

From Fossils to Molecules: The *Metasequoia* Tale Continues

Hong Yang

Recent studies of the wild population in China using the techniques of cuticle micromorphology and population genetics have introduced new ideas about the evolutionary history of *Metasequoia glyptostroboides*, previously limited to hypotheses drawn from the fossil record. The new information suggests that the living *Metasequoia* trees may be recent immigrants to their remote valley in central China, rather than Tertiary relics dating back as far as 15 million years ago.

My first encounter with the genus *Metasequoia* occurred more than fifteen years ago when I was a college student in Wuhan, a city along the Yangtze River in the Hubei Province of central China. In a paleobotany lab session, I was shown a fossil of *Metasequoia* foliage collected from a Tertiary deposit in northeastern China; minutes later I was led outside to inspect the city tree of Wuhan—living dawn redwoods planted along roadsides. Seeing the close resemblance between a fossil imprint preserved in a rock for over 50 million years and the green leaves shining in front of my eyes was a breathtaking experience. Equally astounding to me was the story of *Metasequoia glyptostroboides*, the dramatic discovery of a living tree previously known to science only as a fossil, a story that had unfolded in that same province in the early 1940s (Hu 1948, Merrill 1948). What I could not foresee was that this college exercise had planted a seed in my mind that later grew into a strong professional attachment to this species. The dawn redwood legend has led me twice to "Metasequoia Valley" in central China and engendered a tremendous interest in pursuing its evolutionary history through both fossil records and DNA molecules.

I came to the United States in 1988 for graduate training under Professor Charles J. Smiley at the Tertiary Research Center of the University of Idaho, and it was there, in Smiley's personal library, that I read intensively in the literature on both modern and fossil *Metasequoia*.¹ Smiley had been a graduate student of Professor Ralph W. Chaney, the first Western scientist to travel to Metasequoia Valley, in 1948, and in Smiley's files were copies of remarkable photographs that Chaney and his traveling companion had taken during their trip there shortly after the discovery of the living trees.

In 1988, Smiley was conducting research on the Clarkia Miocene fossil site, an exceptionally well-preserved fossil deposit in northern Idaho that contained abundant *Metasequoia* fossils as well as other warm-temperate plant genera that Chaney had observed during his trip to Metasequoia Valley. I was interested in the theory of "Arcto-Tertiary flora" that Chaney had put forward to explain the origin and distribution of plants around the Pacific basin. He argued that *Metasequoia* and the plants associated with it originated in the high northern latitudes during the Cretaceous period, over 65 million years ago; then the whole assemblage was gradually pushed southward into the modern Metase-

¹ After Dr. Smiley's sudden passing on January 1, 1996, his personal library was donated to the Nanjing Institute of Geology and Palaeontology, the Chinese Academy of Sciences.



The oldest *Metasequoia* tree in Xiaohe Commune, estimated at 440 years of age, photographed in 1997. Photographs taken in 1948 and 1980 can be seen on pages 36 and 49, respectively.

quoia Valley during the Tertiary, beginning around 40 million years ago when the global climate started to cool. A trip to *Metasequoia* Valley to trace Chaney's steps among the "living Tertiary flora" appealed to both Smiley and me.

Historical Biogeography Revealed by Its Fossil Record

In June 1990 Professor Smiley, his wife Peg, Professor Fred Johnson, a forest ecologist from the University of Idaho, and I took only four hours

to complete the journey from Wanxian (known as Wan Hsien in the old spelling) to Moudao (also known as Mo-tao-chi) that Chaney completed in three days in 1948. Still, the narrow road and steep slopes reminded me of a poem by Li Bai, the great poet of the Tang Dynasty, who described traveling in the mountains of Sichuan as being as difficult as climbing to the sky. Although the hardwood forest that Chaney had seen growing alongside the dawn redwoods had been cut down over the previous forty years, the enormous, centuries-old dawn redwood that Chaney had admired in Moudao still stood proudly in the middle of farmland, and I could not help but be amazed by its power to endure time and environmental change. Touching the tree's reddish bark and looking up at its top branches, I had to wonder when and how it got there, and why the species survives only in this remote valley. The answers to my questions, it seemed, were to be found only in the fossil record.

For Chaney, the discovery of living *Metasequoia* provided a critical piece of evidence in support of his theory, but since his time, more fossil *Metasequoia* have been reported. I

wanted to find out if Chaney's theory was still valid in light of new findings from China, Japan, and Russia. Shortly after our trip to *Metasequoia* Valley, I started to compile the *Metasequoia* fossil record from the Cretaceous onward, and a more detailed picture of *Metasequoia* history started to emerge (Yang and Smiley 1991). It is apparent that the story of this remarkable tree encompasses the entire history of the Northern Hemisphere over the past 100 million years, including the changes in land connec-

tions and climates and the evolution of living organisms.

