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THE FOSSIL SEEDS FROM THE TITANOTHERIUM BEDS OF NEBRASKA, THEIR IDENTITY AND SIGNIFICANCE

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A few months ago Dr. W. D. Matthew asked me to describe several specimens of the silicified seeds, and the wood collected in 1925 by Paul C. Miller at the locality in the Titanotherium beds on Hat Creek in Sioux County, Nebraska.¹ This locality is said by Troxell² to have been originally discovered by Mr. Dan Jordan, a local ranchman. It was visited by Hatcher and Peterson in 1900.3 The earliest record of this occurrence that I have been able to find is of a visit by Professor E. H. Barbour in 1895, resulting in the proposal of a name for the seeds, which are the principal subject of the present note. Curiously enough this paper seems to have escaped the attention of Dr. Troxell, and of geologists and paleontologists generally, since it is not recorded in Knowlton's Catalogue of North American Fossil Plants.⁵

Before describing the present material a word or two must be said of Professor Barbour's contribution. In this paper he discusses the preservation and what he calls the double kernels of the nuts, and makes the statements that "These [nuts] are closely related to the genus Hicoria." and that it is "apparent that they have characters sufficiently constant and distinct to constitute a new genus." He then proposes the generic term Archihicoria with siouxensis as the type species, although it can hardly be said that he describes either in a scientific sense.

Although called hickory nuts by both Barbour and, more recently, by Troxell, they can be so-called only by courtesy, and not because they are most closely related to the genus *Hicoria* in the family Juglandaceæ. Nor do they represent a distinct genus in this family, and it is quite absurd to suppose that they constitute a primitive or prænuncial genus,

⁵Knowlton, F. H., 1919. 'A Catalogue of Mesozoic and Cenozoic Plants of North America.' U. S. Geol. Survey Bull. 696.

¹I am indebted to the Walker Museum for additional specimens of the seeds.
²Troxell, E. L., 1925. 'Fossil Logs and Nuts of Hickory.' Scientific Monthly, XXI, pp. 570-572,
³Hatcher, J. B., 1920. 'The Carnegie Museum Paleontological Expedition of 1900.' Science, N.S., XII, pp. 718-720, November 9.
⁴Barbour, Erwin Hinckley. 1898.' Chalcedony-lime nuts from the Bad Lands, Archihicoria siouxensis, gen. et sp. nov.' Nebraska State Hist. Soc., Proc. and Coll., 2nd Ser., II, pp. 272-274, tf.

such as the name Archihicoria suggests, since the existing genera of the family were as old, at the time the Titanotherium beds were deposited, as are the Titanotheriums at the present time.

I have compared the fossils with the seeds of all of our existing species of *Hicoria* and *Juglans*, and I think that it can be shown conclusively that the fossil seeds do not differ in any essential features from those of the genus *Juglans*.

The differences between the seeds of the existing species of Juglans and Hicoria, or Carya as many of our European cousins prefer to call the latter genus, are not profound, since both are constructed upon much the same plan. There are certain features, however, which are distinctive. In general the cotyledons in Hicoria are flatter, with their inner surfaces subparallel, so that the whole seed may be spoken of as compressed, the union of the cotyledons is lower, the radicle is shorter and less prominent, the upper lobes of the cotyledons are closer together and extend above the radicular point, the opposite cotyledons are closer together, and their individual basal lobes are approximated and subtend a long narrow pointed sinus.

In *Juglans*, on the other hand, the seeds are not compressed, the two cotyledons are separated by a deeply and roundly excavated area, so that their inner surfaces are concave and distant; their union is higher up; the radicle is prominent and superior, coming to a point in the apex of the nut above the distal lobes of the cotyledons, which are narrowly rounded and far apart; the radicular prominence is continued downward as a smooth sharp keel to the rounded open sinus which separates the relatively distant basal lobes of the cotyledon.

