THE BEARING OF THE LIVING METASEQUOIA ON PROBLEMS OF TERTIARY PALEOBOTANY

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The discovery of huge living trees in California in 1769, followed by the naming and description of the coast redwood, *Sequoia sempervirens*, by Endlicher in 1847,[1] served as a prelude to the recognition of fossil redwoods in many parts of the northern hemisphere. Leafy shoots from the Oligocene of France, originally assigned to *Taxites langsdorfii* by Brongniart[2] were correctly transferred to the genus Sequoia by Heer in 1855.[3] Heer also identified as members of this genus specimens sent to him from the collections of polar explorers, from Tertiary deposits in Greenland, Iceland, Spitzbergen, Siberia, Sachalin, northern Canada and Grinnell Land.[4] Bringing to North America much of the tradition of European paleobotany, Lesquereux recognized several species of fossil Sequoia in the western United States, including the widely distributed *S. langsdorfii*.[5] During ensuing years the occurrence of Sequoia has been widely noted over the northern hemisphere, at middle latitudes in rocks assigned to middle Tertiary, and at high latitudes in rocks of older Tertiary and Cretaceous age. From the pattern of its occurrence during these later periods of earth history, the paths of its migration southward have been charted.[6, 7] Its environment in past ages has been reconstructed from comparisons with the modern habitat of the coast redwood in California and Oregon.

A fossil cone described as *S. heerii* by Lesquereux[8] from beds of Oligocene age on Medicine Lodge Creek (Sage Creek), Montana, differs from other American cones referred to Sequoia in its attachment on a "naked pedicel." Lesquereux believed that the absence of needles on this "pedicel" (if it had had needles it could not have been properly so designated) had resulted from maceration. In later years identical stalked cones have been found at other Tertiary localities in western North America, such as Bridge Creek, Oregon, and Elko, Nevada; some of the cones figured by Heer as *S. nordenskioldi* from the Eocene of Spitzbergen,[9] and as *S. langsdorfii*[10] and *S. brevifolia*[11] from the Eocene of Greenland are also borne on stems lacking needles. For some time it has been apparent that this type of Sequoia cone is readily distinguishable from those of the living species and of other American fossil species; one of my students has even suggested that there are differences sufficient to justify establishing a new genus.[12]

In 1936 Endo[13] pointed out for the first time a significant character in a

cone of this type, assigned to *S. japonica* from later Tertiary deposits of Japan and Korea. His description and remarks are as follows:

"Description: Cone rather small, spherical, ca. 16 mm. in diameter; cone-scales ca. 16 in number, arranged in 4 longitudinal rows, each row with 4 scales; escutcheon hexagonal, transversely grooved and radially wrinkled, 10 mm. wide, 3 mm. high. Peduncle stout, 2 mm. in diameter.

"Leaves with decurrent base, sessile, arranged in 2 lines; linear, bluntly mucronate at apex, 10 mm. long, 2 mm. wide; upper surface slightly furrowed along the midrib.

"Remarks: The arrangement of the cone-scales in the present species is in longitudinal rows, while being usually spiral in most other species. It has this characteristic feature in common with the cones from the Miocene of John Day valley, once described by Lesquereux as belonging to *Sequoia langsdorfii;* unfortunately the latter is too imperfect for farther comparison with the present materials."

Endo's use of the term "peduncle" is unfortunate, since the stems to which the cones are attached appear in at least two specimens (figures 6, 13) to bear leaves. They may best be considered leafy shoots bearing terminal cones. An obscure photograph (figure 12) of a vegetative shoot shows its needles in opposite position, although Endo does not mention this feature in his description of the leaves. In fact, many fossil shoots with oppositely placed needles had been figured as far back as the days of Heer with no reference to this readily observable character.

It remained for Miki[14] to found a new genus, Metasequoia, in 1941 on the basis of stalked cones and leafy shoots from Pliocene deposits at Osusawa and elsewhere in the clay beds of Central Hondo. His description and discussion (in altered sequence) are here quoted:

"Character: Cone pedunculate, scale decussate, shield-form; peduncle with distichous scars of leaves and scaly leaves at the base. Shoot deciduous; leaf distichous, linear, obtuse, petiolate; stomata parallel to the midrib.

"The remains have usually been referred to Sequoia or Taxodium, indeed the cone is like that of Sequoia and the foliage shoot is somewhat like those of Taxodium.