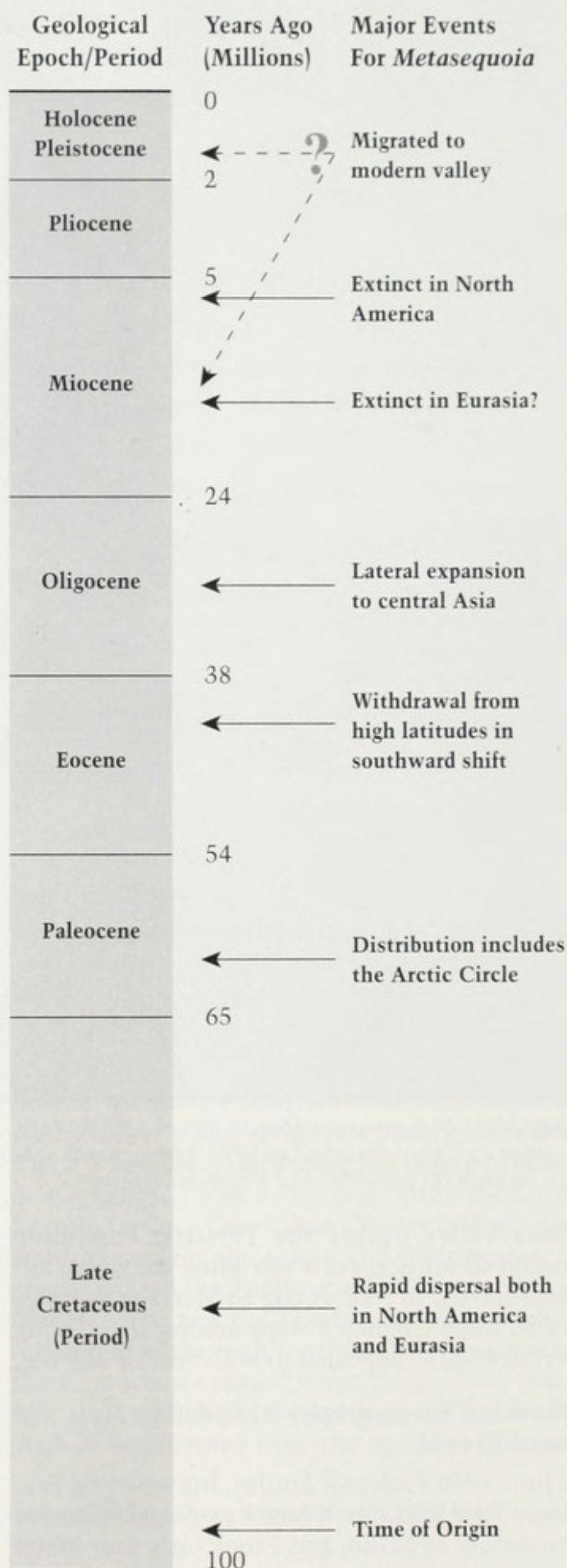
The up-to-date fossil record reveals the following four major phytogeographic events in the history of this genus:

First, it is likely that *Metasequoia* first evolved in eastern Russia (about 60 degrees North) during the early Late Cretaceous period, around 100 million years before the present, as the earliest dawn redwood fossils were reported from this region. Thanks in part to the low temperature gradient across the Northern Hemisphere and the Bering land connection between North America and eastern Eurasia, *Metasequoia* spread very rapidly in two opposite directions shortly after its origin: southward to lower latitudes in eastern Russia, northern Japan, and northeastern China; and northward across the Bering land connection to North America. By the end of the Cretaceous, when dinosaurs became extinct, *Metasequoia* had traveled as far south as New Mexico (about 35 degrees North) in North America and had become a dominant tree in ancient forests of southern Japan (about 36 degrees North) in Asia.

Second, during the Paleocene, about 60 million years ago, *Metasequoia* moved to the high latitudes of North America and invaded northern Europe to become a prominent member in ancient floras circumscribing the North Pole. At the same time, *Metasequoia* maintained the distribution pattern at lower latitudes around the Pacific basin that it had established during the Late Cretaceous.

