PERSPECTIVES: BOTANY

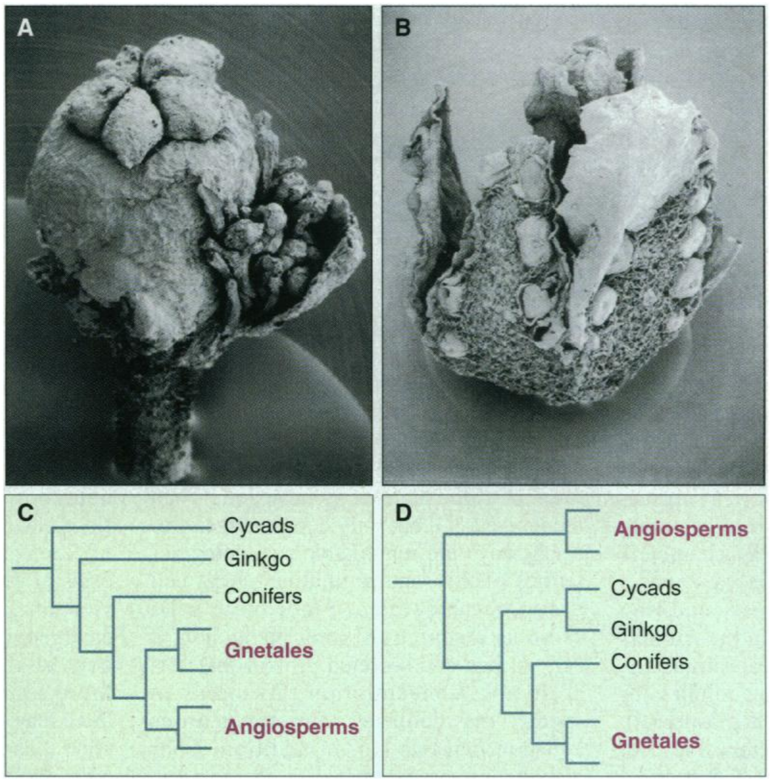
The Abominable Mystery

William L. Crepet

The report by Sun *et al.* (*1*) on page 1693 of this issue describes the first plausible fossil evidence of a Jurassic angiosperm (the type of plants that have flowers and fruits). This finding has important implications for one of evolutionary biology's most enduring puzzles: the origin of, and relationships within, the flowering plants—what Charles Darwin called the "abominable mystery."

The flowering plants are of overwhelming ecological importance, defining most major habitats; they are dominant in plant diversity with over 300,000 species, and they are preeminent in economic importance. Indeed, for over 100 years, botantists have sought to clarify the relationships among angiosperms, which mark a stunning gap in our knowledge. Further intrigue has been added to the mystery by new discoveries (see figure, parts A and B) that reveal highly advanced floral types and taxa in 90-million-year-old deposits, forcing a radical change in our understanding of the timing of angiosperm modernization (*2–6*). This shift compresses the known interval of angiosperm radiation or, alternatively, suggests an earlier, as yet undetected, origin for the group.

Advances in molecular systematics have provided new data that, in theory, have the potential to unravel relationships that are opaque because of apparently intractable morphological variation or convergence. And breakthroughs in software make it possible to analyze large data sets quickly and accurately (*7*). The torrent of analyses, instead of providing clarity, has often yielded conflicting hypotheses of phylogeny. Contrasts among different morphology-based analyses can be ascribed to different character selection, different sized data matrices, and disputes over homology assessment. But even nucleic acid sequences produce different hypotheses of relationship depending on the specific sequences and methodologies employed. Analyses combining different data sets are promising but have not yet resolved these issues (*8*). It is ironic that there is now unprecedented potential in the field of systematic botany, while the most fundamental relationships remain unsolved.