The surface configuration of the seeds is also distinct in the two genera. In *Hicoria* the seeds are corrugated on both sides of the cotyledons and there are usually two prominent longitudinal ridges separated by deep furrows on the outside of each half of a cotyledon—one along the internal margin, and one about half way between the internal and the outer margin, both modified by secondary corrugations. In *Juglans* there is a wide valley on either side of the central keel, marked by inconspicuous transversely radial lines, which on the inside increase in magnitude toward the margin to form the transverse marginal nodes; these lines are even less conspicuous in the valleys on the outside of the cotyledons, where, two-thirds of the distance from a central line to the margin, there is a ridge starting at the apex of the lateral lobe and running subparallel with the cotyledonary keel, until it fades out about midway in its downward course, where the prominent node on the inner

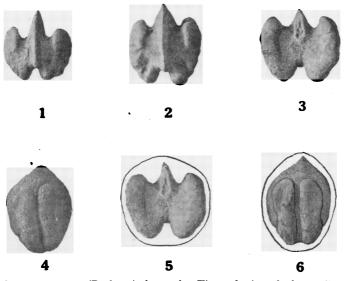
margin of the cotyledonary lobe is most prominent, and marks the upper limit of the ridge which forms the basal margin of the cotyledon.

Whatever the shortcomings of language which preclude a simple and precise statement of the differences between the seeds of the two genera, and whatever the minor variations among the different species, the objects themselves are easily recognized and readily differentiated, and I do not think that anyone would be at a loss to distinguish them.

The fossil seeds are especially like the seeds of the existing Juglans nigra Linné, and I can see no basis for the generic term Archihicoria. The Oligocene species becomes then:

Juglans siouxensis (Barbour)

It may be described in much the same language as a preceding paragraph in which I attempted to characterize the generic features of Juglans seeds. The radicle is high, and where complete is sharply pointed and laterally keeled. In perfect specimens its point is 5 to 6 millimeters higher than the upper margins of the cotyledonary lobes. The largest specimen of seed seen is 2.2 centimeters high and about 2.15 centi-



Juglans siouxensis (Barbour) from the Titanotherium beds on Hat Creek, Nebraska.

- Fig. 1. Outer view of a smaller cotyledon with a very long radicle.

 Fig. 2. Outer view of a larger cotyledon.

 Fig. 3. Internal view of a large cotyledon showing radial markings in the valleys.

 Fig. 4. Entire seed viewed from one side, 90° from preceding. The specimen is slightly compressed but shows the profile of the radicle and its keels above and outside the faintly outlined cotyledonary

 - Fig. 5. Facial view of a cotyledon with the shell outlined.
 Fig. 6. Same view as Fig. 4, with shell outlined and cotyledonary lobes retouched.

meters wide. One of the features which seems to have impressed Barbour was an apparent doubling of the cotyledonary lobes by the development of a saddle-shaped narrow lobe in the main sinuses on either side of the radicle. This might represent an abnormality of actual structure, but it seems to me to more likely represent a secondary deposit of siliceous filling after the cotyledons had become silicified, and before the shell had entirely rotted away. This seems the more probable since such filling occurs, in my material, in but a few specimens in which the whole kernel is present, and in no case do the specimens of single cotyledons show such anomalies. I have seen somewhat similar abnormalities in occasional recent seeds of both Juglans and Hicoria, but whichever explanation is the true one, they have absolutely no systematic importance.

As I have already mentioned, this Oligocene seed is most like those of the existing Juglans nigra. Next among existing forms in point of resemblance is Juglans rupestris major Torrey, and comparisons with the latter have some interest because of the present distribution of that species, a subject to which I will return in a subsequent paragraph. The seeds of Juglans rupestris major are somewhat smoother, the lower lobes of the cotyledons are more incurved than the fossil seeds, and the latter will average fifty per cent larger.

A very moderate estimate of the thickness of the shell of the fossil gives, for the larger of the seeds, profiles for the nut (exclusive of husk) of the size shown in the accompanying figures (Figs. 5, 6).