Third, when major global cooling occurred during the Late Eocene, 40 million years ago, and the cooler climate persisted, the distribution pattern changed dramatically: *Metasequoia* disappeared from high latitudes. By the Early Oligocene, 35 million years before present, *Metasequoia* had moved to lower latitudes and undertaken a longitudinal expansion to arrive in central Eurasia along the foothills of the Ural Mountains. During the Middle Miocene, when the climate again warmed up, *Metasequoia* re-entered the Arctic Circle. It had vanished from Eurasian fossil floras by the Middle Miocene and from North America by the end of the Miocene.

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Fossil Remains of *Metasequoia*

The discovery of living *Metasequoia* in China more than fifty years ago shed light on the study of fossil Taxodiaceae, the family of redwoods and bald cypresses. After his trip to China, Chaney (1951) reassigned to the genus *Metasequoia* many fossils that had been misidentified as *Taxodium* or *Sequoia*. Since then, new *Metasequoia* fossils have been reported from the Northern Hemisphere, the oldest dating back to the Late Cretaceous. *Metasequoia* foliage and cones are among the most common fossils in Paleocene and Eocene floras around the Pacific Ocean. From small branchlets to single shoots, the leaves of *Metasequoia* show morphological characteristics that differ from those of other members of Taxodiaceae.

The graceful, opposite arrangement of leaves allows quick, sure identification in the field (figure a). However, reliable identification is difficult in pollen and wood fossils of *Metasequoia*: separated from the male cone, *Metasequoia* fossil pollen grains are almost indistinguishable from those of members of Cupressaceae, Taxaceae, or other Taxodiaceae; likewise, its wood anatomy is very similar to that of other members of the same family.

Metasequoia fossils have been reported from exceptionally well preserved deposits, revealing morphological and anatomical details of dawn redwoods that lived millions of years ago. For example, three-dimensional *Metasequoia* fossil cones from the Clarkia Miocene lake deposit in Idaho yielded seeds that give an accurate

description of *Metasequoia* seeds in Miocene time (figure b). Mummified *Metasequoia* leaves found in an Eocene deposit on Axel Heiberg Island in Canada's Arctic archipelago have permitted detailed anatomical studies of its soft tissue, and leaves trapped in amber for more than 50 million years at Fushun, a Paleocene-to-Eocene coalfield in northern China, offer a remarkably detailed snapshot of an ancient *Metasequoia*.



HONG YANG

Metasequoia leaves trapped in amber found in a Paleocene coal mine in Fushun, China.



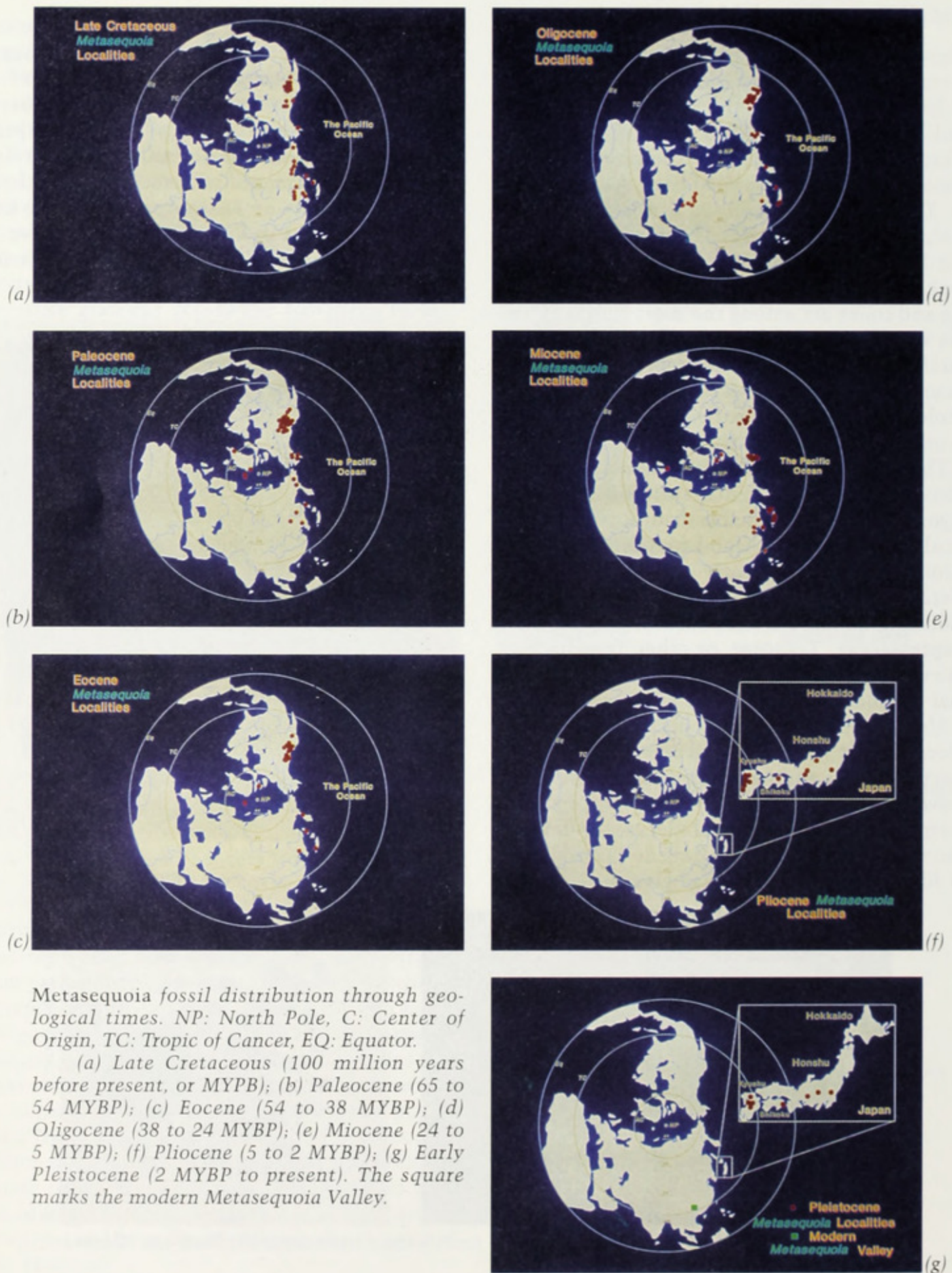
(a)

