and “pollen” appear in it)<sup>2</sup> and, formally, by taxonomist Antoine Laurent de Jussieu in *Genera Plantarum*, 1789.<sup>3</sup>

Darwin in 1879 in a letter to Hooker called the sudden appearance of angiosperms (about 200 million years ago) in the (very incomplete then) fossil record, an “abominable mystery.”<sup>4</sup> To update the much worked over angiosperm phylogeny that includes such highly evolved oddities as bacteria-sized *Wolffia*, and to zero in on angiosperm origin, Pamela Soltis, Douglas Soltis and Yin-Long Qiu in 2000 compared selected genes in the chloroplasts, mitochondria, and cell nuclei of more than a hundred diverse living flowering species. *Amborella*, a little-known flowering shrub (small, greenish-yellow flowers and red fruit), which grows wild only on the South Pacific island of New Caledonia, turns out to be the least derived (a living fossil); water lilies next, and then a group with star anise.<sup>5</sup>

The flowering plants are evolved from nonflowering predecessors, as persist today as pine trees and related plants (and not from magnolia- or waterlily-like plants once regarded to be ancestor candidates for their lack of many advanced features).

Most flowers consist of concentric whorls of: sepals in the first whorl, petals in the second whorl, stamens in the third whorl, and carpels in the fourth whorl. How the four types of floral organs develop from what would otherwise be leaves, is not fully understood. However, genetic studies using floral homeotic mutants have led to the ABC model of flower development in which: class A genes specify sepals, class A and B genes specify petals, class B and C genes specify stamens, and class C genes specify carpels.<sup>6</sup> The subtleties are still being worked through but, for our purposes, whereas the structural difference between the flowering plants and non-flowering plants is small, the result for evolution was enormous.<sup>7</sup>

The earliest known angiosperm fossils are in freshwater Cretaceous sediments that record climates as widely different as, then, polar southeastern Australia, and subtropical to tropical New Jersey.

In their cold climate (Australia) first appearance, flowering plants were a minor component of Cretaceous flora (now lignites and coals in which they are identified by a sprinkling of their different pollens). Because the tilt of Earth's axis varies little (courtesy of orbiting, heavy, Moon),<sup>8</sup> high latitudes have always been subject to winter nights that last for weeks and, near the pole, for months. Nevertheless, according to Robert T. Gregory, a temperate paleoclimate is indicated by the ratio oxygen-18 / oxygen-16 trapped in Cretaceous sediments for southeastern Australia (then inside the Antarctic Circle).<sup>9</sup> Then this area supported conifers (pines), ginkgos, ferns, cycads, bryophytes, and horsetails. Of these, the evergreens had thick cuticles and other structural features that indicate adaptation to cold or dryness (perhaps brought on by winter freezing). The abundance of ferns and bryophytes indicate that all the seasons (except perhaps winter) were moist. The deciduous plants (ginkgos) seem to have shed leaves by mass (all at once) falls brought on by winter cold or darkness.

In their warm climate (New Jersey) first appearance, whole fossil flowers have been obtained from fluvial sediments of the Turonian Raritan fm, Upper Cretaceous stage. Exquisite preservation of floral morphology, and the often perfect retention of cell-by-cell anatomical details of these, approximately 90 million year old angiosperms, allows exacting comparison with modern flowers. Some 100 species have been described, inclusive of dicotyledonous flowers and fruits, and the earliest known monocotyledonous flowers. Together, the paleoflora (flowers, pollen, various leaves and reproductive structures of conifers and fern vegetative and reproductive structures) indicate a subtropical to tropical paleoclimate.

Lower Cretaceous (Aptian stage and older Barremian stage) assemblages of flowers, fruits and seeds, from Vale de Agua, Buarcos, Catefica, Famalicão, and Torres Vedras, Portugal, sort into some 150 angiosperm taxa, most (85 %) of which are either plants at the magnoliid grade or are monocots. In these oldest sediments known to contain angiosperm flowers, the discovery of fossil water lilies (Nymphaeales) (these are tiny), supports the early diverging position of magnoliid families, indicated by molecular phylogenetic analyses of extant angiosperms.<sup>3</sup> □

Figure h3.1<sup>10</sup> Linnaeus's key to the sexual system for the classification of plants.

