DOCTORAL DISSERTATION SERIES

PUBLICATION: 5727

AUTHOR: Richard Albert Scott, Ph. D., 1953
University of Michigan

TITLE: FOSSIL FRUITS AND SEEDS FROM THE EOCENE CLARNO FORMATION OF OREGON

University Microfilms, Ann Arbor, Michigan, 1953

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by

Richard A. Scott

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy in the
University of Michigan
1952

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Abstract

One of the uncommon occurrences of fossil fruits and seeds in the Tertiary beds of western United States is found in the Eocene Clarno formation of north central Oregon. The fruits, which are mostly siliceous locule casts surrounded by carbonized endocarpal remains, were obtained from a single locality in two unstratified beds of highly indurated rock of volcanic origin. About four hundred specimens have been collected.

Ten species of fruits and seeds have been identified from the Clarno locality. They represent eight genera and seven families. Eight of the species and three of the genera have not been described previously.

Fossil leaves are also known from the Clarno formation, and from them Chaney has identified seventeen angiosperm genera in fourteen families (unpublished data). There is little agreement between the lists based on the two types of remains. There is not a single genus in common, and only four families, the Vitaceae, Lauraceae, Menispermaceae, and Nyssaceae are found on both lists.

Although correspondence is slight, the affinities of the fruits and seeds bear out the previous interpretations of the

Clarno and other early Tertiary floras known chiefly from leaves. These floras indicate humid, sub-tropical conditions in Oregon during the Eocene. One of the families represented by fruits and seeds, the Icacinaceae, is now exclusively tropical, and another, the Menispermaceae, is almost exclusively tropical. The major components of the western early Tertiary Flora, the Paleotropical, Neotropical, and temperate to warm temperate elements, are each represented by fruit and seed forms.

The numerically dominant form among the Clarno fruits and seeds is a new species of walnut (Juglans). This is the first walnut fruit known with certainty from rocks as old as the Eocene. This occurrence of Juglans demonstrates that the fruits of the walnut and the hickory (Carya) were generically distinct during Eocene time. It has been suggested previously that, although the leaves of the two genera are known to have been distinct during the Eocene, their fruits were not differentiated until later.

About two-thirds of the genera to which the Clarno fruits and seeds belong are extinct. This figure, comparable to that for the considerably larger fruit and seed flora from the Eocene London Clay, is much higher than is found for the American Eocene floras known principally from leaves. The higher proportion of extinct genera among the Clarno and London Clay fruit and seed assemblages than among the Eocene floras based on leaves suggests that the leaves of some early Tertiary plants may have differentiated along modern generic lines before their reproductive organs. Although the evidence is as yet

PREFACE

Investigation of this problem was suggested by Professor C. A. Arnold, whose assistance is gratefully acknowledged. Most of the work was done at the British Museum (Natural History) and at Kew Herbarium during the 1951-52 academic year, while the writer was a Fulbright Scholar at Bedford College, University of London. The opportunity provided by this appointment, through the United States Department of State, has been deeply appreciated. The writer is most grateful to Mr. W. N. Edwards, Keeper of Geology, for making available the facilities and collections of the British Museum (Natural History), particularly the fruits and seeds described by Reid and Chandler in the London Clay Flora. The outstanding work of these investigators has been the source of much information. Mr. Edwards also gave access to Miss M. E. J. Chandler's manuscript of the initial volumes of the Tertiary Floras of England, ensuring that the Clarno forms described by the present writer do not duplicate any of the numerous fruits and seeds to be described in the forthcoming publication of the Museum. Sir Edward Salisbury, Director, Royal Botanic Gardens, Kew, kindly allowed examination of material in the Herbarium of that institution.

The courtesy of Professor R. W. Chaney, University

of California (Berkeley), in furnishing a list of genera from his unpublished work on the Clarno flora, and of Professor L. Hawkes, Bedford College, University of London, in examining thin sections of the matrix in which the Clarno fossils occur is gladly acknowledged. A grant from The Research Club of the University of Michigan made possible the examination of material in the seed collection at the United States Department of Agriculture, Beltsville, Maryland, and in the United States National Herbarium, Washington, D. C. The writer wishes to express his sincere appreciation to the following, who, by allowing access to herbaria, by loaning or donating specimens, or by suggesting possible affinities for the fossils, have aided this study: Professor E. S. Barghoorn, Biological Laboratories, Harvard University; Professor H. H. Bartlett, Department of Botany, University of Michigan; Doctor R. W. Brown, United States National Museum; Miss M. E. J. Chandler, Lymington, England; Mr. W. N. Croft, Department of Geology, British Museum (Natural History); Mr. A. W. Hancock, Portland, Oregon; Mr. H. F. Hastings, Walnut Canyon National Monument, Arizona; Doctor Theodor Just, Department of Botany, Chicago Natural History Museum; Professor C. D. LaRue, Department of Botany, University of Michigan; Professor W. E. Manning, Botanical Laboratories, Bucknell University; Doctor H. N. Moldenke, New York Botanical Garden; Doctor P. A. Munz, Rancho Santa Ana Botanic Garden, Anaheim, California; Professor W. S. Phillips, Department of Botany, University of Arizona;

Mr. P. G. Russell, United States Department of Agriculture, Beltsville, Maryland; and Doctor George Taylor, Herbarium, British Museum (Natural History).

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INTRODUCTION

A most unusual occurrence of fossil fruits and seeds in the Tertiary beds of western United States is found in the Clarno formation of Oregon. The existence of these fossils has been known to amateur collectors and paleobotanists for a number of years, and the desirability of studying them has been pointed out by Chaney (15). The material has not, however, been investigated previously. It is the purpose of this study to describe the available Clarno fruits and seeds, and to determine their relationships with modern and early Tertiary plants.

Although cellular structure has not been preserved in the Clarno fossils, the morphology of most forms is sufficiently distinctive to permit identification. A majority of the fruits are drupes preserved as carbonized endocarps in which the seed is represented by a chalcedony cast of the locule. The details of preservation differ somewhat among them, and will be mentioned in the separate descriptions.

Previous knowledge of the Clarno flora is based almost entirely upon leaf remains, which have been found at several localities. Plants from the formation were described long ago by Newberry and Lesquereux, but the first comprehensive account is contained in Knowlton's Fossil

Flora of the John Day Basin, published in 1902 (32). After summarizing the early work on the flora, he listed 22 forms from the "lower" Clarno and an additional 45 forms from a locality along Bridge Creek, which he regarded as "upper" Clarno. Chaney (11) has since shown that this Bridge Creek locality is not in the Clarno, but belongs in the overlying John Day formation.

In recent years leaves from the Clarno formation have been extensively collected and studied by Chaney. He has described the general subtropical aspect of the flora in his several discussions of the Tertiary floras from western United States, the most recent of which appeared in 1948 (13). In the following year Chaney (14) pointed out the occurrence in the formation of an altitudinal ecotone with Metasequoia as its most prominent member. Arnold (1, 2) has recently described two new species of the fern Osmundites from silicified material occurring in the Clarno formation. However, Knowlton's paper remains as the most extensive single treatment of the Clarno flora. Prof. Chaney has supplied from his unpublished notes the names of the genera which he now tentatively regards as composing the flora. These genera are listed in a later section of this paper.