REGARDING THE METHOD OF PETRIFICATION:—Barbour studied his specimens mineralogically, and concluded that the material was an intimate mixture of chalcedony and calcium carbonate. My specimens showed but slight acid traces of lime, which I took to mean that they were siliceous replacements, since the interstices of the lobes were sometimes filled with crystalline calcite, but I have not examined them petrographically. Doubtless some of them preserve more or less of the cellular structure of the original seed, but since a description of this would shed no light on their relationship, it did not seem to warrant the sacrifice of good specimens.

There are no traces of the shell among my material, although Troxell (loc. cit.) mentions its partial preservation in some of his specimens. As stated above, the seeds seem to me to represent replacements and not casts of the seed cavity of the nuts. I conclude this from the form of the fossils, the fact that many are incomplete, the secondary siliceous material clearly apparent in some specimens, and the calcite filling in others. Its determination is of no great importance in so far as the botanical relationship is concerned.

I have had sections of the associated wood cut. This wood is partly

siliceous and partly calcareous, and appears to have been very badly decayed before petrification, so much so that it is absolutely undeterminable. Although quite possibly true, it is a pure assumption that the wood is related to the seeds. The only statement that can be made concerning the wood is that it is obviously dicotyledonous, since a few vessels can be made out, but my specimen is too far gone to show any generic features or seasonal changes. It is quite possible that if one were to go to the expense of cutting a large number of sections some might show better preservation, but I do not regard this as very hopeful. I am indebted to Dr. Troxell for a considerable fragment of the wood collected by him but it does not look as promising to me as the American Museum specimen that I sectioned.

The chief paleontological interest in this Oligocene walnut centers in any light which it can be made to shed upon the environmental conditions at the time of the formation of the Titanotherium beds. This is possibly of less significance than it might be since these seeds are known from but a single locality, and this might represent a stream margin, and therefore a local and more mesophytic environment than prevailed generally throughout Nebraska and adjacent states at that time, exactly as at the present time several of our southeastern mesophytic trees extend for long distances into the plains country along streams.

Considerable has been written concerning the conditions under which the White River beds were deposited, perhaps the most exhaustive study being that by Wanlass¹ in South Dakota, who concluded that they were mainly fluviatile in that area, although earlier Matthew² had concluded that they were mainly eolian in Colorado. Doubtless there was considerable variation in local environments, with the usual diversification of habitats as represented by channel, flood plain, and eolian sediments in a region of mature topography and sluggish streams; and it cannot be too strongly emphasized that the ecological significance of a fairly large-fruited species of Juglans cannot be extrapolated beyond the horizon and locality at which the fossils are found.

In a general way it is rather universally admitted by those who have studied the question that there was considerable climatic fluctuation during the time of deposition of the White River beds, with local and perhaps more general breaks in sedimentation. Sinclair's studies³

Wanlass, H. F., 1922, 'Lithology of the White River Sediments.' Proc. Am. Phil. Soc., LXI, pp. 184-203. 1923, 'The Stratigraphy of the White River beds of South Dakota,' Idem, LXII, pp. 190-269.

²Matthew, W. D., 1899, Amer. Naturalist, XXXIII, pp. 403-408. ³Sinclair, Wm. J., 1921, Proc. Am. Phil. Soc., Lx, pp. 456-466.

bring this out rather definitely. The earlier White River or Titanotherium time was a time of more or less humid climatic conditions, with a considerable rainfall and rapid accumulation of mostly fluviatile deposits, reflected in the bedding and in the practical absence of caliche or other salt deposits. This is the horizon of Juglans, and of wood said by Chaney (as quoted by Wanlass) to be that of Celtis, as well as remains of a large fauna. The overlying Oreodon beds indicate a much lessened rainfall and a more arid, or perhaps better, a more prairie type of country, with land snails and turtles, and considerab's caliche formation. The later or Protoceras beds seem to show a great humidity than during Oreodon time, but less than during Titanotherium time.

