Magnolias in Stone

Exploring an ancient Magnolia forest in northern Idaho

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In April of 1990 when I first heard of the successful extraction of DNA from a 17 to 20 million year old Magnolia leaf found in Idaho (Golenberg et al, 1990), I was immediately captivated by this incredible event and had to learn more about the fossil Magnolia latahensis (Berry) Brown, and this remarkable paleobotanical site located near Clarkia, Idaho. My quest led me to one of the authors of that paper, Dr. Charles J. Smiley of the University of Idaho, Moscow, Idaho. Dr. Smiley was the site manager for the Clarkia fossil site and had authored or co-authored many papers on it since its discovery in 1971. With Dr. Smiley's help I was able to access much of what had been published on Clarkia. Later, in 1991 Dr. Smiley invited me and my wife Anita to actually visit and collect at the Clarkia fossil site!

The fossil beds are located about 50 miles northeast of Moscow, Idaho in the valley of the St. Maries River near the townsite of Clarkia. The type locality (known as the P-33 site) resides on the property of Mr. Francis Kienbaum. In September 1971, Mr. Kienbaum was grading a section of his land for use as a snowmobile racetrack. While bulldozing, he noticed many black leaves being turned up in the soft shale, some even blowing around in the wind. Fortunately, it aroused his curiosity. Noticing that most of these leaves appeared to be from broadleaf trees not common to Idaho, Kienbaum telephoned the University and eventually contacted Dr. Smiley. What Kienbaum had uncovered is now regarded as the best preserved Miocene plant fossil site in the world. Those black leaves were the organic remains of leaves that fell there at least 17 million years ago.

In the ensuing years Dr. Smiley and his team of researchers would discover upwards of 130 different plant species in the 9 meter thick fossil sediments including 2 or perhaps 3 species of Magnolia as well as fossil equivalents of many of its present day associates including Liriodendron, Liquidambar, Taxodium, Quercus (even one similar to extant Q. phellos), Diospyros, Persea, Nyssa, Fagus, etc. Also present in the fossil record are several genera now confined to Eastern Asia, such as Metasequoia, Cunninghamia, Cercidiphyllum, Zelkova, and Paulownia (Smiley & Rember, 1985). Though the assemblage of plants most closely matches the present flora of S.E. North America, it appears the Miocene Clarkia flora was probably more diverse than any existing flora of temperate North America.

Origin of the Clarkia Fossil Beds

During early Miocene time (about 20 million years before present) extensive volcanic activity was underway in the Pacific Northwest. One of the largest known lava flows overspread eastern Washington at that time and is evidenced today as the Columbia River basalts. Further east, in the proto-St. Maries River valley, similar volcanic activity occurred, and one of the resulting lava flows suddenly dammed the valley creating a deep narrow lake (Smiley and Rember, 1979). The lake must have been cold bottomed and oxygen limited with very little microbial or scavenger activity, thus favoring the preservation of any plant parts that would be deposited from the nearby shore. The lake silted in fast, probably due to airfall ash, clays, silt and other products of erosion, perhaps filling in completely within 1000 years or less. This gentle but rapid infilling of sediment on the lake bottom entombed the leaves and fruits in the lacustrine sediments where they remained virtually unaltered and water-saturated to the present. Finally, these sediments were never to have been eroded or modified by weather, water-loss, glaciers, or other geological processes as most of the earth has during the past 20 million years! Everything had to go right and it did.

Exploring Clarkia

We arrived in the Clarkia area by way of the University of Idaho campus in Moscow in early July 1991. Though nearly midsummer, it looked strangely spring-like in northern Idaho as black locust trees (Robinia pseudoacacia), used as ornamentals here, were still in bloom. After a brief meeting with Dr. Smiley, we embarked on the hour long car ride to the Clarkia fossil site. Along the way Dr. Smiley provided detailed geological and botanical narration to the roadside scenery. Evidence of the Miocene lava flows was indicated by basalt extrusions in the roadcuts. These were often interbedded with clay-like "Latah" sediments (which are sometimes fossil bearing). As we traversed the gently rolling topography, the existing flora-consisting of grand fir (Abies grandis), douglas fir (Pseudotsuga menziesii), western white pine (Pinus monticola), western larch (Larix occidentalis), subalpine fir (Abies lasiocarpa), quaking aspen (Populus tremuloides), etc.-contrasted markedly to my mental image of the rich Magnolia-Beech-Baldcypress forest that once existed here in Miocene time.