A collection of the Clarno fruits and seeds was made in the summer of 1949 by a field party from the Museum of Paleontology, University of Michigan, headed by Professor C. A. Arnold and including Mr. Robert Linsley and the present writer. The writer spent two weeks at the locality in

July 1950, and obtained additional material. On both occasions Mr. John Silvertooth, Antelope, Oregon, gave valuable field assistance. The combined collections, numbering approximately 400 specimens, form the main basis for this study. Material from the Clarno locality in the collections of the United States National Museum has also been examined through the cooperation of Dr. R. W. Brown. Mr. A. W. Hancock has kindly donated a number of representative specimens from his private collection. Unless otherwise indicated, all specimens described are in the Museum of Paleontology, University of Michigan.

GEOLOGIC OCCURRENCE

The fossil fruit and seed locality occurs in the Clarno formation about 1½ miles east of Clarno's Ferry (now a bridge), in the SE ¼, Sect. 27, T. 7 S., R. 19 E., Wheeler County, Oregon (Plate I). This location, in the basin of the John Day River, is near the type locality of the formation, which crops out in an area of several hundred square miles in north central Oregon. The Clarno formation was named and described by Merriam (39) in 1901, and since that time has been mentioned frequently in the abundant literature concerned with the geology and paleontology of the John Day Basin. Hodge (25), in his description of the geology of north central Oregon published in 1942, has discussed the Clarno formation and mapped its areal extent. Portions of the formation have recently been examined in considerable detail by a United States Geological Survey party during a study of the Horse Heaven mining district (48).

The beds which compose the Clarno formation are almost entirely of volcanic origin and, so far as has been exposed, were deposited upon the eroded surface of Mesozoic marine rocks. They were originally up to 3000 feet in maximum known thickness, and include conglomerates, tuffs, breccias, ashy layers, and lava flows. The predominately andesitic material has undergone alteration both hydrother-

mally and by weathering. The layers are often highly indurated and resistant to erosion and, most notably in the coarser basal portions, form cliffs with odd, roundly weathered faces referred to locally as "castle rocks" (Plate II, Fig. 1).

The formation represents a long period of intermittant volcanic activity. Many of the intervals were long enough for soil surfaces and vegetation to develop. During these intervals erosion was active, and many of the original lava and detrital deposits have been reworked. After the formation was deposited it was folded in a NW-SE direction and eroded to its present variable thickness, which is often only a few hundred feet. The overlying John Day formation, whose lower member is of upper Oligocene age, was deposited upon the Clarno topography.

In his original description of the Clarno formation, Merriam considered it to be of Eocene age. This determination was Knowlton's and was based upon correlation of the fossil plants from the formation. Since then it has been assigned ages ranging from lower Eocene to lower Miocene. Since 1935 Chaney, quoted by Sanborn (45), on the basis of his study of the fossil leaves, has regarded the Clarno as upper Eocene and this age has been generally accepted.

The difficulty in determining the age of the formation arises in part from the lack of animal fossils. The only known occurrence is a single tooth belonging to the rhinoceros genus Hyrachyus which was found near the fruit

and seed locality. This tooth was described in 1944 by Stirton (47) in a paper which also contains a summary of the previous opinions on the age of the Clarno. According to this author, the tooth clearly places the formation within the Eocene and indicates its probable middle Eocene age.

The affinities of the fossil fruits and seeds, chiefly subtropical, substantiate the Eocene age of the formation, but do not contribute to a closer determination. Only two of the species have been described previously, both from the lower Eocene of England; and their correlative value is dubious. The upper Eocene age suggested by Chaney for the Clarno formation is based upon the most extensive evidence, but there is some evicence that the formation may be slightly older.

At the fruit and seed locality from which the present collection was made the exposure consists of beds of volcanic tuff dipping 20 degrees to the NW and overlain by about 200 feet of the purple to gray shale of the lower John Day formation (Plate II, Fig. 2). The fossils occur about 25 feet below the top of the Clarno in this immediate area. They are limited to two beds of indurated tuff separated by a two to three inch layer of clay. The lower bed, containing most of the remains, is about two feet thick; the upper bed, containing chiefly walnuts, is only one foot thick (Plate II, Fig. 3). The fruits and seeds seem to be confined to an area about twenty-five feet wide, although an

occasional specimen can be found farther away. Within each layer the components of the rock show no traces of stratification, and the fruits and seeds are distributed irregularly. They are accompanied by leaf fragments, Equisetum stems, and segments of silicified branches. Silicified logs occur near by but do not appear to be in situ. Although no identifiable leaves were found by the writer, Chaney[1] mentions having collected determinable leaf remains, including a cycad, from the locality. Stems of Equisetum, in their original position of growth, are preserved about 300 feet to the northeast in what is either a continuation of the lower fossiliferous bed or an equivalent bed at the same level. The beds in the area lens out so that it is difficult to trace individual layers for more than short distances.

As an aid in interpreting the conditions under which the Clarno fruits and seeds were buried, Professor Leonard Hawkes has examined thin sections of the fossiliferous matrix. He has furnished the following description:[2]

> The thin sections (A, 621, 622) show fragments of lava rocks, oligoclase, and carbonaceous material in a very fine grained matrix of weakly doubly-refracting substance, presumably 'clay minerals'. No detrital quartz is present, but in section 622 some irregular areas are infilled with chalcedony.
>
> The lava fragments are largely felspathic. Most are fine-grained with flow texture--some have porphyritic oligoclase. Ferro-magnesian minerals are sparse and altered--some fresh biotite can be recognised. The lavas are of latite and allied types.

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[1]Letter dated April 3, 1952.

[2]Letter dated March 17, 1952.

There is no glass or 'shard' structure to indicate the presence of contemporaneous volcanic ash in the deposit, which is unbedded and heterogeneous in grade. The impression is of a deposit resulting from the erosion of a terrain of lavas.

This interpretation of the lithology indicates that the layers were not formed as the result of ash falls. The lack of stratification and the presence nearby of vertical Equisetum stems indicates that the sediments accumulated rapidly. Arnold (2) has suggested that these nut-bearing tuffs were deposited during a flood.

First-hand information regarding the accumulation of potentially fossil plant parts in an area of eroding volcanic material has been furnished by the recent deposits at Paracutin, Mexico. It should be noted that at Paracutin there has not yet been sufficient time for erosion to affect the lava, so that juvenile material is being transported rather than weathered lava fragments which compose the Clarno beds. Dorf (22), who has studied the Paracutin deposits, recognizes seven environmental facies of which three, the valley bottom, valley slope, and lacustrine facies, suggest the Clarno occurrence. The sediments in these three facies are chiefly water-deposited, and the included plant remains are numerous only within 100 feet of the forest edge.