Among the flowers. **(A)** A 90-million-year-old fossil flower of the family Clusiaceae (*5*). **(B)** Another 90-mIllion-year-old flower representing a group of closely related species in the Heath family. Flowers in this complex include such derived characters as clawed petals, spurred anthers, and pollen in polyads (*2*). **(C)** Phylogeny of living seed plants based on morphological characters (*10*) showing a close relationship between the Gnetales and angiosperms. **(D)** A contrasting phylogeny of living seed plants based on cpITS sequences (*13*). In this analysis, the Gnetales are more closely related to other gymnosperms than to the angiosperms.

Even the growing consensus on the identification of the groups most closely related to the flowering plants is being challenged. In virtually all morphology-based data sets, the angiosperms are placed in a monophyletic "anthophytes" with two groups that have at least some genera with flowerlike reproductive structures (see figure): the relictual Gnetales and the extinct order Bennettitales (*9–12*). Yet a growing number of analyses of different nucleic acid sequences suggest that Gnetales are more closely related to the rest of the gymnosperms than to the flowering plants (see figure, parts C and D) (*13*, *14*). Remarkably, the status of every group purported to be "ancestral" to the flowering plants has been challenged by at least one contravening analysis.

There is similar uncertainty over which living taxa are basal ("primitive") within the angiosperms. Different morphology-based, nucleic acid sequence–based, and combined data phylogenetic analyses accord this status to taxa embedded in the poorly resolved subclass Magnoliidae (*15*). Some taxa now posited to be among the basal angiosperms have flowers that are complex, large, and multiparted, whereas others have very small, simple flowers. Obviously, contrasting alternative archetypes have vastly different implications for the pattern of angiosperm floral evolution. Fossil evidence is indecisive, but simple-flowered angiosperms are among the oldest fossils, supporting the notion that, in contrast to traditional thinking, the earliest angiosperms may have had small, simple flowers, as suggested by a growing number of phylogenetic hypotheses.

There is so much uncertainty about angiosperm relationships that bona fide evidence of very early angiosperms should be greeted with an enthusiasm fueled by desperation. Such fossils have the potential of retaining informative ancestral characteristics while pointing unambiguously to an archetype. In effect, they could point both up and down the evolutionary ladder. Zeal for such a finding may have spurred the many reports of pre-Cretaceous angiosperm fossils, but they have been unconvincing, from younger deposits than initially purported, or based on attributes too generalized to be definitive.

The taxon, *Archaefructus*, reported by Sun *et al.* (*1*), however, provides manifest evidence of a combination of characters

The author is at the L. H. Bailey Hortorium, Division of Biological Sciences, Cornell University, Ithaca, NY 14853, USA. E-mail: wlc1@cornell.edu

that are now restricted to the flowering plants in what appear to be Jurassic deposits. But does this fossil taxon provide insights into angiosperm ancestry based on retained characters shared with nonangiosperms? *Archaefructus* does not share substantial features with modern Gnetales, adding some support to recent nucleic acid sequence–based phylogenies that challenge a close gnetalean-angiosperm relationship (*13*, *14*). Comparisons with bennettitalean reproductive structures also fail to support the possibility of a close relationship. Having found little to link the fossils with the anthophytes, the authors succumb to the temptation to compare the fossils with seed ferns because of some similarities. Yet there is a gap, and the fossils indicate that angiosperms were isolated from other seed plants by the end of the Jurassic, suggesting that it will be difficult to reconstruct ancient angiosperms from comparative studies based only on existing taxa (*16*).

But what are the implications of these fossils for relationships within angiosperms? Do they favor any of the groups that have been hypothesized as primitive? Sun *et al.* note that *Archaefructus* lacks some features of the Chloranthaceae (*1*). It is also substantially different from the flowers or fruits of other putative basal angiosperms. However, *Archaefructus* shares certain characters with Magnoliales and even Magnoliaceae. They may prove even more like the flowers of Magnoliales if stamens are found attached at the base of the floral axis in new specimens, but with a substantial difference. The fossils are a combination of strongly magnolialean characters and a notable nonmagnolialean one: a missing perianth, an unusual condition found only in some species in the families Chloranthaceae and Piperaceae (ironically, families competing with Magnoliales for primitive stature within the angiosperms). This combination of characters does not occur in any extant group of flowering plants, and Sun *et al.* appropriately recognize a new subclass of angiosperms on the basis of *Archaefructus*.