"The cones were never found connected to branches, but as the leaf-scars on the peduncle are also distichous, it is conceivable that the cones and the shoots belonged to the same plant. The foliaged shoots seem to be lateral branches shedding in autumn, because their length is usually constant and the proximal end is covered by scaly leaves, although they have no scaly bud on the top and the branches two or more years old have two or more bud scars on the nearly same point as in Fig. 8 Ge.

"The cone is distinguished from that of Sequoia by the decussate arrangement of scales and by the delicate peduncle having scale leaves at the base. The foliaged shoot differs from Sequoia by distichous arrangement of leaves and by the brittle petiole. At a glance the shape of the shoot of fragmental remain seems to be Taxodium or Cephalotaxus but it differs from Taxodium by distichous leaf and parallel arrangement of stomata on it and from Cephalotaxus by short delicate shoot without scaly bud at the terminal and by the obtuse top of leaf.

"The decussate arrangement of cone-scales is not found in living Taxodiaceae, but a common character in Cupressaceae. The shedding of lateral foliaged shoot with linear leaves is common in Glyptostrobus and Taxodium. So it is sure that the remains

belong to Taxodiaceae but as the characters do not harmonize with those of the living forms, a new genus Metasequoia is established."

Since several of the cone-stems which he figures (*A—g, h, i, j, k*) show scaly leaves or leaf scars, it seems clear that they are modified leafy shoots rather than peduncles. Miki uses the term "distichous" to describe the position of needles on the foliage shoots; whether he meant to indicate their opposite position (and I am inclined to believe from his phrasing that he did) is uncertain, but in any event the term carries no such implication; Sargent[15] even defines "distichous" as "leaves arranged alternately in two vertical ranks," though the word may be equally well used for opposite position. The significant feature of Miki's description is his recognition of the association of cones bearing decussate scales with leafy shoots which were deciduous. He assigns two species to Metasequoia, of which one, *M. disticha*, was originally described as *S. disticha* by Heer[16] from the Eocene of Spitzbergen on the basis of leafy shoots. The second, *M. japonica*, is the species originally described by Endo as *S. japonica* from Miocene and Pliocene deposits in Japan and Korea; it is distinguished from *M. disticha* by the shape and fewer numbers of its cone-scales, distinctions which may not prove to be of specific significance in the light of our present knowledge of the genus. Miki's assignment of these fossil cones and shoots to a new genus, and his conclusion that even though they do not occur in direct attachment they are parts of the same deciduous plant, represent an outstanding discovery in Tertiary paleobotany. It is all the more remarkable, coming as it did only a few years before a second major discovery.

Miki's paper had probably not been read by any paleobotanist or botanist outside of Asia when it was announced, in the spring of 1946, that three trees of Metasequoia had been found living in Central China. Tsang Wang, attached to the Bureau of Forestry of the Ministry of Agriculture, had brought back to Nanking specimens collected at the village of Motao-chi, in eastern Szechuan, about 140 miles northeast of Chungking. This material was studied by W. C. Cheng, Professor of Forestry at National Central University, and H. H. Hu, Director of the Fan Memorial Institute of Biology, both of whom have a wide knowledge of the living plants of China. They soon realized that it represented no known living tree, and comparisons showed that the cones and leafy shoots were essentially the same as those described by Miki from fossil specimens in Japan. Additional collecting by C. J. Hsueh in 1946 resulted in the discovery of several additional trees, and greatly augmented the material available for study. During the fall of 1947, C. T. Hwa, also a student of Professor Cheng, spent several months in the region, with financial support provided by the Arnold Arboretum of Harvard University through the coöperation of E. D. Merrill,[17] and with a small grant from the University of California.