The valley bottom facies at Paracutin includes channel fills, lenses, flood plain deposits, and alluvial fans. The plant remains are found chiefly in pockets or lenses, and consist of fragments of leaves, broken twigs

and cones, and some portions of larger branches. Although Dorf did not describe them specifically, the accumulations of plant parts in the intergrading valley slope facies are presumably similar to those found in the valley bottom.

The lacustrine facies, found in lakes formed by craters or impounded by lava flows, is characterized by fine grained, thinly bedded ash deposits containing well preserved plant remains. This facies as described by Dorf is unlike the Clarno beds; however, his characterization is based on the examination of only one of the several lakes in the area. A paper by Eggler, who has also done field work in the Paracutin area, contains the following description (23, p. 425):

> The drainage pattern of a part of this area has been changed. Lava flows have cut across and filled some stream channels. Now, upon reaching the lava, streams are ponded and drop their sediments. There are numerous playas, formed in that way, east, south and north of the lava flows. Debris has accumulated to a depth of many feet, and consists of a great mixture of ash, old soil, leaves, branches of trees, logs, and disseminules of many plants.

The similarity of the localized and fragmental plant remains in the Paracutin valley and lake deposits to those at the Clarno locality is apparent. Both locations show rapid deposition of sediments. The Clarno fossils are little worn, indicating that they were not transported far. Most of the plant material in the deposits at Paracutin originated in the forests bordering the water. The number of fruits and seeds included would be expected to vary with the type of vegetation and the time of year at which the

sediments were deposited.

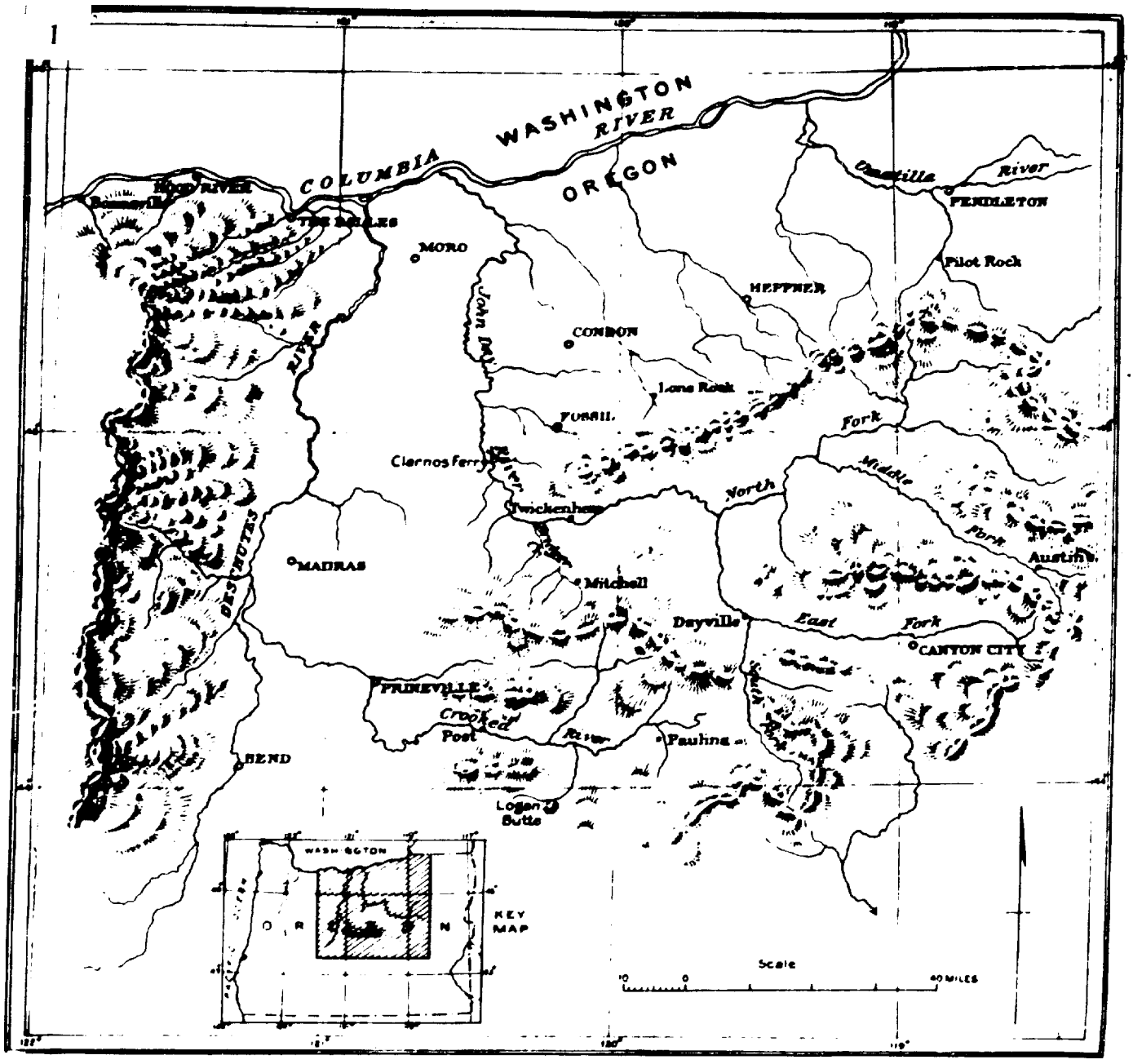
It seems probable that the plants which produced the Clarno fruits and seeds lived adjacent to a stream, perhaps on a flood plain. As will be shown later, the situations in which their modern relatives grow support the supposition of a riparian habitat for the Clarno species. The fruits may have fallen directly into a stream, or may have been carried to it by the collapse of undercut banks or by mudflows; or they could have been moved entirely by flood waters. After being transported a short distance they were concentrated in a spot where the current was slowed, possibly near the entrance to a shallow, lava dammed lake. It is likely that the fruits in each bed, or perhaps in both beds, were laid down during a single season, possibly during periods of autumn rains.

EXPLANATION OF PLATE I

Fig.

1. Map of north central Oregon. The fossil fruit and seed locality is marked by a cross.

PLATE I



MAP OF NORTH CENTRAL OREGON

EXPLANATION OF PLATE II

Fig.

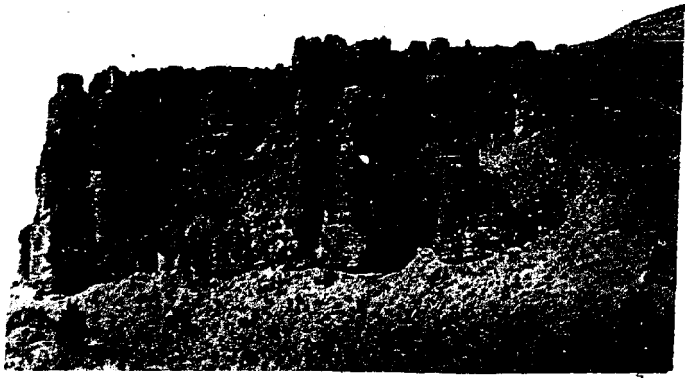
1. The Clarno formation along the road southeast of the nut locality.