At last, a sign on the left which read, "Fossil Bowl" (the name of the racetrack), signaled that we were indeed at the P-33 site. Bill Rember, Yang Hong and other members of Dr. Smiley's research team were already at the site and in the process of obtaining drill cores of stream and lake sediment. After introductions, Rember provided an account of a "really big leaf" that was found here at P-33 that was believed to have been a Magnolia, perhaps belonging to section Rytidospermum. As we talked I kept looking at the ground - leaves, black leaves, all over the place, mostly of Taxodium. Within minutes, I had picked up pieces of shale containing Metasequoia, Liquidambar, Castanea, and yes even Magnolia! Dr. Smiley suggested that better specimens could be obtained if we "chopped" them fresh from the sediment.

This method calls for using a pulaski axe to chop out small blocks of the soft shale sediment. One would then split off individual bedding surfaces using a pocket knife. Each bedding surface usually reveals one or more fossil leaf compressions many of which still show original green or red pigmentation for a short time before finally turning black. Sometimes fruits and

twigs are also present.

That is the way we "explored" this ancient forest. I would chop, Dr. Smiley would split and identify, while our wives Peg Smiley and Anita Figlar wrapped and labeled specimens. As we lifted these leaves from the ancient sediments, my sense of time often became lost and confused—for these 20 million year old leaves looked like present day leaves, and, in most cases, they appeared to be in better condition than those which fell into my own pond last fall. Digging them today had the effect of feeling Miocene time in the present—a strange experience. We had time to dig for only an hour or so, but in that short time we collected fossil leaves of numerous Miocene species including those of Magnolia latahensis and what appears to be a second species of Magnolia, one that resembles extant M. acuminata of section Tulipastrum.

Later, we visited the main fossil collection at the Tertiary Research Center at the University of Idaho. There, Dr. Smiley showed us many of the better specimens of Magnoliaceae and other genera from Clarkia. Most impressive in this collection is an exceptionally well preserved fossil impression of an immature Magnolia fruit aggregate. Even more remarkable is the extraordinary resemblance of this fossil fruit to that of present day Magnolia grandiflora of Section Theorhodon. Close examination (morphology and scar marks of flower parts) of the fossil aggregate indicates 9 tepals, approximately 250 stamens, and some 120 carpels-all of these being well within the ranges for M. grandiflora. Three similar fossil aggregates were in the collection but were of lesser quality. Also impressive were the quality and quantity of fossil Liriodendron leaves and fruits. I proceeded to take many close-up photographs of the various leaves, the fruit aggregates, and both types of Magnolia leaves (latahensis and acuminata types) for further study.

Discussion

The possibility of two Magnolia species in the Miocene Clarkia flora was first described by Smiley and Rember (1981) as part of a stratigraphic analysis of a 7.6 meter column of Clarkia sediment. In the study column they found trends for plant species that favored specific communities or associations. Some parts of the column revealed fossil evidence of swamp association species such as Taxodium, Nyssa, and Magnolia (as latahensis), whereas other sections of the column reflected a mesic slope association dominated by Quercus, Fagus, and Metasequoia. In this latter association, Smiley and Rember

found fossil leaves of a species of *Magnolia* whose leaf morphology was suggestive of living *M. acuminata*. Smiley further indicates (1991, pers. comm.) that, unlike those of *M. latahensis*, these were uncommon fossils that were typically found in a more fragmented, transport abraded, condition.