In the region to the south, in western Hupeh, Hwa found several hundred additional trees of Metasequoia, made a comprehensive collection of the woody plants of this general area, and brought out a large quantity of viable seeds. With adequate material for study at hand, Hu and Cheng have recently published an account of this new tree under the name *M. glyptostroboides*.[18] In an earlier paper, Hu[19] had mentioned the discovery of this living tree in his brief discussion of another fossil species, *S. chinensis*, which had been described by Endo from the Oligocene flora of Fushun, Manchuria;[20] Hu correctly transferred it to the genus Metasequoia on the basis of its stalked, decussate-scaled cones. The leaves and cones of the living trees of Metasequoia, as described by Hu and Cheng, differ in no essential respects from those of the fossils on which Miki based his generic description. But there are four additional characters, of particular interest to paleobotanists, which are mentioned by these authors: (1) "opposite, distichously arranged foliage shoots"; (2) "leaves—opposite"; (3) "staminate flowers axillary and terminal, opposite, on racemose or paniculate flowering branchlet-system"; (4) cone-bearing twigs "with decussate linear leaves before maturity, and with conspicuous leaf scars and with persistent bracts at the base in winter." This paper by Hu and Cheng, describing the occurrence and external characters of *M. glyptostroboides*, represents a major contribution to the botany of China and of the world.

With this significant information regarding Metasequoia, both fossil and living, coming over from Japan and China, I have reëxamined with graduate students at the University of California[21] the abundant conifer material in our Tertiary collections from the western United States, and later the collections at the United States National Museum. We have also studied the descriptions and illustrations of Heer and others, covering material from Cretaceous and Tertiary horizons elsewhere in the northern hemisphere. All of the specimens previously referred to *S. heerii*, and many of those assigned to *S. langsdorfii* and several other fossil species, have the cone or foliage characters of Metasequoia. In addition, staminate aments like those of the living species have been found in the Bridge Creek flora (Oligocene) of Oregon, and the Elko flora (Miocene) of Nevada, in association with typical cones and leafy twigs of Metasequoia. These fossil aments and twigs from Nevada had previously been referred to Taxodium.[22] It has become increasingly apparent that many of the specimens assigned to Sequoia and Taxodium from the Cretaceous and Tertiary floras of North America are properly referable to Metasequoia. A generic revision of some of these is now in preparation, under the auspices of the American Philosophical Society and the Carnegie Institution of Washington. At this time it seems desirable to rewrite the description of Metasequoia on the basis of the paleobotanical evidence. In this description

and the following discussion the data provided by fossil specimens will be the primary consideration, though in some cases our knowledge of corresponding parts of the living tree has enabled us better to interpret them. All consideration of fossil stems is here omitted, since study of the wood of Metasequoia, modern and fossil, has not progressed to a point where significant distinguishing characters between it and Sequoia have been noted.

Genus Metasequoia Miki.—Description.—Foliage shoots straight, decussate; alternate pairs which come out from top and bottom of branch are twisted approximately 90° into horizontal plane of laterally disposed pairs so that all lie along one plane on branch, in opposite pairs; pairs originating in vertical plane often missing and represented by scars preserved on top surface of branch; diverging at angles approaching 90°, commonly ranging in length up to 8 cm., deciduous. Needles decussate, twisted with their decurrent bases to form two oppositely paired ranks, closely spaced, diverging at angles approaching 90° in typical, mature specimens; up to 1.8 cm. long, averaging about 8 mm., longest on proximal half of shoot and gradually reduced in length toward its tip; up to 2 mm. in width; obtusely tipped, narrowed and twisted at point of attachment to decurrent base; midrib well defined, with stomata parallel to it on ventral surface. Staminate cones ovate, up to 5 mm. long, with decussate bracts; closely spaced, sessile and decussate on elongate spikes; rotated into one plane so that they appear to be attached in opposite pairs. Ovulate cones globose to ovoid or elliptic, up to 2 cm. long and 1.5 cm. wide, averaging 1.5 by 1.2 cm. (at one American locality (Mollala) they are globose, 1.6 to 2.4 cm. in diameter, open cones slightly broader); cone-scales 12 to 24, decussate, peltate on broad-based stalks, discs lenticular to hexagonal, with transverse, medial grooves. Seeds about 3 mm. long, 1 mm. wide, the surrounding wings asymmetrical, notched at the apex, with over-all length of 4 to 5 mm., width of 3 to 3.5 mm. Cones terminal on stout, straight or curved shoots; cone-bearing shoots probably lateral, up to 4 cm. long and 2 mm. in diameter, more slender at the middle, bearing scaly leaves at base in complete specimens, rarely with scaly leaves or leaf-scars preserved along the shoot, probably widely spaced and evidently decussate.

