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## STATUS OF AN ASIATIC MEMBER OF THE JUGLANDACEAE REGARDED AS A 'LIVING FOSSIL'<sup>1</sup>

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THE DESCRIPTION of a living representative of a genus known previously only from the fossil record is a rare event of considerable interest to both neo- and paleobotanists. The extent of this interest may be measured in part by the large number of papers concerned with *Metasequoia glyptostroboides* since the discovery of this 'living fossil' was reported in 1948. Recently Dr. Hsen-Hsu Hu (1952), who had a part in the discovery of the modern *Metasequoia*, has concluded that a member of the walnut family now found in China and Indo-China is a living species of *Juglandicarya*, a genus previously known only from fossil fruits occurring in the Eocene London Clay formation of England. The writer, who recently examined the material of *Juglandicarya* in the collections of the British Museum (Natural History), believes that this assignment is in error. The following discussion reviews the available information on the living and fossil species as a basis for the contention that the species are not congeneric.

Unlike *Metasequoia glyptostroboides*, this Recent species has been known to botanists for a number of years. However, a lack of reference to the pertinent literature, in part unavoidable, by authors dealing with this species has led to much confusion with regard to its systematic position and nomenclature.

Fruits of the species were described as *Carya sinensis* by Dode (1912), but his description was overlooked until 1950. Meanwhile the species was again described from other material by Chevalier (1941), who placed it in a new genus, *Annamocarya*. Although naming this plant *A. indochinensis*,

*sis*, Chevalier also inexplicably referred to it as *Juglans indochinensis* in the same paper. Later in the same year Kuang (1941) independently proposed another new genus, *Rhamphocarya*, whose single species, *R. integrifoliolata*, is also based upon material of the plant under discussion.

Hjelmqvist (1948), overlooking the earlier descriptions by both Dode and Chevalier, transferred the species from *Rhamphocarya* to *Carya*, creating the new combination *C. integrifoliolata* (Kuang) Hjelmqvist. W. Y. Chun had previously referred the species to *Carya* as *C. tsiangii*, but this combination was never published (Manning and Hjelmqvist, 1951).

Leroy (1950) concluded that the species constitutes a distinct genus and, with full knowledge of the pertinent literature, proposed the new combination *Annamocarya sinensis* (Dode) Leroy as its name. Leroy's reason for taking the species out of *Carya* was based chiefly upon the vascular structure of the fruit (1951a, b). He reported that the vascular strands extend from the base to the apex within the inner wall of the fruit rather than within the primary partition as is the case for both *Carya* and *Juglans*.

Manning and Hjelmqvist (1951), after examining all available herbarium material but without knowledge of Leroy's work, reaffirmed Hjelmqvist's earlier opinion that this Asiatic species belongs in *Carya*. As Leroy had done earlier, they linked Dode's description of *Carya sinensis* to the material at hand. After rejecting the possibility that the species is closely related to *Juglandicarya*, they concluded that its name should remain as *Carya sinensis*.

The first intimation that this Recent species might be a 'living fossil' was made by Chevalier when he described it as *Annamocarya indochinensis*. He considered that its fruits showed features suggesting both *Juglans* and *Carya*, and that the species might represent a form ancestral to these two genera. Merrill (1948), using the name *Rhampho-*

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*carya*, regarded the plant as a living representative of the fossil genus *Caryojuglans* Kirchheimer. The monotypic *Caryojuglans*, described from fruits found in European brown-coal beds, is regarded by Kirchheimer (1938) as an intermediate between *Juglans* and *Carya*. Mädlar (1939) believes that its single species should be assigned to *Juglans*, and Leroy (1952) assigns the species to *Carya*. The fruits of *Juglans* and *Carya* have several features in common and, particularly in the fossil state, are sometimes difficult to distinguish. Their characteristics have been discussed by Mädlar and by Kirchheimer (1951). Both Kirchheimer (1951) and Manning and Hjelmqvist (1951), after examining fruits of the Recent '*Rhamphocarya*', have rejected the possibility that it is a species of *Caryojuglans*. Kirchheimer has also expressed the opinion that the Asiatic species does not belong to *Juglandicarya*.

Hu's (1952) transfer of the problematic species to the fossil genus *Juglandicarya* is the most recently published opinion regarding its affinities. Of the papers cited above, Hu referred only to Kuang's work. It should be noted, however, that because of the length of the period during which Hu's paper was in press, he could not have seen any of the papers published during 1951. Hu considered the earliest previous name for the species to be *Rhamphocarya integrifoliolata* and created the new combination *Juglandicarya integrifoliolata* (Kuang) Hu to designate it.

The net result of this involved sequence is that since it was first described this one juglandaceous species has been associated with six generic names: *Carya*, *Juglans*, *Annamocarya*, *Rhamphocarya*, *Caryojuglans*, and *Juglandicarya*. There are currently three independent proposals regarding its designation in the literature: *Annamocarya sinensis* (Dode) Leroy, *Carya sinensis* Dode, and the one to be discussed here, *Juglandicarya integrifoliolata* (Kuang) Hu.