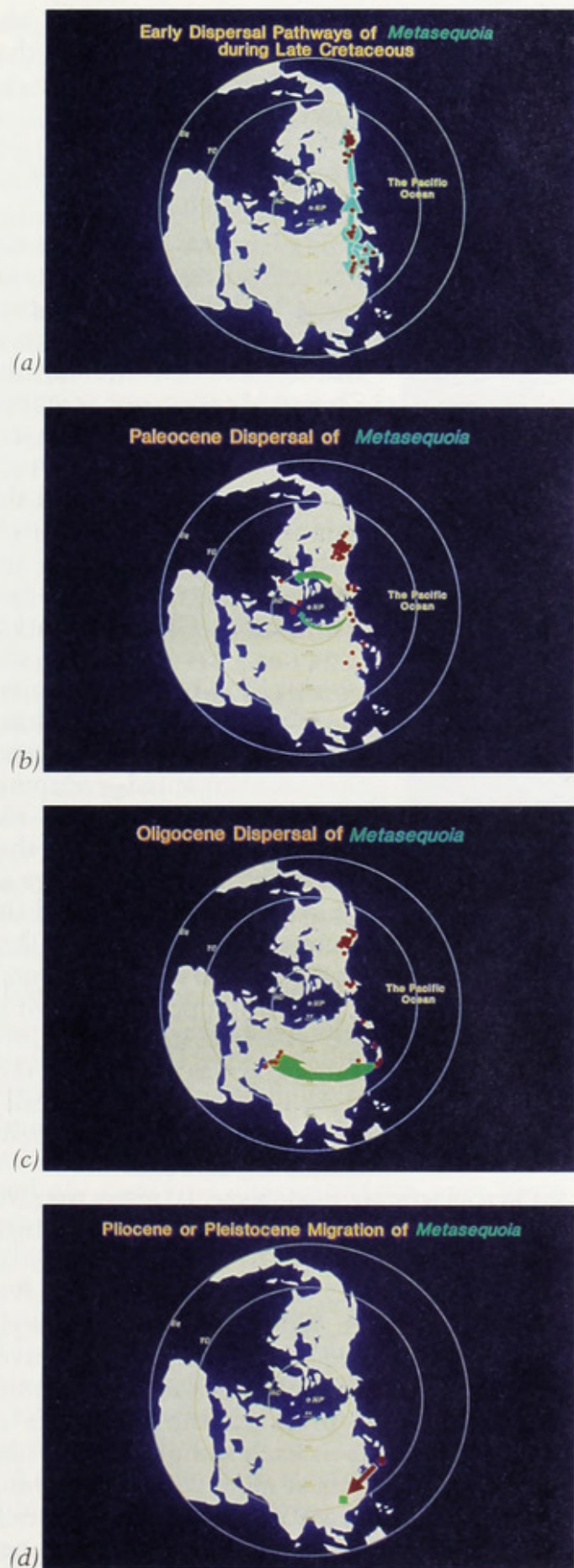


COURTESY OF C. J. SMILEY

(b)

Metasequoia fossil remains: shoots (a) and female cone with seeds (b) from the Clarkia Miocene deposit in northern Idaho.