Discussion.—It is unusual to find leafy shoots attached to branches in the fossil record. Their position is decussate in every instance, though the shoots that come out at right angles to the plane of the branch are commonly missing, and may be represented only by scars which show on the exposed surface of the slab. These fossil shoots average somewhat longer than those of the living *M. glyptostroboides* which we have examined. Some specimens, especially those from Elko, Nevada, and Mollala, Oregon, both of Miocene age, have slender, curving shoots with needles more

openly spaced and directed distally at higher angles than the typical specimens from Bridge Creek and other localities; studies of foliage of living trees have not progressed to a point where we can determine whether there is corresponding variation in *M. glyptostroboides*. Differences of opinion have been expressed regarding the mode of attachment of the needles. I agree with Stebbins[23] that their position is decussate; this may be readily observed at the tips of young shoots on seedlings which we have growing in Berkeley. The older shoots on herbarium specimens, as well as the leafy shoots preserved as impressions on our fossils, also show clearly the alternating position of attachment of successive pairs of needles and the twisting of their decurrent bases to bring all the pairs of needles into a single plane. Thomas Morley, graduate student in botany at the University of California, has at my suggestion sectioned the stem of a leafy shoot of the living *M. glyptostroboides* (sheet No. 753369, Univ. Calif. Herbarium). He finds the leaf gaps opposite at each node, with each successive pair at right angles to the pair below. However, in alternating nodes the leaf gaps and the decurrent leaf bases are twisted approximately 90°, which brings all the points of attachment of the needles into essentially the same plane along the shoot. An original decussate arrangement is thus confirmed by Morley's slides. No difficulty has been experienced in recognizing the opposite position of the needles in well-preserved fossils of Metasequoia; under low magnification the relations of needles and leaf bases to the shoot are as clear as with modern material; both living and fossil specimens are distinguishable at a glance from leafy shoots of Sequoia and Taxodium in which the needles are alternately disposed along the shoots. Like the pairs of needles, the decussately attached staminate cones are twisted into a single plane along the twig so that they are disposed in opposite or nearly opposite pairs. The staminate cones of a fossil specimen from the Oligocene Bridge Creek flora of Oregon are much smaller than those from Elko, and appear to represent a less-developed stage; in the living species there is a similar range in size. A specimen from Elko shows six spikes, in close association like those of the living species. The considerable range in size and shape of the ovulate cones, and in the numbers of their cone-scales, is no wider than is to be found in cones of the living species, and we have no present basis for determining whether such variation will provide criteria for recognizing two or more species.

As stated in the description, needles are commonly lacking from the cone-bearing shoots, and even their attachment scars are difficult to make out on most fossil specimens. The scars are readily visible on shoots of the living plant, and needles may remain in attachment while the cone is on the tree. When it has fallen, the needles are shed; the fossil record is made up exclusively of cones which have fallen to the ground, and the presence of needles on their shoots is not to be expected. Since this dis-

cussion deals with fossil material, in which the cones and leafy shoots are not commonly attached to branches, we have had to qualify certain of our statements regarding their mode of attachment. However, there is little doubt that this follows the general pattern of the living *M. glyptostroboides*, in which the vegetative and reproductive shoots, and their needles and scales, are prevailingly decussate.

A survey of the characters of Metasequoia as seen in fossil material, and a comparison of these characters with those of Sequoia and Taxodium, provides the following bases for distinguishing this Chinese genus:

(1) Leafy shoots decussate, disposed distichously in opposite pairs along the branches in Metasequoia; spiral, disposed distichously and alternately in Sequoia and Taxodium.

(2) Leafy shoots deciduous in Metasequoia and Taxodium; remaining on the branches 3 to 4 years in Sequoia.

(3) Needles decussate on the shoots of Metasequoia, twisted and disposed distichously in opposite pairs; spirally disposed, commonly distichous, on the shoots of Sequoia and Taxodium.

(4) Stomata in parallel bands on each side of the midrib in Metasequoia and Sequoia; irregularly transverse in Taxodium.

(5) Staminate cones decussate on spikes, twisted into distichous, opposite pairs, in Metasequoia; spirally disposed on spikes in Taxodium; solitary in the axils of terminal needles in Sequoia.

(6) Pistillate cones terminal on elongate, probably lateral, leafy shoots in Metasequoia (they are lateral in the living species), the needles widely spaced, deciduous, leaving a naked cone-shoot on shedding; terminal on short scaly shoots which develop at the ends of leafy shoots of the preceding year in Sequoia; cones at the ends of branches in Taxodium.

(7) Cone scales decussate in Metasequoia; spirally disposed in Sequoia and Taxodium.