The genus *Juglandicarya* was founded by Reid and Chandler (1933, p. 140) to contain "Fruits which, although clearly referable to the Juglandaceae, are of doubtful generic relationship both to living genera and to one another." It includes four published species, one of which, *J. crassa* (Bowerbank) Reid and Chandler, was based on material which had disintegrated in storage before the latter authors transferred it to *Juglandicarya*. The original description is not adequate for comparisons. Opinions regarding the possible affinities of the other three species are shown in table 1. These diverse opinions bear out the conclusion of Reid and Chandler that the species assigned to *Juglandicarya* do not constitute a single natural genus. It is often necessary for paleobotanists to erect genera of this sort; unfortunately, botanists who work chiefly with modern plants do not always recognize the element of artificiality inherent in them.

As would be expected where relationships can be established clearly only to family level, the observ-

TABLE 1. Summary of opinions regarding the possible affinities of the species of *Juglandicarya* Reid and Chandler.

<i>Juglandicarya</i> Species	Nearest Modern Relative		
	Reid and Chandler (1933)	Kirchheimer (1951)	Manning and Hjelmqvist (1951)
<i>J. lubbocki</i>	<i>Juglans</i>	<i>Engelhardtia</i>	<i>Pterocarya</i> ,
<i>J. cantia</i>	<i>Juglans</i>		<i>Engelhardtia</i> ,
<i>J. depressa</i>	<i>Pterocarya</i> ,	<i>Pterocarya</i>	<i>Juglans</i>
	<i>Juglans</i>		<i>rupestris</i>
<i>J. crassa</i>	Specimens disintegrated in storage		

able features of the species of *Juglandicarya* are for the most part general ones typical for the walnut family and not necessarily limited to any one modern genus. Reid and Chandler's diagnosis of *J. cantia* is representative (1933, p. 142):

"Endocarp globular, smooth, and without external nodulations, dehiscing into equal valves, one-loculed, one-seeded; walls thick, without cavities. Seed erect, orthotropous, conforming to the shape of the locule, simple above, two-lobed below, each lobe being slightly emarginate at the base. Diameter of endocarp about 12 mm."

The similarities upon which Hu bases the supposed congeneric relationship between '*Rhamphocarya*' and *Juglandicarya* are stated in this quotation (1952, p. 264):

"*Rhamphocarya* has a smooth, globular to ellipsoid, one-loculed and one-seeded endocarp with thick wall without cavities. Its seed is erect, orthotropous, conforming to the shape of the locule, simple or emarginate above, deeply two-lobed below, the lobes again being shallowly two-lobed by a secondary septum. Its contours are smooth. These characteristics are similar to those of *Juglandicarya*; only the size of the endocarp is much larger."

This description of the fruit of '*Rhamphocarya*' is obviously similar to the diagnosis of *Juglandicarya cantia* and is also like that of *J. lubbocki*. Of the species of *Juglandicarya*, Hu found these two to agree most closely with the modern species. The correspondence which he points out is not, however, adequate evidence for congeneric relationship. Hu's characterization of '*Rhamphocarya*' is a generalized one which is also applicable in most respects to fruits of other genera in the walnut family, for example, *Juglans* and *Carya*. The only feature in which the agreement might indicate close relationship to *Juglandicarya* is the stated lack of cavities in the wall of the modern nut. Wall cavities, absent in *Juglandicarya*, are usually lacking in *Carya* but do occur in at least three species; they are always present in *Juglans* although sometimes greatly reduced. This similarity between '*Rhamphocarya*' and *Juglandicarya* is not a reliable one, however, for Manning and Hjelmqvist (1951) have

described and illustrated cavities in the wall of the nut near the apex in the modern species.

Except to note the much larger size of the fruit of the Asiatic species, Hu did not consider the differences between it and the species of *Juglandicarya*. Internal ridges, typical for *Carya*, are present on the nutshell of the modern form but are absent from *Juglandicarya*. As Manning and Hjelmqvist have pointed out, the seed of the modern species is compressed in the plane parallel to the primary partition rather than at right angles to this plane as are the seeds of *J. cantia* and *J. lubbocki*. The primary embryo lobes of *J. cantia* are entire at the base; *J. lubbocki* has a secondary partition which is as wide as the primary partition. The modern nut is prominently apiculate, but the nuts of these two *Juglandicarya* species are rounded.

The resemblances of the Asiatic species under consideration to the two species of *Juglandicarya* are only general ones, and there are significant differences between them. Through the courtesy of Miss M. E. J. Chandler and Mr. W. N. Edwards, Keeper of Geology, British Museum (Natural History), the writer was permitted to consult the manuscript of Miss Chandler's forthcoming publication in which additional species of *Juglandicarya* are described. None of these new species appears to be any more closely related to '*Rhamphocarya*' than are *J. cantia* and *J. lubbocki*. No substantial evidence for the relationship of '*Rhamphocarya*' to the fossil genus has been presented by Hu, and his transfer of the modern form to *Juglandicarya* is unjustified.