2. The fruit and seed locality. The fossils are found at the base of the outcrop. The overlying John Day formation is seen in the background.

3. The two fossiliferous beds. The head of the hammer is at the clay parting between them. A cavity occupied by a walnut appears near the top of the upper layer, directly above the hammer.

PLATE II

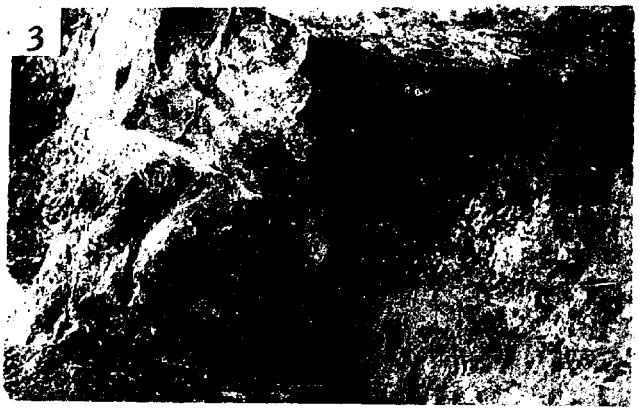
1



2



3



SYSTEMATIC RELATIONSHIPS

Family JUGLANDACEAE (Walnut family)

JUGLANS Linnaeus

1737. Gen. Pl., Ed. I, p. 291; 1754. Ed. V, p. 431.

Juglans clarnensis n. sp.

Plates III, IV, IV A

DESCRIPTION: Endocarp.--Globose to ellipsoidal, occasionally somewhat pointed at the apex; length 14 to 24 mm., diameter 13 to 22 mm.; relatively thick-walled, walls 2 to 3 mm. thick. Dehiscing into two valves in a plane which bisects the embryo lobes longitudinally. Outer surface longitudinally furrowed, the furrows shallow, 8 to 12 in number, usually parallel and converging at base and apex but occasionally anastomosing. Inner surface without internal ridges. Locule divided at right angles to the plane of dehiscence by a primary partition, the two cells thus formed continuous above through an oval orifice in the partition extending about half the length of the locule; locule usually shallowly 4-celled at the base, divided in the plane of dehiscence by a secondary partition which, when present, is as thick at its base as the primary partition, but is low and occasionally lacking. Endocarp wall containing prominent cavities which are not connected across the

plane of dehiscence; the cavity within the wall of each valve extending from base to apex, bifurcate at the base and for over half its length, but united above, appearing in median transverse section as two separate, laterally flattened wall cavities opposite the lobes of the cotyledons. Two intraseptal cavities present near the middle of the primary partition, but cavities lacking in the endocarp wall opposite its ends.

Locule cast.--Rounded to elongate, scutiform in outline in the plane of dehiscence, not compressed laterally, or appearing slightly compressed at right angles to the primary partition of the endocarp in median transverse section. Apical end entire, compressed laterally at right angles to the primary partition; deeply bilobed below, forming two primary embryo lobes. Surface of the lobes smooth, with a prominent median longitudinal ridge extending from the base to the apex of the locule cast and marking the line of union of the cotyledons; outline of the lobes sloping or squared but not recurved in the shoulder region; varying from conspicuously notched to entire at the base, hence secondary lobing shallow to absent. Length 12 to 19 mm., width in the plane of dehiscence 10 to 17 mm., with at right angles to this plane 10 to 15 mm.; maximum depth of secondary lobing 1/5 the length of the seed.

REMARKS: This walnut is by far the most abundant fossil at the Clarno locality. The complete collection contains about 200 specimens; among these are found both endo-

carps[1] and separate locule casts. The number of specimens furnishes evidence of considerable variation within the species.

Most of the fossil endocarps are more or less carbonized although two specimens are silicified. The best preserved nuts are hard, black, and have an almost pitch-like consistency; others are soft, brown, and crumble easily. White lines of chalcedony are frequent on the outer surface; these represent fillings of the shallow furrows, and in part, cracks formed during fossilization (Plate II, Fig. 1).

When found, most of the fossilized endocarps were enclosed in a thin (0.5 mm.) layer of chalcedony that was attached to the matrix. This layer is either a replacement of the husk or the filling of a space resulting from the shrinkage of the endocarps during fossilization.

Both the locule and the cavities in the wall of the fruit have been filled with chalcedony. A thin brown layer on the surface of the locule casts probably represents the testa; thus the seeds conformed to the shape of the locule as in modern Juglans. Fragments of the parenchymatous tissue which originally occupied the wall cavities have been preserved in the chalcedony fillings (Plate III, Figs. 4, 5). In most specimens the locule and wall cavities have been filled with chalcedony without any silicification of the tissues of the endocarp. The endocarp has crumbled from a

---

[1]In the strictest sense, the hard portion of the fruit of Juglans should be referred to as a tryma rather than an endocarp. This term has not, however, come into general use; hence the more familiar, if less accurate term endocarp.

number of specimens, leaving the locule and cavity casts. A few of these show a silicified "stalk" extending from the region of the placenta toward the base of the nut. This "stalk" represents the course of the vascular strands to the seed (Plate III, Figs. 11, 12).

Successive transverse sections of two of the fossil walnuts were prepared, using an instrument designed by Croft (18) for grinding serial sections at measured intervals. (Plates IV, IV A). Recent species having similar endocarps, including Juglans major (Torr.) Heller, J. microcarpa Berl., and J. californica S. Wats. were sectioned by the same method for comparison.

AFFINITIES: The nuts of Juglans and Carya are similar in several respects, and fossilized representatives are often difficult to distinguish. Separation of the nuts of the two genera has been discussed by Mädler (36) and Kirchheimer (31). It is difficult to draw up a list of characteristics which are consistently limited to one genus. However, the combination of features in the Clarno nuts offers conclusive evidence that they belong to Juglans rather than to Carya or some intermediate genus. These features are:

1. Broad, symmetrical cavities extending from the base to the apex within the wall of the nut.
2. Longitudinal ridges absent from the inside surface of the wall of the nut.
3. Exterior of the nut furrowed; not quadrangular.
4. The secondary partition, when developed, as broad at its base as the primary partition.