Our conclusion that Metasequoia rather than Sequoia was the dominant conifer of the Arcto-Tertiary Flora, whose southward migration from high latitudes has been so well established,[6, 7] calls for reconsideration of the paleoecology and floristics of the Tertiary period. It is of primary significance to note that it was not an evergreen but a deciduous conifer which ranged northward to latitude 82° in Grinnell Land during the Eocene. The deciduous habit of Metasequoia was wholly consistent with that of the majority of its angiosperm associates in the older Tertiary floras from high northern latitudes. This same group of trees, only slightly altered in composition, is widely known at middle latitudes, both in North America and Asia, during middle Tertiary time. The need for determining the associates of the living *M. glyptostroboides* becomes at once apparent, for they may represent a closer approach to the Arcto-Tertiary Flora than any modern vegetation as yet studied. It is necessary also to learn as much

as possible about the modern environment of Metasequoia, to serve as a guide for the reconstruction of its habitats in past ages.

In February and March, 1948, with Dr. Milton Silverman, Science Writer for the San Francisco *Chronicle*, I made a brief trip to western Szechuan and eastern Hupeh under the auspices of the Save-the-Redwoods League, and with the cordial coöperation of Chinese scientists and of Chinese and American officials. It was our good fortune to have accompanying us C. T. Hwa who had previously collected extensively in this area. The redwoods of China live in valley bottoms and slopes at altitudes from 4000 to 4450 feet. The discovery trees at Mo-tao-chi, Szechuan, including the largest tree observed[24] with a diameter of 64 inches above the buttress and a height of 98 feet, are growing in the midst of rice-paddies, and no other trees occur within 100 yards. But in the valley of Shui-hsa-pa, in western Hupeh, scores of Metasequoias were observed not only on the borders of rice-paddies on the floodplain, but extending up ravines under conditions which appeared to be relatively natural.[25] This is in no sense a forest, for trees occur largely in isolated ravines in association with other conifers and with deciduous hardwoods which show every evidence of being second growth. These associates had been widely noted at corresponding elevations during our 5-day trip into the area, and the plant formation has been described by Cheng[26] as occurring between 400 and 2000 meters elevation in this area. Among the more common hardwoods noted in immediate association with Metasequoia are chestnuts (*Castanea henryi* and two other species), a small-leafed oak (*Quercus glandulosa*), sweet gum (*Liquidambar formosana*), and cherry (Prunus) of an undetermined species. An evergreen shrub related to our spice-bush (Lindera) is one of the most abundant members of the understory. On adjacent higher slopes the birch (*Betula luminifera*) and the beech (*Fagus longipetiolata*) are common, and in one ravine there is a large tree of katsura (*Cercidiphyllum japonicum*, var. *chinensis*). Four evergreen conifers, *Cunninghamia lanceolata*, *Cephalotaxus fortunei*, *Pinus massoniana* and *Taxus chinensis*, are of regular occurrence here, and small fan palms (*Trachycarpus fortunei*) were noted at various places in the Shui-hsa-pa area. This assemblage is essentially the same as that recorded in the fossil record of the Eocene from high latitudes; many of the figured specimens of Metasequoia from Greenland and Alaska have on the same slabs leaf impressions of katsura or birch; the Oligocene and Miocene floras from the John Day Basin of Oregon and other localities in the western United States include all of the angiosperm genera (except the palm) above recorded, in association with fossils of Metasequoia. Numerous genera which are common members of the Arcto-Tertiary Flora, both in the Eocene of high latitudes, and in middle Tertiary deposits at middle latitudes, have not yet been noted in immediate association with Metasequoia

at Shui-hsa-pa; however, our field work was of limited duration and carried on at a season unfavorable for easy recognition of deciduous trees. We already know that species of Alnus, Acer, Carpinus, Ostrya and Ulmus have been observed within a few miles of Metasequoia trees, and it is probable that other genera known in the fossil record will be recorded during the field season of 1948 while Professor Cheng and his associates are working in this region.