This is potentially a big discovery. Although its age and chimeric nature imply that *Archaefructus* may represent the most "primitive" angiosperm yet discovered, final confirmation of its basal status and its angiospermous nature depend on precise phylogenetic context. Phylogenetic analysis is also necessary to rationalize the conflicting combination of characters now found in opposing models of primitive angiosperms. Can such an analysis be accomplished to everyone's satisfaction with the characters now available in *Archaefructus*? Probably not, because too many important characters are now missing, especially stamen position and structure, pollen morphology, and leaf and seed structure. However, through my experience in fossil collecting, I have learned that the discovery of a few specimens of a new fossil taxon is seldom a unique event—there will be new specimens of *Archaefructus* and the kinds of characters critically needed are also the kinds likely to be preserved. Given the potential informative value of this taxon and the recent pace of innovation in studies of angiosperm systematics and paleobotany today, I predict that the great "abominable mystery," with us for over 100 years, will not last another 10.

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PERSPECTIVES: NEUROSCIENCE

The When and Where of Floor Plate Induction

Jane Dodd, Thomas M. Jessell, Marysia Placzek

The floor plate is a transient embryonic organizing center located at the ventral midline of the neural tube that profoundly influences the development of the vertebrate central nervous system. The specialized histological features of floor plate cells have long been recognized (*1*), but only comparatively recently have the remarkable patterning activities of this ventral midline neural cell group been revealed. Floor plate cells serve as a source of Sonic hedgehog, a cell surface and secreted protein that acts at distinct concentration thresholds to specify the identities of motor neurons and interneurons (*2*). In addition, floor plate cells secrete netrin-1, a chemotropic factor that directs the axonal trajectories of commissural interneurons and certain motor neurons (*3*). Appreciation of the specialized signaling properties of the floor plate has thus brought an enhanced interest in the origins of this neural organizing center.

Many studies have provided evidence that the differentiation of the floor plate requires inductive signals provided by axial mesodermal cells of the notochord that lie under the midline of the neural plate (*4*). Notochord signals can induce floor plate differentiation both in vitro and in vivo. Conversely, selective elimination of the notochord in vivo, without removal of floor plate precursors, results in the failure of floor plate differentiation (*4*). On the basis of these findings, a relatively simple view of floor plate differentiation initially emerged, emphasizing the notochord as a key cellular source of inductive signals. More recent data, however, suggest that there may be more to floor plate differentiation than a single inductive signal provided by the notochord. Indeed, one recent review has questioned the entire concept of induction of the floor plate (*5*).

Here we discuss recent advances in the understanding of the molecular steps of floor plate development, findings that have begun to shed additional light on the timing and position within the embryo at which floor plate differentiation is initiated. We argue that while these findings may indicate new complexities, they nevertheless do not erode the basic case for the operation of an inductive signal that directs floor plate differentiation. The issues at stake can be reduced to three basic questions: Does inductive signaling have a critical role in floor plate differentiation? What are the molecules that control floor plate differentiation? When and where is floor plate differentiation initiated?

J. Dodd is in the Department of Physiology and Cellular Biophysics and Center for Neurobiology and Behavior, Columbia University, New York, NY 10032, USA. T. M. Jessell is at the Howard Hughes Medical Institute, Department of Biochemistry and Molecular Biophysics, Columbia University, New York, NY 10032, USA. E-mail: tmj1@columbia.edu. M. Placzek is in the Developmental Genetics Programme, Krebs Institute, University of Sheffield, Sheffield S10 2TN, UK.