In addition to the question of affinity there are other objections to the use of the name *Juglandicarya integrifoliolata* (Kuang) Hu for the species under discussion. It has been established that this species was first described by Dode as *Carya sinensis*; hence Hu's combination is illegitimate. Article 68 of the new International Code of Botanical Nomenclature, which came into effect after Hu submitted his manuscript for publication, provides that when a taxon of Recent plants, except algae, and a taxon of the same rank of fossil or subfossil plants are united, the correct name of the former taxon must be accepted even if it is antedated by the latter. Thus use of the name *Juglandicarya*, based on fossil material, is now illegitimate for modern plants. If the relationship pointed out by Hu were correct, it would be necessary to transfer the related species of *Juglandicarya* to the genus to which the modern Asiatic species belongs. The underlying wisdom of this Article is well illustrated in this case, for the transfer of a living species to *Juglandicarya* would place the species in a taxon whose members are of uncertain generic relationship to one another.

If this modern species is not related to *Juglandicarya*, what are its affinities? Two opinions remain: Manning and Hjelmqvist consider it to be a species of *Carya*, while Leroy believes that it constitutes a

separate genus. Further investigation is needed before this question can be settled finally. Both the anatomy of the secondary xylem (Heimsch and Wetmore, 1939) and the morphology of the pollen (Heimsch, 1944) are useful in delimiting the genera in the Juglandaceae and for the most part support the relationships suggested by Manning (1938) on the basis of his study of the floral morphology of the family. Thus it appears that when sufficient material becomes available to permit application of the varied approaches of modern taxonomy to this enigmatic Asiatic species, it may become possible to establish its correct affinities. Meanwhile, it seems advisable to refer to the plant as *Carya sinensis*, in the genus to which it was originally assigned and which Manning and Hjelmqvist (1951) have lately reaffirmed as correct. One thing seems certain, however; the species is not a 'living fossil' in the sense of being a closely related survivor of those members of the walnut family that formed a part of the Paleotropical assemblage known to have flourished during the Eocene in the region of present-day England.

#### SUMMARY

Dr. Hsen-Hsu Hu has concluded that a member of the walnut family now found in China and Indo-China is a living species of *Juglandicarya*, a genus based on fossil fruits from the Eocene London Clay formation of England. The genus *Juglandicarya* was founded to include fossil juglandaceous fruits identifiable to family only, and its species are of doubtful relationship to one another. The features which Hu found to be common to the living species and *Juglandicarya* are for the most part general ones also shared by other genera in the family. He ignored important differences that exist between the modern and the fossil fruits. In the opinion of the present writer, these differences are sufficient to preclude their generic identity. There are also nomenclatorial objections to the use of the name proposed by Hu. This modern Asiatic species cannot be considered to be a 'living fossil' in the sense of being a closely related survivor of any of the extinct species included in the genus *Juglandicarya*.

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## BIOSYSTEMATIC STUDIES IN ASTER. I. CROSSING RELATIONSHIPS IN THE HETEROPHYLLI<sup>1</sup>

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THE COMPLEXITY of species pattern in the genus *Aster* has long been noted. Much of the taxonomic difficulty has been ascribed to the blurring of species boundaries by hybridization. The only previous experimental hybridization studies of asters were conducted by Wetmore and Delisle (1939) with *Aster novae-angliae* and *A. ericoides* (*multiflorus*). Several floristic studies of asters have been made recently (Shinners, 1941, 1945; Rosendahl and Cronquist, 1949) but the group under consideration here has never been subjected to cytogenetic analysis.

The present study concerns a group of nine closely-related aster species generally known as the HETEROPHYLLI. It is the purpose of this study to examine the concept of hybridization as a prominent cause for the taxonomic difficulty of the group and to examine those factors which may be operative in directing the evolutionary pattern of these species. The present paper is designed primarily to present a preliminary survey of the crossing relationships among seven of the heterophyllous species. The evolutionary consequences of the speciation pattern will be discussed elsewhere (Avers, 1953).

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The species under consideration here are morphologically similar in many respects. Varieties have been largely ignored in the present treatment. Many of the varieties now recognized are merely the result of hybridization and local ecological variation and their taxonomic recognition would burden the literature without elucidating the genetic relationships among the species.

The heterophyllous asters are perennial herbs which are most frequently found in small populations in shaded woodlands. The species occur in eastern North America except for the boreal *A. ciliolatus* Lindl. which extends from coast to coast. While several of these taxa are allopatric, many are sympatric over a large part of their range.

CYTOLOGY.—Determinations of chromosome numbers from pollen mother cells were made using the acetocarmine squash technique after preliminary fixation in chloroform-ethanol-acetic acid, 4:3:1. The basic chromosome number in this group is 9, with diploid, tetraploid, and octaploid species represented. No multivalents were apparent in examinations of wild material of the parent species. Table 1 shows the chromosome numbers of the HETEROPHYLLI, which are here reported for the first time.

Meiotic behavior in the hybrids was examined and all F<sub>1</sub> hybrids evinced regularity of chromosome pairing although a small percentage of pollen mother cells contained two to four unpaired chromosomes. Hybrids between homoploid species showed no evidence of multivalent associations.

Pollen fertility was determined by relative stain-