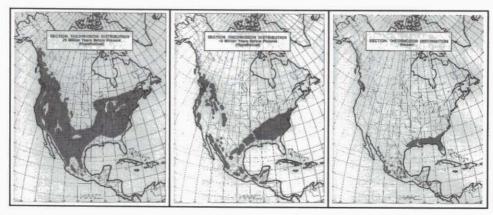
Using both close-up photographs and actual fossil material. I compared leaf structures and venation patterns of the two fossil magnolias to each other and to numerous living species of Magnolia (Figlar, 1991). Despite the small sample size of fossil material, the specimens were in excellent condition and showed fine details of leaf venation even down to the ultimate structures (areoles and veinlets). The comparative analysis of these characters indicated that the two fossil species (M. latahensis and the "slope species") showed a closer resemblance to living M. grandiflora and M. acuminata, respectively, than to each other or to any other extant Magnolia species used in the study. In fact, the structural dedails and venation parameters for each of the fossil species were well within the ranges for each of their proposed living analogues. Smiley's comments on the typically abraded leaves of the slope magnolia, which suggests membranous-deciduous rather than coriaceous-evergreen leaves, further supports the slope magnolia affinity with living M. acuminata [See illustrations on pages 16-17.].

Regarding the resemblance of *M. latahensis* to living *M. grandiflora* of Section Theorhodon, both the leaf architecture and the stratigraphic evidence (swamp association) are indicative of possible affinities. In addition, the extraordinary morphological similarity between the fossil seed aggregate and those of modern *M. grandiflora*, makes for an even more convincing case for the *latahensis/grandiflora* affinity. But since the fossil aggregate wasn't found with leaves attached, it is impossible to prove that it was produced by *M. latahensis*. However, probability suggests that since only one type of *Magnolia* fruit was found at Clarkia, it must have come from the species that produced the most leaves—that is, *M.*

latahensis.

Perspective

Later on in the middle and later parts of the Miocene Epoch, the Cascade Range formed, producing a rainshadow



Distribution maps for Section Theorhodon for (left) 25 MYBP, (center) 15 MYBP, and (right) the present.

The maps for 25 and 15 MYBP are hypothetical.

effect over Clarkia and surrounding areas. Not only would the rising Cascades to the west cause precipitation and humidity to decrease, this climatic barrier would allow more frequent invasions of artic air masses from the north. These combined effects would eventually doom *Magnolia latahensis* and the rest of the mesic Miocene Clarkia flora, in favor of more xeric and boreal floral elements similar to those in evidence today throughout interior western North America. With similar orogeny taking place farther south in the Sierras, this kind of change probably occurred throughout much of western North America and the Great Basin at that time.

Other Miocene fossil records, though less well preserved, indicate that many Clarkia-type floras existed throughout western North America. Fossil Magnolia corrallina Chaney, from the Miocene San Pablo (Neroly) flora of west central California (Condit, 1938) is said to resemble present day M. grandiflora (Chaney & Axelrod, 1959). Chaney and others suggest the same for M. latahensis from the Miocene Latah flora near Spokane, Washington, and M. californica Lesquereux, of the Miocene Puente flora of the Los Angeles area (Axelrod, 1939).

Recently, in a study of fossil magnolia seeds of Oligocene(?) Brandon Lignite of west-central Vermont, Tiffney (1977) describes two fossil Magnolia species, M. septentrionalis and M. waltonii, whose seed morphologies suggest alliance to

extant species of section Theorhodon and section Tulipastrum, curiously in parallel with the affinities described here for

Clarkia fossil Magnolias.

The Clarkia evidence, which suggests close morphological and DNA similarity of the Miocene M. latahensis to present day M. grandiflora and other section Theorhodon species, supports the view (Parks & Wendel, 1990) that species which persist in the same mesic habitats as their Miocene counterparts tend to retain their ancestor's morphological characteristics, the best examples being illustrated by Liquidambar and Liriodendron which have obviously changed little since Miocene time (Baghai, 1988). Conversely, species that survived in more xeric habitats today generally show greater morphological disparity from their Miocene ancestors.

Speculative epilogue

One could speculate that some 25 MYBP (million years before present) during the late Oligocene/early Miocene, a grandiflora-like section Theorhodon species formed a continuous distribution from (what is now) far western Canada southward through the Great Basin into Mexico and Central America, then back up through south-central US into New

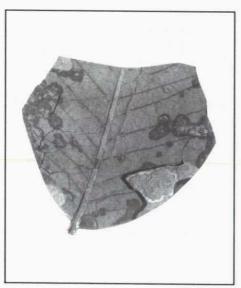
England and perhaps beyond.