The genus Juglans has been divided into three sections whose species are listed by Manning (37). The section Rhysocaryon Dode is the largest, with 17 exclusively American species. Nuts belonging to this section have shallowly furrowed or, less commonly, prominently ridged (J. nigra) exteriors. The primary embryo lobes of their seeds show well developed secondary lobing at the base and are recurved in the shoulder region. The section Dioscaryon Dode contains the single Old World species J. regia L., which has a relatively smooth surfaced endocarp. The embryo lobes of J. regia are also recurved in the shoulder region and show prominent secondary lobing at the base. There are four species in the section Cardiocaryon Dode, three of which are Asiatic. One species, J. cinerea L. occurs in eastern United States. The nuts in this section are somewhat elongate or are pointed at the apex. They may be almost smooth, but more often are deeply sculptured with the predominant ridges arranged in longitudinal lines. The embryo lobes are sloping or squared in the shoulder region rather than recurved, and are entire at the base due to the absence of secondary lobing.

The endocarps of the Clarno walnuts are comparable to those of the section Rhysocaryon, and are particularly like those of Juglans major (Plate III, cp. Figs. 2 and 3). The fossil endocarps are similar to this species in size, variably globular to elongate shape, and also have shallow longitudinal grooves on their outer surfaces. On some speci-

mens the grooves anastomose as do those of J. major; on others, however, they remain parallel from base to apex. The symmetrical, compressed wall cavities are slightly narrower than those of J. major in median transverse section, and remain simple toward the apex.

The similarities and differences among the endocarps of Juglans clarnensis, J. microcarpa, and J. major are shown by the serial sections on Plates IV and IV A. The nuts of J. microcarpa are smaller than a majority of the fossils, and the wall cavities are greatly reduced. The most conspicuous difference between the fossil and these two living species is that the shoulder regions of the fossil embryo are not recurved. This is illustrated by the 5-celled condition of the locule of the two living species (Plate IV, Figs. B 12, B 13, B 14, C 9, C 10, C 11) in comparison with the simple state exhibited by the fossil (Plate IV, Figs. A 8, A 9, A 10, A 11). J. californica has larger, more inflated wall cavities than any of these species, and its larger endocarp is commonly sub-globose.

The seeds or embryos of Juglans clarnensis resemble the section Cardiocaryon closer than any of the other sections of the genus. The fossil conforms to this section in not being recurved in the shoulder region. The shoulder region of J. clarnensis can vary from sloping to nearly square on the two sides of the same primary embryo lobe. The differences between the sections Cardiocaryon, as represented by J. microcarpa and J. major, are shown on Plate III,

Figs. 9, 13, 17. The embryo of J. clarnensis is shown on Plate III, Figs. 7, 11, 15.

The sections Rhysocaryon and Dioscaryon uniformly possess well developed secondary lobing of the embryo, which the section Cardiocaryon consistantly lacks. The fossil species is variable in this respect, and individual specimens may be either notched or entire at the base (Plate III, cp. Figs. 7, 11, 15). Even in the most deeply lobed fossil specimens the notch is V-shaped and less fully developed than the broad, U-shaped indentation found in Rhysocaryon species. The more pronounced secondary lobing in the fossil species does not necessarily accompany squared shoulders.

The seeds of all species of the section Rhysocaryon are flattened parallel to the primary partition. The only living form which is flattened at right angles to this partition is Juglans ailantifolia var. cordiformis, in the section Cardiocaryon. The seed of J. cathayensis, also the latter section, is about equidimensional laterally. J. clarnensis, which is equidimensional or slightly flattened at right angles to the primary partition, resembles members of the section Cardiocaryon in this respect.

The Clarno walnut shows features which are intermediate between the sections Cardiocaryon and Rhysocaryon. Its seeds are more like that of the former section, but are transitional between the curved shoulder region and entire base of the primary embryo lobe characteristic of it, and the recurved shoulder and deep secondary lobing found in

Rhysocaryon species. The features of the endocarp are those of the section Rhysocaryon with the exception that the upper portion of the locule is simple rather than 5-celled due to the absence of recurvature in the shoulder of the embryo.

One American species of fossil walnut, Juglans orientalis, which furnishes evidence of relationship to modern Asiatic members of the section Cardiocaryon has been described by MacGinitie (34) from the lower Oligocene Weaverville flora. He states that this species, based on leaves, shows a much closer resemblance to J. cathayensis Dode, J. stenocarpa Maxim. from eastern Asia than to American species.

Although the genus Juglans has a long and extensive fossil record, much of it is based on leaf remains. Only a few well characterized nuts have been described from the American Tertiary. Silicified locule casts from the Oligocene of Nebraska have been described by Berry (6) as J. siouxensis (Barbour). Berry considered this species to be closest to the living J. nigra, and also compared it with J. major. The primary embryo lobes of these seeds show the deeply recurved shoulder regions and well developed secondary lobing characteristic of the section Rhysocaryon, and thus are distinct from the Clarno species. Additional material referrable to J. siouxensis has recently been obtained from the lower Oligocene White River formation, Wyoming, by Mr. Charles Bass and Mr. Arthur Tressler. One specimen loaned to the writer by Mr. Tressler shows part of the exterior surface of the endocarp, not previously known for

this species. It is relatively smooth except where marked by longitudinal furrows, and closely resembles the nuts of J. major (Plate III, Fig. 3), and J. microcarpa. The locule casts are similar except for their larger size to those of the latter species. It seems probable that J. siouxensis has a nearer relationship to these two closely related species than to J. nigra.

Berry (7) has described one silicified specimen of a walnut from the Miocene of Nevada as Juglans nevadensis. On the basis of its relatively smooth exterior he suggested possible affinities to the Asiatic species J. regia and J. sieboldiana. Axelrod (3) has re-examined the specimen and concludes that it is most closely related to J. californica. He has assigned a part of the material of Juglans from the middle Pliocene Mt. Eden flora that he originally described as J. beaumontii, to J. nevadensis, and emended the diagnosis of the former species. J. beaumontii emend. is according to Axelrod, most like J. rupestris (J. microcarpa). J. nevadensis has primary embryo lobes which are recurved at the shoulder and deeply lobed at the base. Although the embryo of J. beaumontii is not described, from its indicated affinities, it should also possess these features. Consequently, both species are distinct from J. clarnensis.

The only known South American fossil walnut is a late Tertiary species from Ecuador described by Brown (9) as Juglans Linki. It is an apically acute, quadrangular form which he considers to be nearest to the recent J. Honorei Dode.

American forms that have been assigned to Juglans, but which are not described in sufficient detail to permit comparisons, include J. brandonianus Perkins from the Brandon lignite, J. calvertiana Berry, and an unnamed Juglans sp. listed by Knowlton from the lower Oligocene of the John Day Basin.

Fossil juglandaceous fruits are more common in the Tertiary of Europe than America, and several European forms that combine to varying degrees characteristics now absent or found separately in Juglans and Carya have been described. They include J. ventricosa (Sternberg) Brogniart, J. costata (Presl) Unger, both ranging from the middle Oligocene to the upper Miocene; and the species of two monotypic genera, Caryojuglans Kirchheimer and Antweileria Kirchheimer, both lower Oligocene in age. The oldest European species of Juglans is J. lacrymabunda (Koenig) Kirchheimer (J. schweiggeri) from the lower Oligocene of Germany. The Clarno walnut bears little resemblance to these species, and the differences between it and these and other European species are apparent from their descriptions.