The fossil record shown on the preceding page was compiled from published paleobotanical literature, using only clearly illustrated fossil leaves and cones. These records give a feeling for the extensive distribution of *Metasequoia*. The oldest was found in Late Cretaceous rocks (about 100 million years old) in northeastern Russia. At the other extreme, the youngest *Metasequoia* fossil was collected from Pleistocene deposits in southwestern Japan: the lower part of the Osaka Group—about 1.6 million years old—marks the extinction of *Metasequoia* from Japan.

The highest latitude at which a *Metasequoia* fossil has been reported is 82 degrees North in northeastern Greenland, where abundant Paleocene fossils have been found. The prize for southernmost distribution goes to the Shihti Formation, a Miocene deposit in Taiwan at a latitude of 25 degrees North. To the west, *Metasequoia* fossils have been reported from Oligocene deposits in central Asia as far as 60 degrees East.

Possible *Metasequoia* dispersal and migration routes: (a) center of origin; (b) Paleocene dispersal paths showing invasion of higher latitudes; (c) lateral Oligocene dispersal paths; (d) Late Pliocene or Early Pleistocene migration direction.

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Fourth, the post-Miocene history of *Metasequoia* has been less studied, yet it is critical to the explanation for its survival in central China. *Metasequoia* fossils from the Pliocene and Pleistocene epochs—roughly from 5 to 1.7 million years ago—have been found only in central and southern Japan. Non-marine Pliocene and Pleistocene deposits have been commonly reported in eastern China, but no *Metasequoia* fossil has been found. If we read the fossil record literally, it suggests that the living *Metasequoia* is geologically a newcomer to its valley at the juncture of Sichuan, Hubei, and Hunan Provinces in central China, most likely having immigrated from Japan during the Late Pliocene or



These isolated trees are located in a field inside an iron fence in the remote Longshan area of Hunan Province, about 70 miles southeast of Metasequoia Valley.

Early Pleistocene, only 2 million years or less before the present.

It is interesting to note that the morphology of *Metasequoia* has changed little during the 100 million years since its origin. A recent taxonomic revision of *Metasequoia* fossils by Liu et al. (1999) has reassigned twenty of what were formerly twenty-one species (excluding only *M. milleri*) to a single species: *M. occidentalis*. This merger suggests a considerable degree of morphological stasis and implies a slow rate of morphological evolution. This would explain the striking similarity in morphology between

the Tertiary fossil and the modern *Metasequoia* twig that I compared fifteen years ago in Wuhan.

Morphological Variation at the Population Level

In 1997, seven years after my first trip, I revisited Metasequoia Valley with colleagues from the Nanjing Institute of Geology and Paleontology, the Chinese Academy of Sciences. The aim of the second trip was to collect modern *Metasequoia* leaf samples from trees in the wild for study of both cuticle and genetic variations at the population level. In the past few years, China's market economy has reshaped the country, and I was eager to see how these trees had weathered the environmental changes that accompanied economic reform. To my surprise, the rapid economic growth that has taken place elsewhere in China had not penetrated the remote Metasequoia Valley. And thanks to the *Metasequoia* conservation program, most of the wild trees are still healthy, although I was sad to learn that eight huge trees under which we picnicked in 1990 had died a couple of years ago.

On this trip, we made a special effort to travel to the remote Longshan area of Hunan Province, about 110 kilometers (70 miles) southeast of Metasequoia Valley, to visit and sample leaves from several large, wild trees that have rarely been seen by outsiders. We also sampled leaves from large *Metasequoia* trees in eight natural dawn redwood groves in the provinces of Sichuan and Hubei. Each sample was divided into two sets: one for study of cuticle micromorphology and another for DNA analysis. Cuticle from each tree was prepared and examined under a scanning electron microscope by Qin

Leng, a paleobotanist at the Nanjing Institute of Geology and Paleontology. We were not surprised to find that the cuticular characteristics among living trees within *Metasequoia* Valley display little variation, but Leng did make an exciting discovery: the sample collected from an isolated wild tree in Paomu, Longshan, showed some variation. Among other noticeable differences, the internal surface of the lower cuticle in the Longshan leaves possesses a uniquely even cuticular membrane between the stomatal zone and the non-stomatal zone—a characteristic that is not observed in any of the groves.²