Prior to the study of the trees of this region, the nearest surviving equivalents of the Arcto-Tertiary Flora which I have seen are the mixed bald cypress (Taxodium)—hardwood forest of the Wabash river valley in Illinois and Indiana, and the hardwood forests with associated conifers at middle altitudes on the Island of Hondo in Japan. The occurrence in the Shui-hsa-pa region of Metasequoia and Cercidiphyllum now restricted to Asia,[27] together with many angiosperm genera which occur today in North America as well, gives these groves in the ravines of western Hupeh a closer resemblance to the Eocene floras of Greenland, Spitzbergen and Alaska, and to the Oligocene-Miocene floras of Oregon and Manchuria than any living group of plants known to me. Not only has Metasequoia come down through the ages to survive in Central China, but the whole assemblage of which it is a part has had a long geologic history, and has participated in wide migrations. During these movements covering thousands of miles, and continuing for millions of years, some genera have disappeared and others have been added; minor changes in leaf or fruiting characters which are the basis for specific distinctions have appeared; but the Arcto-Tertiary Flora as we know it from early Tertiary rocks at high northern latitudes is so fully represented in the Metasequoia groves of Central China that there can be no question as to the holarctic origin of this modern vegetation.

That being the case, we may turn to this region for suggestions regarding the physical environment occupied by the Arcto-Tertiary Flora at many localities in the northern hemisphere during past ages. The nearest station which provides climatic data is Chungking, 140 miles to the southwest, and at an elevation more than 3000 feet lower. Annual precipitation here (43-year record) is 43.1 inches, of which 2.3 inches fall in the winter, 11.1 inches in the spring, 17.7 inches in the summer, and 12 inches in the autumn. The mean annual temperature (44-year record) is 66.2°F., ranging from a low of 48.6° in January to a high of 84.4° in August; the mean monthly minimum (6-year record) ranges from 35° in January to 70° in August, and the extreme lowest recorded temperature in 25 years is 28.9°; the mean monthly maximum (6-year record) ranges from 59° in January to 104° in August, and the extreme highest recorded temperature in 25 years is 111°. Relative humidity averages about 82% (16-year record), and there is little monthly variation. It seems probable that at

Shui-hsa-pa, 4000 feet in elevation, there is higher rainfall and a wider range in temperature. At the time of my visit in March, temperatures were mild and light rains fell daily. Villagers reported that there is no snow or frost, and the general aspect of the understory, made up of evergreen shrubs in the Lauraceae, Theaceae, Euphorbiaceae and Palmae, is suggestive of winter temperatures which rarely fall below freezing. Discussing the climate of the Red Basin of Szechuan, on the eastern rim of which our area is located, Cressey has stated:[28] "The climate is temperate and mild. Despite the location in the interior of the continent, it is protected from extremes of temperature by the surrounding mountains, and the contrast between summer and winter is not great. Summer temperatures seldom exceed 100°F., while during the winter the thermometer does not usually drop below freezing."

The only vegetation in North America which is closely comparable with Metasequoia and its associates of Central China is the bald cypress-hardwood forest of the south Atlantic coastal plain and the Gulf of Mexico,

TABLE 1

SHOWING PRECIPITATION AND TEMPERATURE IN REGIONS OCCUPIED BY METASEQUOIA, TAXODIUM AND SEQUOIA

	ALTITUDE, FEET	PRECIPITATION, INCHES					FAHRENHEIT TEMPERATURE		
		WINTER	SPRING	SUMMER	AUTUMN	ANNUAL	MEAN ANNUAL	EXTREME MAX.	EXTREME MIN.
Chungking	754	2.3	11.1	17.7	12.0	43.1	66.2	111	28.9
Brunswick, Ga.	14	9.3	9.8	18.6	12.0	49.7	68.4	103	13.0
Glennville, Ga.	175	9.7	9.9	17.4	9.9	46.9	67.1	106	11.0
Hammond, La.	44	14.9	14.0	18.1	11.2	58.5	67.5	106	1.0
Eureka, Calif.	62	19.5	10.2	1.0	8.3	39.0	51.6	85	20.0

extending northward up the Mississippi Valley to Illinois and Indiana. This is a lowland forest, reaching a maximum altitude of about 475 feet in the valley of the Wabash River. At latitudes corresponding to Shui-hsa-pa in Louisiana and Georgia, this forest lives within a few tens of feet of sea level, ranging up to about 200 feet in Georgia. As in Central China, precipitation is well distributed and adequate over all this region (table 1), with more than half falling in the spring and summer months. In the southeastern United States at the latitude of Shui-hsa-pa, temperatures show essentially the same mean average, but the extreme minima are much lower.