A combination of the distribution of the existing species of Juglans and their geological history should furnish some information regarding the probable environment of this Nebraska Oligocene species. The existing species number 10 or 11 and their range is shown, somewhat exaggerated, on the accompanying sketch map (Fig. 7). This map is not new, but is somewhat more accurate than previous attempts, and is introduced primarily to show that something more definite than geographical location of a plant must be known before any deductions regarding past climates can be drawn from its extinct relatives.

One might assume that Juglans californica in southern California, or Juglans rupestris in our arid southwest, or even the really disconnected range of Juglans regia from Greece to China, indicated a semi-arid type of tree. This is decidedly not true, however. All of the existing species require plenty of water and most of them thrive only in rich and moist soils. In regions where this becomes restricted you find Juglans withdrawing to stream margins, as is the case with the species mentioned above.

The norm of environmental conditions for the genus, and that which I believe to more nearly approximate the primitive conditions, is that demanded by such modern forms as Juglans nigra and Juglans cinerea. The existing California form is a tree of stream banks and bottom lands; Juglans rupestris of our arid southwest is usually reduced in size to a many-stemmed shrub from an unusually deep root which has enabled it to linger on in stream valleys under adverse and progressively drier climatic conditions. It has a variety, major, in central New Mexico and Arizona, which is a larger form. This occurs in a region with a somewhat greater rainfall, and its actual habitat is the rich, well watered soil of canyon bottoms.

As a question of actual relationship I believe that major is really the

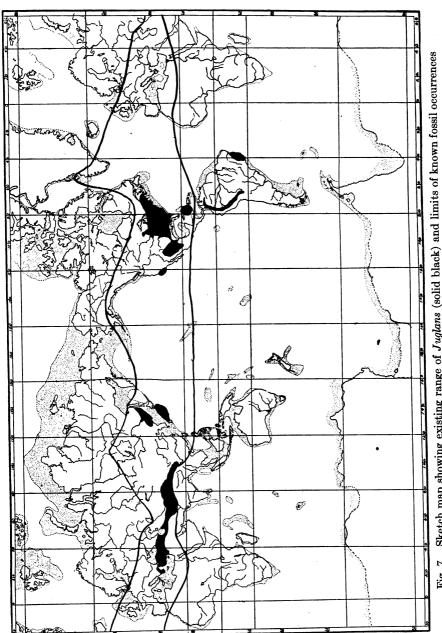


Fig. 7. Sketch map showing existing range of Juglans (solid black) and limits of known fossil occurrences (within irregular latitudinal lines).

ancestral form, now confined to relict situations, and *rupestris* is a derivative, evolved during the progressive desiccation of the southwest.

The geological history of Juglans extends back to the mid-Cretaceous, and the type became essentially cosmopolitan during the earlier Tertiary, at which time the present outlying forms in the Andes and in eastern Brazil were probably connected with the balance of the stock. The known northern and southern limits within which fossil species of Juglans have been discovered are indicated by the irregular latitudinal lines on the accompanying sketch map. The most northern known fossil forms have been found in western Greenland, and in the Aldan region of Siberia. The most southern occur in the Fayûm in Africa, and in the Antilles. Much remains to be learned about the Tertiary floras of the equatorial regions, but it has generally been assumed that Juglans was of equatorial origin.

This somewhat tentative conclusion is based upon the pinnate leaves, on the discontinuous distribution of the existing species, and on the habitat and range of this and other genera of the family. There is considerable validity for this view, especially if we envisage an upland equatorial center of origin.

The Juglans of the Titanotherium beds, as indicated by the size of its fruits, and by the demands of Juglans nigra, its most closely related existing relative, required a rich, deep soil, a mesophytic environment, and an ample water table. This may have been realized by its having been restricted to Oligocene river banks, but the abundance and character of the associated animal life seem to me to indicate that there were considerable areas of forested country in that region, surviving from the earlier Tertiary, and in so far as its features permit of conclusions Juglas siouxensis may very well stand close to the ancestral stock from which the modern Juglans nigra and Juglans rupestris major took their origin—the former more nearly representing the characters and habitat of this stock, and the latter representing more of a climatic modification in the direction of Juglans rupestris.