The form genus Juglandicarya has been erected by Reid and Chandler (44, p. 140) for juglandaceous fruits of uncertain affinities, and contains four species from the London Clay. The material on which one of these, J. crassa (Bowerbank) Reid and Chandler, was based had disintegrated in storage before the latter authors transferred the species from Cupressites. The transfer was based on a figure, and

the original description is not adequate for discussion. J. depressa was compared by Reid and Chandler with Pterocarya. It is a very small, dorsi-ventrally compressed form not at all like the Clarno wlanut. J. lubbocki and J. cantia were considered by the original authors to be most closely related to Juglans. Kirchheimer (31) considers them to be near Engelhardtia, whereas Manning and Hjelmquist (38), considering all three species, state that they are perhaps referrable to the vicinity of Pterocarya or even Engelhardtia, or possibly Juglans microcarpa.[1]

The three species of Juglandicarya mentioned above agree in the complete lack of cavities in the endocarp walls, a fundamental difference from Juglans. In both Juglandicarya lubbocki and J. cantia the outside surface of the endocarp is smooth. Although the primary embryo lobes of the former are not recurved in the shoulder region, they are deeply notched at the base. The primary embryo lobes of J. cantia are also not recurved in the shoulder region, but they are emarginate instead of notched at the base. Except for slightly smaller size, the seed (but not the endocarp) of this species is much like some of the Clarno locule casts.

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[1] A paper by Hsen-Hsu Hu, titled "On a living species of Juglandicarya found in south Yunnan" (Sahni Memorial Vol., pp 263-265, 1952) reached the writer too late to be included in the list of literature cited in the present report. In his paper Hu states that the recent species discussed as Carya sinensis (Dode) by Manning and Hjelmquist (38) is a living representative of Juglandicarya. This assignment is in error for reasons pointed out by the later authors, whose paper Hu had not seen.

As the above discussion shows, the exact affinities of any of the species of *Juglandicarya* are not known with certainty. However, there seems to be little reason to assume that the genus is intermediate between *Juglans* and *Carya*. In spite of the implications of the name, *Juglandicarya* was meant only as a genus for fruits referrable to the Juglandaceae. Reid and Chandler compared it with *Carya* only because of its lack of wall cavities.

Although Brown (9, p. 555) refers to undescribed specimens from the Paleocene of Montana, Wyoming, and Colorado as "the earliest fossil nuts recognizable with certainty as walnuts or at least as being closely related to walnuts", the Clarno walnuts are the oldest fruits of *Juglans* yet described and named.

EXPLANATION OF PLATE III

Fig.

Juglans clarnensis n. sp.

1. Exterior of the endocarp, showing the chalcedony fillings of the furrows and line of dehiscence. x 2.
2. The same, another specimen. x 2.

Juglans major (Recent)

3. Exterior of the endocarp. x 2.

Juglans clarnensis n. sp.

4. Transverse section of the fruit near the base. The plane of dehiscence is horizontal. The tips of the four secondary lobes are inside the wall cavities. x 2.
5. The same, median transverse section. x 2.
6. The same, transverse section near the apex. Only the wall cavities show. x 2.
7. A locule cast. The plane of dehiscence is in the vertical plane at right angles to the plane of the paper. x 2.
8. The same, at right angles. The plane of dehiscence is in the plane of the paper. x 2.

Juglans cathayensis (Recent)

9. The seed, oriented similarly to Fig. 7. Note the resemblance to Fig. 7 in lack of recurvature in the shoulder region and absence of secondary lobing. x 2.
10. The same, at right angles. x 2.

Juglans clarnensis n. sp.

11. Another locule cast. Note the cast of the vascular supply at the base. x 2.
12. The same, at right angles.

Juglans microcarpa (Recent)

13. A metal locule cast. Note the prominently recurved shoulders and deep secondary lobing. x 2.
14. The same, at right angles. x 2.

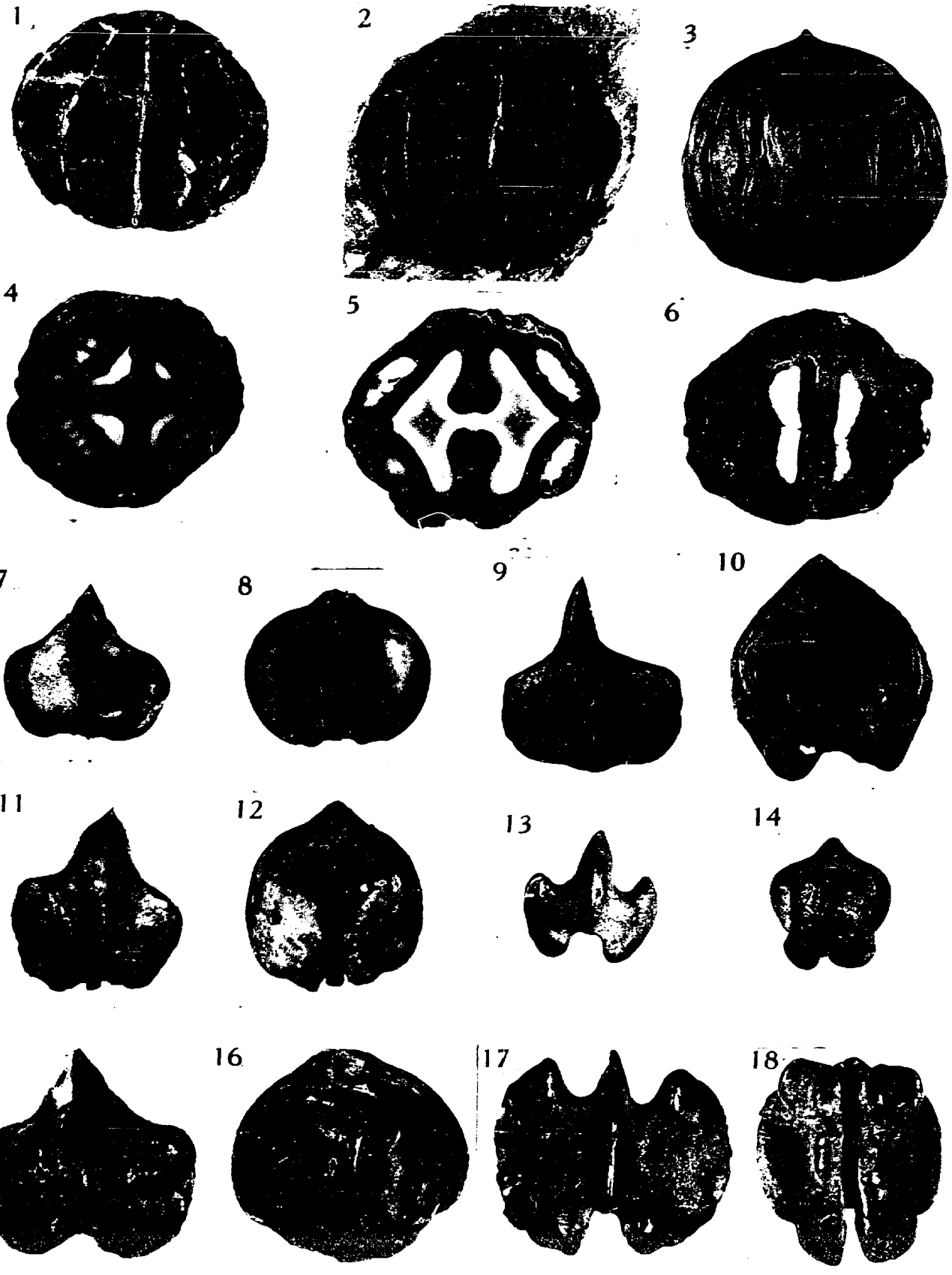
Juglans clarnensis n. sp.