Moreover, compared with all other samples, the Paomu sample also showed variation in the micromorphology of its guard cells. The differences in these features are great enough to warrant designation of two separate cuticle types, and the data imply that the isolated tree in Hunan Province may have preserved some characteristics that do not exist in the trees in *Metasequoia* Valley. Is this an indication that this isolated dawn redwood possesses a slightly different gene pool? If so, it is exciting news for the endangered *Metasequoia* population, whose genetic variability is expected to be very low. New morphological features found in the wild population may signal an increase of genetic diversity, which would help to alleviate its endangered state.

Clues from DNA Molecules

The past fifty years have witnessed the rapid development of molecular biology, and the impact of DNA-based biotechnology is felt in almost all subdisciplines of biological science. Earlier genetic work on *Metasequoia* has examined chromosome characteristics and, more recently, electrophoretic patterns of enzyme polymorphism (Kuser et al. 1997), but population structure at the DNA level for wild *Metasequoia* remained unexplored. Accordingly, a set of leaf samples collected during our 1997 trip was used to assess genetic diversity; the project is still in progress, but some preliminary data are intriguing.

As a small population with a very limited number of individuals living in a restricted geo-



In 1992, the post office of the People's Republic of China issued stamps celebrating dawn redwood as well as other prominent Chinese conifers.

graphic area, we would expect the modern *Metasequoia* population to display a very low level of genetic diversity, especially since the morphology of several of its features has shown considerable homogeneity at the population level. However, preliminary DNA analysis, using a RAPD (random amplified polymorphic DNA) technique, by Dr. Qun Yang and his student Chunxiang Li at the Nanjing Institute of Geology and Paleontology indicates that the species possesses a moderate genetic diversity that exceeds that of other endangered Chinese conifers, such as *Cathaya argyrophylla*. Further, the RAPD analysis also reveals that the genetic differences among sampled *Metasequoia* trees is primarily related to the geographic distance between them (Li et al. 1999). This interesting revelation suggests several possibilities: First, the genetic constitution of isolated trees in Hunan Province may have helped to increase the overall genetic diversity of the population. If this is true, the data from molecular analysis could fit with the findings in the comparison of cuticle morphology, which also imply a slightly different gene pool for the grove in Hunan Province from that of the groves in *Metasequoia* Valley.

Second, the unexpected level of genetic diversity may reflect a relatively recent establish-

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² Q. Leng, H. Yang, Q. Yang, and J-p. Zhou. 1999. Variation of cuticle micromorphology in native population of *Metasequoia glyptostroboides* Hu et Cheng (Taxodiaceae) (in progress).

A Glimpse of the Living Population

Cuticle is a waxy layer covering the outer cell walls of the plant leaf that serves as an effective barrier against water loss. Both botanists and paleobotanists are interested in plant cuticle because their faithful impressions of epidermal cells provide valuable physiological and sometimes taxonomic information. The cuticle's stable chemistry allows it to be preserved in sedimentary rocks for millions of years; therefore, it is particularly valuable for paleobotanists, who use it to classify fossil plants and infer their paleoenvironment. However, for both botanist and paleobotanist, studies of fossil cuticle are greatly improved when preceded by analysis of the cuticle micromorphology of living plants, and the limited distribution of existing *Metasequoia* will simplify this task of examining the variability of cuticle micromorphology within the species. Thus, the results of these studies will be very useful for interpreting cuticular features in the fossil material.

In the laboratory, cuticle from both sides of *Metasequoia* leaves can be prepared, and both internal and external surfaces of each piece can be examined. Cuticle is separated from the leaf by means of an acid solution. After the material is washed in distilled water and dried in the air, it can be coated with platinum and then amplified hundreds of times under a scanning electron microscope. In addition to the cuticle's thickness, micromorphological features of taxonomic or physiological value include the shape of epidermal cells, size and shape of stomata, shape of guard cells around stomata, and patterns on various cell walls.

Two types of cuticle micromorphology were observed by Qin Leng in the wild *Metasequoia* population. The isolated tree growing in the Longshan area of Hunan Province exhibits slightly different cuticle characteristics from those of trees in the Sichuan and Hubei groves, some 110 kilometers (70 miles) away. For example, epidermal walls in the Paomu sample from Longshan are more regular, with a defined boundary, and the shape of the guard cells around stomata differs from those of the Sichuan and Hubei samples. These differences point to a possible source of morphological variation in the wild population.