The bald cypress, *T. distichum*, of the American forest has its best development in swamps and on swamp borders, but its occurrence with hardwoods on moist floodplains more closely resembles the environment of Metasequoia in Central China. All of the angiosperm associates in the groves at Shui-hsa-pa have been noted with the exception of Cercidiphyllum and Trachycarpus which are confined to Asia; Sabal takes the

place of the latter genus in the southern United States. In spite of their geographic separation and marked topographic differences, the general aspect of the Taxodium-hardwood forest is surprisingly similar to that of the Metasequoia-hardwood assemblage. This resemblance is the more significant since during middle Tertiary time Taxodium and Metasequoia lived together in western North America and in northeastern Asia, in association with the same angiosperms; during early Tertiary time, these two conifers were widely distributed at high latitudes and with the same genera of hardwoods. Taxodium is almost as widely distributed in the Arcto-Tertiary Flora as Metasequoia. We conclude that this forest type had its origin at the north, in Eocene and Cretaceous time, in a region with a summer-wet and winter-cool climate; the deciduous habit of all the dominant trees, including Metasequoia and Taxodium, is consistent with such a climate. By Oligocene and Miocene time, a similar forest was widely established as far south as Oregon and Nevada, and down into Japan and Manchuria. By the end of the Miocene, Metasequoia appears to have disappeared from this continent; with a changing climatic regime in western North America, the surviving Taxodium-hardwood forest has been confined to southeastern North America. In Asia Taxodium is rare or absent in Pliocene floras; here Metasequoia has continued down to the present, though it is now confined to a limited area where environmental factors are favorable. This tree is reproducing on a limited scale, but its continued existence will be determined by the pressure put upon it by a people whose land, fuel and timber resources are wholly inadequate. A conservation committee has recently been organized in Nanking, and we may hope for its success in protecting some of the groves in which Metasequoia and its associates are living. Glyptostrobus, a close relative of Taxodium, has survived in the lowlands of South China. Sequoia, the living genus most similar to Metasequoia, is likewise a relict genus, restricted to the California and Oregon coast. Here the rainfall regime is wholly different from that in Central China, though the temperature, somewhat lower at this more northerly latitude, resembles that of western Szechuan in its equability (table 1). Our present knowledge of the Tertiary floras of Europe indicate that Heer was correct in his original reference of material from the Miocene of Switzerland to this genus, and that Sequoia rather than Metasequoia lived on this continent during the Tertiary period. Wide-spread submergence in western Europe at this time appears to have provided living conditions which favored Sequoia, although Metasequoia may be found in the fossil record of the Tertiary interior, farther to the east.

Having in mind the deciduous habit of Metasequoia and Taxodium, the deciduous hardwood associates of these genera, both in living forests and in the fossil record, and the modern environments in Central China and southeastern North America, we may suggest certain physical conditions

which may have been best suited to the origin and development of the Arcto-Tertiary Flora. A summer-wet climate appears to have been the primary requisite, with a total annual rainfall in excess of 40 inches. Moderate temperature seldom falling below freezing is also indicated, though a winter characterized by lower temperatures is indicated by the prevailing deciduous habit. The apparent absence of polar ice-caps during at least the early part of the Tertiary period, and postulated ocean circulation, makes it reasonable to accept the occurrence of Metasequoia and its associates as far north as Grinnell Land; possibly it was the darkness of the arctic night rather than low winter temperatures which brought about the annual shedding of the leaves of these trees, a habit which has been retained in Metasequoia even though winter temperature in its habitat in Central China seems not to make the deciduous habit a modern necessity. It is doubtful whether the present altitude of the Metasequoia occurrence, at about 4000 feet, has always been an essential requirement. More probable is the assumption that the high valleys occupied by these trees provide the only existing habitat which is suitable. Farther to the north at lower altitudes, extremes of temperature or precipitation characterize the climate of China, and although the fossil record shows that Metasequoia has lived there in the past, it can no longer do so. The limited area in eastern Szechuan and western Hupeh where the trees are known to have survived is surrounded by mountain ranges which protect them from the climatic extremes which characterize other inland environments. An equable climate rather than a high altitude appears to be the determining factor in the modern occurrence of Metasequoia.