15. Another locule cast. Note the increase in the height of the notch producing secondary lobing in the series Figs. 7, 11, 15.
16. The same, at right angles. x 2.

Juglans major (Recent)

17. An artificial locule cast. x 2.
18. The same, at right angles. x 2.

PLATE III



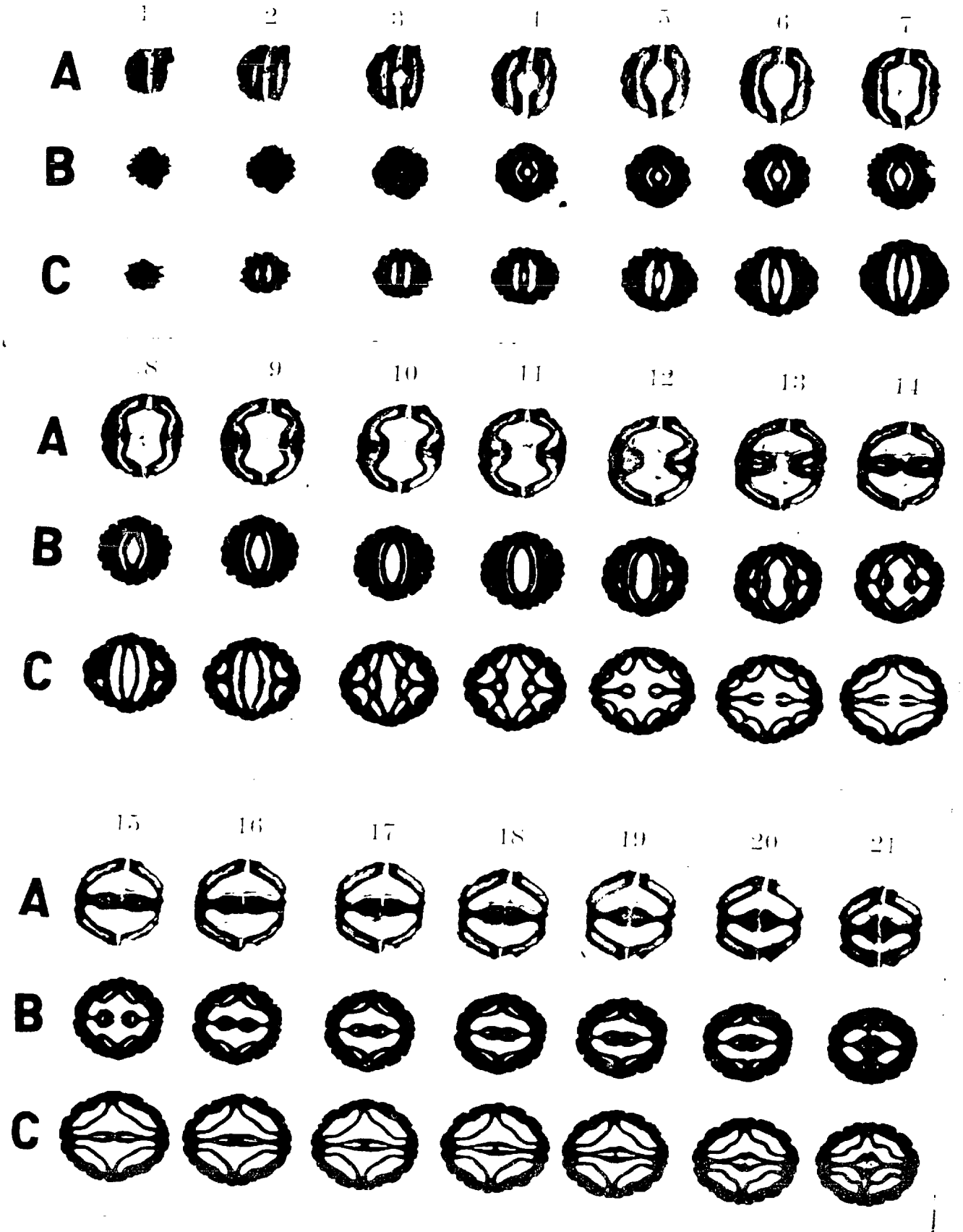
EXPLANATION OF PLATE IV

Serial sections of the endocarps of three species of *Juglans* (numbered from apex to base):

A. *J. clarnensis* n. sp.
B. *J. microcarpa* (Recent)
C. *J. major* (Recent)

The sections were made transversely from the apex to the base of each endocarp at intervals of one thirtieth of its length. (The three initial sections of each series have been omitted.) The sections were prepared using the instrument designed by Croft (18). The endocarp of *J. clarnensis* was embedded in plaster and the sections photographed; those of the two Recent species were inked and printed directly on paper. (Continued on Plate IV A)

PLATE IV



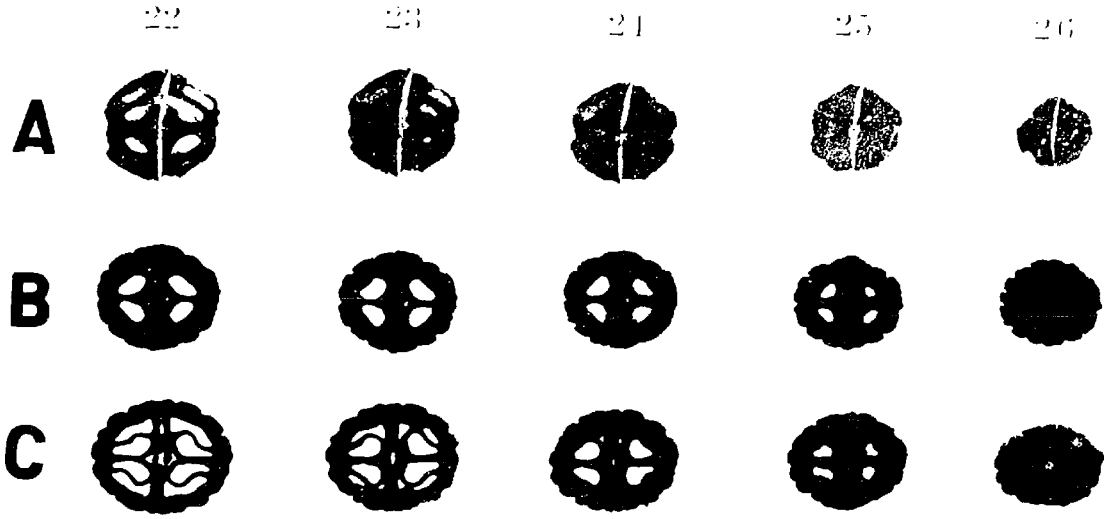
EXPLANATION OF PLATE IV A

Serial sections of the endocarps of three species of *Juglans* (numbered from apex to base):