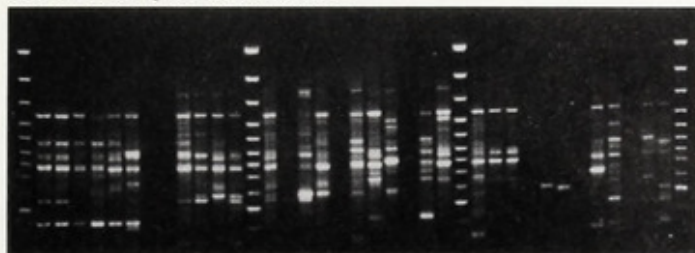
COURTESY OF Q. LENG

Cuticle micromorphology of living Metasequoia magnified 200 times; both show the internal surface of the cuticle on the underside of the leaf, comparing the two cuticle types: (a) from an isolated tree in Longshan, Hunan Province, (b) from Metasequoia Valley in Lichuan, Hubei Province.

DNA from *Metasequoia*

Only recently have molecular approaches been applied to the field of paleobiology, providing evolutionary biologists with an independent data set that helps compensate for the incomplete fossil record. In higher plants, DNA molecules reside in the nucleus and in two organelles, chloroplast and mitochondria. A biochemical procedure permits a mixture of the three types of DNA to be extracted and purified from plant cells. Then, using a new molecular technique called polymerase chain reaction (PCR)—a kind of molecular copy machine—selected portions of the DNA can be amplified into millions of identical copies. Depending on the goals of the research, amplified DNA fragments can be sequenced to reveal nucleotide base pairs or can be cut by various enzymes to detect variations. It is the variation in DNA molecules that is the genetic basis

COURTESY OF Q. YANG AND C.-X. LI



Agrose gel electrophoresis pattern showing RAPD amplifications derived from 27 different wild *Metasequoia* trees.

for morphological variability and population diversity.

RAPD (random amplified polymorphic DNA) analysis, a PCR-based technique, is a new molecular tool that has proved powerful in detecting genetic diversity at the population level. Primers—small synthetic pieces of DNA—will locate any regions of the chromosome (“priming sites”) that exhibit sequences complementary to the primers’ sequences. PCR will amplify all complementary fragments of DNA; if, due to a mutation, a priming site is absent from an individual, then PCR will skip over it. Thus, by counting the number of fragments shared by two individuals we get a crude measure of their genetic difference.

When fragments from each *Metasequoia* sample are separated and stained according to their size, a series of bands is created. Variations in amplification patterning among the samples mirror the underlying DNA variation of the *Metasequoia* population. Therefore, the amount of genetic variation within the population can be measured by the pattern of banding after amplification. By comparing amplified bands, computer-based statistical programs are able to calculate the genetic divergence among examined *Metasequoia* samples. For DNA collected from any two individual trees, the more differences among the bands, the larger the genetic distance.

Only in the past few years has ancient DNA from amber been extracted and sequenced. I have cracked open an amber from Fushan containing a *Metasequoia* shoot similar to that shown on page 63, hoping to find ancient genes that had survived for over 50 million years. Despite repeated efforts, I have been unable to find DNA; perhaps this goal will be achieved in the future.

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ment of the living population. In theory, the longer a population exists in a confined area, the more homogeneous its genetic diversity would become as inbreeding increases.

Third, the unexpected level of genetic diversity may also indicate divergent evolution of small, isolated populations due to habitat fragmentation from a once genetically homogeneous, large population. Unfortunately, our current data are insufficient to prove or disprove these possibilities. The RAPD technique used in this study is a rough, molecular-level survey and, moreover, the sample size is not large enough for a meaningful statistical test. DNA sequences of appropriate genes derived from individual *Metasequoia* may yield more quantitative information. Nonetheless, the available DNA data reveal an interesting level of genetic variation in the wild *Metasequoia* population.

When Did *Metasequoia* Arrive There?

Traveling through Metasequoia Valley in 1948, Chaney thought that he had seen a Tertiary fossil flora come to life. Based on the close resemblance between fossil remains that he had studied in Tertiary deposits around the Pacific basin and living plants that he encountered in Metasequoia Valley, Chaney believed that *Metasequoia* and its Tertiary associates had taken refuge in central China since Tertiary time. He asserted that *Metasequoia* “participated in wide migrations” from north to south and “continued down to the present Metasequoia valley” (Chaney 1948). In other words, he viewed the living *Metasequoia* as a Tertiary relic. However, the detailed fossil record seems to tell a slightly different story.