Later in Middle Miocene time, 15 MYBP, a large gap in the distribution would develop in the American Southwest as increased aridity pervaded that region. Also, mountain building along the western coast ranges would begin starving off moisture to other Theorhodon populations in western North America and Central America, resulting in many disjunctions. The New England leg of the distribution would shrink southward as the Miocene and Pleistocene climates cooled.

The western North American populations would vanish by the end of the Miocene. Eventually in Quarternary time, perhaps as recently as 10,000 years ago, climatic change would force another separation of the Theorhodon distribution between Texas and the disjunctions in Mexico. These Central American disjuncts, having been genetically isolated for so long, have become separate allopatric species (Vazquez-G., 1990). Magnolia grandiflora, which still has a sizable continuous distribution in S.E. USA, is all that remains of the original continental distribution.

Leaf architecture comparison between Magnolia acuminata and a Miocene (Clarkia) Magnolia species

Secondary Veins



Fossil leaf impression (specimun RBF-20) of Miocene Clarkia Magnolia sp. (resembling extant M. acuminata).



Extant M. acuminata leaf.

M. acuminata leaves typically have 10 to 14 secondary veins per each side of the midrib. The angle of divergence of the secondaries from the midrib is mostly 45 to 65 degrees with the angle becoming more acute towards the apex. Frequently, the secondaries on the basal half of the leaf are more or less recurvate, particularly in the proximity of the midrib. Extrapolation suggests the fossil leaf (above left) contained 12 to 14 secondaries. The patterns of secondary veins of the fossil are very distinct and appear indistinguishable from those of modern cucumber tree (above right).

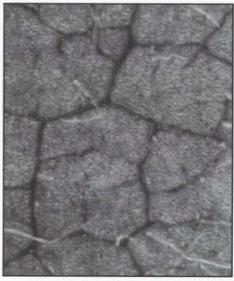
Other magnolia species, with leaf shapes comparable to *M. acuminata*, are distinguished by having less acute (*M. grandiflora* 60 to 70 degrees, *M. campbellii* up to 90 degrees, and *M. delavayi* up to 90 degrees) or more acute (*M. denudata* < 45 degrees) angles of divergence. Leaves of section Rytidospermum magnolias are separated by having far more secondary veins (usually more than 20).

Leaf architecture comparison between Magnolia acuminata and a Miocene (Clarkia) Magnolia species

Ultimate Venation



Ultimate leaf venation of Miocene Clarkia Magnolia sp. (resembling extant M. acuminata), specimen RBF-20.



Ultimate leaf venation of M. acuminata (white lines are pubescence).

Under x 40 magnification the ultimate venation structure in *M. acuminata* leaves is evidenced by areoles which are usually pentagonal of quadrangular shaped and measure 0.5 to 1.0 mm across. Typically more than half of these areoles contain simple veinlets which "dead end" inside the areoles. These features are clearly visible in the fossil (above left) and appear to closely match those of extant *M. acuminata* (above right).

Comparable magnolias (M. campbellii, M. sprengeri, and M. delavayi) are distinguished by having larger (2 to 3 mm) areoles, while in M. grandiflora and fossil M. latahensis veinlets are rarely present or are indiscernible (because of coriaceous leaves?).

A similar migration could be posited for the ancester of the cucumber magnolia (M. acuminata) except that, being a more temperate species, its range may have extended farther north, perhaps well into Alaska during the early Miocene epoch. The fact that the closest living relative to cucumber magnolia, M. liliiflora, is found in Asia suggests that the ancestral species could still have been genetically "communicating" across the continents via the Alaska land bridge to Asia during or shortly before the early Miocene. This relatively short period of isolation, about 25 million years, might have resulted in the morphological and chromosomal similarities that exist between the two extant Section Tulipastrum species, M. acuminata and M. liliiflora.

These scenarios seem plausible, but for now they are largely conjectural, given the fragmentary fossil evidence. But just as the amazing findings at Clarkia have brought us much closer to understanding Magnolia's past in North America, future studies there might someday unlock still more secrets.

Dedication

While this manuscript was being prepared my mother, Adelene Greenwood Figlar, passed away. She was a kind loving lady and, probably because of me, developed a great fondness for magnolias. This paper is dedicated to her memory.

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