We may summarize our current knowledge of the fossil occurrence and history of the genus Metasequoia as follows:

(1) Many of the fossil leaves and cones from the Cretaceous and Tertiary rocks of high northern latitudes, and from middle latitudes in North America and Asia, which have previously been referred to Sequoia and Taxodium, are now known to be Metasequoia on the basis of recent descriptions of fossil and living members of this genus in Asia.

(2) Vegetative and reproductive units in the fossil record differ in no essential respect from those of the living *M. glyptostroboides* of Central China. Like those of this tree, they are characterized by the decussate arrangement of their shoots, leaves and scales, and by the deciduous habit of leafy and cone-bearing shoots.

(3) Occurrence of Metasequoia in the Arcto-Tertiary Flora, at high latitudes in the Eocene epoch, at middle latitudes in the Oligocene and Miocene, provides evidence of the northern origin of this Flora, and of its southward migration during the Tertiary period.

(4) Survival of Metasequoia in Central China, in association with many of the hardwood genera recorded with it in the fossil records of the

northern hemisphere, provides a basis for reconstructing the climatic conditions under which the Arcto-Tertiary Flora had its origin and subsequent migration. A humid climate with summer rainfall, and with moderate temperatures not regularly falling below freezing, may be suggested as best suited to this deciduous forest during its past history.

[1] Endlicher, S., *Syn. Conif.*, 197–198 (1847).

[2] Brongniart, A., *Prodrome Hist. Veg. Foss.*, 108 (1828).

[3] Heer, O., *Flora Tert. Helv.*, **1**, 54, pl. 20, f. 2; pl. 21, f. 4 (1855).

[4] Heer, O., *Flora Foss. Arct.*, 7 vols. (1868–1883).

[5] Lesquereux, L., *U. S. Geol. Surv. Terr.*, VII, 76 (1878).

[6] Chaney, R. W., *Bull. Geol. Soc. Am.*, **51**, 473 (1940).

[7] Chaney, R. W., *Ecol. Mon.*, **17**, 144–146 (1947).

[8] Lesquereux, L., *U. S. Geol. Surv. Terr.*, VII, 77, pl. 7, f. 13 (1878).

[9] Heer, O., *Flora Foss. Arct.*, **2, 3**, 36, pl. 4, f. 4a (1870).

[10] Heer, O., *Ibid.*, **2, 4**, 464, pl. 43, f. 1 (1869).

[11] Heer, O., *Ibid.*, **3, 3**, 5, pl. 2, f. 8 (1874).

[12] Ashley, J. F., in an unpublished report, written in 1938 when a graduate student, he suggested that stalked cones from Elko might be placed in a genus intermediate between Sequoia and Taxodium.

[13] Endo, S., *Proc. Imper. Acad. (Tokyo)*, **12**, 172, f. 5, 7–13 (1936).

[14] Miki, S., *Jap. J. Bot.*, **11**, 261–263, f. 8 (1941).

[15] Sargent, C. S., *Manual of Trees of North America*, p. 894 (1922).

[16] Heer, O., *Flora Foss. Arct.*, **4, 1**, 63, pl. 12, f. 2a; pl. 13, f. 9–11 (1876).

[17] Merrill, E. D., *Arnoldia*, **8**, 1–8 (1948).

[18] Hu, H. H., and Cheng, W. C., *Bull. Fan. Mem. Inst. Biol.*, **1**, 153–161, pl. 1 (1948).

[19] Hu, H. H., *Bull. Geol. Soc. China*, **26**, 105–107 (1946).

[20] Endo, S., *Jap. J. Geol. and Geog.*, **6**, 27–29, pl. 7 (1928).

[21] Acknowledgment is due T. R. Pray and R. H. Shan for their assistance.

[22] Lesquereux, L., op. cit., 73, pl. 6, f. 13.

[23] Stebbins, G. L., *Science*, **108**, 95–99 (1948).

[24] Hwa reports seeing a tree more than 7 feet in diameter and over a hundred feet tall near Shu-hwi-chang, Hupeh.

[25] It is not possible to determine, in our present state of knowledge, that any of the Metasequoia trees are truly native. However, their association with the same conifers and angiosperms at several places strongly indicates that they have a natural place in this plant formation.

[26] Cheng, W. C., *Trav. For. Toulouse*, **1**, 150 (1939).

[27] *Ginkgo biloba* is also living here, but was noted only near villages and is probably not native.

[28] Cressey, G. B., *China's Geographic Foundations*, pp. 312–313 (1934).