The absence of post-Miocene *Metasequoia* fossils in China suggests that the dawn redwood is a relatively recent arrival in central China. The youngest *Metasequoia* fossils found in China are from Middle Miocene deposits (about 15 million years before present) in Jilin Province, more than 2,000 kilometers (1,240 miles) northeast of Metasequoia Valley, and in Taiwan, an island more than a thousand kilometers (620 miles) east of

the present native population. Despite fifty years of intensive searching (Li 1995), no post-Miocene *Metasequoia* has ever been found in China. It is possible, of course, that younger *Metasequoia* fossils are waiting to be discovered in central China, but it is also conceivable that the chronological and geographical gap in the fossil record reflects the tree's absence during the period of more than 15 million years between the Middle Miocene and Early Pleistocene.

Pliocene and Pleistocene *Metasequoia* fossils have been found only in central and southern Japan. Geological evidence shows that the land link between southern Japan and eastern China (at about 34 to 36 degrees North) was available most recently during the late Pliocene to early Pleistocene interval, during the same period that *Metasequoia* trees are known to have lived in southern Japan. This land connection could have provided a migration route for its westward relocation (Wang 1985).

There is also evidence that, while the climate in Japan during the Pliocene appears to have been suitable for *Metasequoia*, the aridity of central China in that period would not have allowed it to survive. Conversely, during the Pleistocene "Ice Age," southern Japan may have become too cold for *Metasequoia* (Momohara

1992), while central China, which was not significantly influenced by continental glaciation, thanks to the intervening mountains, could have been a protected haven for the species. One possible interpretation of the fossil distribution and climate data is that *Metasequoia* migrated southward during the Late Pliocene or Early Pleistocene from Japan to the modern *Metasequoia* Valley.

Finally, the preliminary RAPD data seem to be compatible with the fossil record, suggesting the recent establishment of *Metasequoia* in its present range. Unfortunately, it offers no precise information regarding the antiquity of the living population, but further molecular study may yield better data.

Conservation Efforts

During my second visit to *Metasequoia* Valley, I was happy to see promising results from local conservation efforts, including preservation of large trees in the wild, a plantation of grafted trees, and reintroduction of seedlings to other parts of China and throughout the world. Despite a very limited budget, a *Metasequoia* conservation station in Xiaohe, with Mr. Shenhui Fan as the director and only employee, has maintained a large *Metasequoia* seedling farm and a plantation grown from grafts of wild

PETER DEL TREDICI



Long He, Hubei, 1994. In China, *Metasequoia* has been planted in groves and along roads in great numbers, and many nurseries have been established to produce seedlings for cuttings. The rooting efficiency of cuttings decreases with the age of the source tree; the best source of cuttings is from seedlings aged one to three years.

trees. Local people still worship the giant trees, believing they bring the family good luck (nowdays translated into prosperity) and bless their children with healthy bodies and bright minds. Educational programs are increasing, as is local awareness of the significance of these trees. Many articles in the Chinese press have featured *Metasequoia*, describing its discovery, scientific value, and current conservation programs.

Over the next fifteen years or so, the *Metasequoia* trees will witness the construction of the controversial Three Gorges Dam on the Yangtze River, not far from their native land. The huge manmade lake behind the dam is bound to affect the local climate and related ecosystems. It is my hope that the remarkable resilience of this species will again enable it to cope with dramatic environmental changes, as it has so successfully done throughout its history.

Fifty years may be short for the dawn redwoods, whose lifespans easily exceed hundreds of years, but it is long enough for political, economic, and technological changes to occur around their native valley. Our knowledge of these magnificent trees has grown substantially over the past fifty years, thanks to new technologies and to several generations of industrious scientists. As studies of the species continue to provide scientists with new inputs for new ideas and hypotheses, the fascinating *Metasequoia* tale will continue to evolve.

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Acknowledgments

This article is dedicated to two scientists of previous generations whose work brought me to *Metasequoia*: Dr. Ralph W. Chaney, whom I never met, but whose thinking on *Metasequoia* and other fossil plants has always intrigued me; and Dr. Charles J. Smiley, with whom I shared the joys of both the *Clarkia* fossil site in Idaho and *Metasequoia* Valley in China. I would like to thank my colleagues at the Nanjing Institute of Geology and Paleontology and the Zhongshan University for their collaboration. The research is supported by a Bryant College course release and by summer stipends. My trips to China have been supported by grants from the Chinese National Science Foundation, China Bridge International, and the K. C. Wong Educational Foundation.

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