A. *J. clarnensis* n. sp.
B. *J. microcarpa* (Recent)
C. *J. major* (Recent)

The sections were made transversely from the apex to the base of each endocarp at intervals of one thirtieth of its length. The sections were prepared using the instrument designed by Croft (18). The endocarp of *J. clarnensis* was embedded in plaster and the sections photographed; those of the two Recent species were inked and printed directly on paper. (Continued from Plate IV.)

PLATE IV A



Family MENISPERMACEAE (Moonseed Family)

Tribe Tinosporeae Diels

ODONTOCARYOIDEA gen. nov.

DIAGNOSIS: Endocarp one-loculed, one-seeded, elongate, straight or slightly curved from base to apex; apically acute, with a reniform hollow in the endocarp wall on each side immediately below the apex; basally blunt, with the margins of the endocarp extended to form a deep reniform hollow across the base. Dorsal surface convex, ventral surface concave. Condyle elongate, hollow; condylar cavity one-chambered, open to the exterior. Locule cast deeply boat-shaped, its margins non-faceted.

GENERITYPE: O. nodulosa

Odontocaryoidea nodulosa n. sp.

Plate V

DESCRIPTION: Endocarp.--Elongate, up to 30 mm. long, straight or slightly curved from base to apex. Dehiscent in a median longitudinal plane at right angles to the ventral surface; bisymmetric about the plane of dehiscence. Apically acute, with a reniform hollow on each side immediately below the apex (the hollows represented in the fossil state by two nodules of matrix material). Basally blunt,

the margins of the endocarp extended arcuately to form a deep, reniform hollow (also represented by a nodule of matrix material) across the base; the inner surface of the extension of the endocarp wall which bounds the basal hollow ventrally possessing a short, tapered, median ridge which is occasionally developed into a partition dividing the hollow into two chambers (this condition indicated in the fossil state by two nodules). Dorsal surface convex, with a slight median ridge; ventral surface deeply concave, the concavity formed by the condyle. Condyle elongate, hollow, open to the exterior; wall of the condylar cavity marked by an external median ridge along the ventral suture and parallel striations which diverge at approximately right angles from this ridge. Endocarp wall about 1 mm. thick, other dimensions probably about 2 to 5 mm. larger in each case than those given for the locule cast (length 18 to 25 mm., width 8.5 to 11 mm., thickness 5 to 8 mm.), but not measurable exactly due to carbonization of the endocarp.

Locule cast.--Elongate, length 18 to 25 mm., width 8.5 to 11 mm., thickness 5 to 8 mm.; deeply boat shaped. Apically pointed, the shoulder region sloping; basally blunt or slightly angled, with a small median projection. Dorsal side convex, smooth or with a slight median groove marking the suture. Ventral side concave, its broad, deep hollow variably elongate, length 13 to 19 mm., width 5 to 6.5 mm.; margins of the ventral hollow prominently or only slightly rounded, but not faceted; position of the raphe shown by a

median longitudinal ridge in the ventral hollow; seed attached at a median, subapical point at the margin of the ventral hollow.

REMARKS: All of the 27 specimens are boat shaped locule casts. The casts of the condylar cavity and the nodules representing the hollows at the ends of the endocarp are present with some specimens; on others they were lost during collection.

A thin (0.5 mm.) layer of chalcedony cemented to the enclosing matrix is present with some speciments, and probably represents the exocarp. No traces of a mesocarp have been observed. The casts of the apical and basal cavities are either adherent to the thin layer of chalcedony or are continuous with the matrix. In the former instance the fine sediment that filled the cavities presumably filtered through breaks in the exocarp. When comparable living forms are dried, the pulpy mesocarp virtually disappears and the tough exocarp appresses upon the endocarp, roofing over its hollows. Prolonged soaking does not restore the original turgid condition, hence the hollows would remain enclosed during transport and deposition in water.

During fossilization the exocarp, when present, and the seed, except for its testa, decayed, leaving the hollow, woody endocarp. As the exocarp and seed decayed, the cavities remaining became filled with chalcedony deposited from percolating siliceous solutions. Sometime after the locule had been filled with chalcedony, the relatively impermeable

endocarp was carbonized. One locule cast which has been broken transversely shows in outline the slightly shrivelled testa of the single seed, which conformed in shape to the locule (Plate V, Fig. 8). The transverse furrows visible in the ventral hollows of some of the locule casts may represent ruminations on the ventral surfaces of the seeds (Plate V, Fig. 2).

Whenever a fruit was encountered while removing the material from the matrix, the carbonized endocarp would crumble and the locule cast drop out. Hence, the nodules and the casts of the exocarp and condylar cavity, all of which were externally attached, were usually lost. Thus the evidence is not complete, but the one-chambered condition of the basal hollow of the endocarp seems to have been more common than the two-chambered condition. Only one specimen showing two basal nodules has been saved, but several specimens have a single large nodule at the base.

Although the shape of the endocarp is revealed by the associated casts, its actual remains, except for one partially silicified specimen, are limited to carbonized pieces.

AFFINITIES: The ventral hollow which forms a conspicuous feature of the seeds in many genera of the Menispermaceae results from development upon an enlarged placenta. This structure, projecting into the cavity of the ovary and indicated in the mature fruit by a ventral infold of the endocarp, is termed the condyle.

Genera with endocarps straight or only slightly curved from base to apex occur in three tribes of the Menispermaceae: the Peniantheae, Fibraureae, and Tinosporeae. In the Peniantheae the condyle is longitudinally lamelliform; in the Fibraureae it is lamelliform or lacking. Straight endocarps possessing broad, deep condyles are found only in the Tinosporeae.

Among the genera of the Tinosporeae with somewhat similar endocarps, the Clarno fossil most closely resembles Odontocarya Miers. Seeds of the two species examined, O. tamoides (D. C.) Miers (Plate V, Figs. 10, 11) and O. paupera (Griseb.) Diels are strikingly like the fossil locule casts. They are similar in conformation, with a pointed apex, blunt base, deep ventral hollow with a median raphe, subapical attachment, and possess a deep, unpartitioned candylar cavity (Plate VI, Fig. 1). The differences concern size, proportions, and exterior configuration of the endocarp.

The largest endocarps of O. tamoides measured at Kew Herbarium are 14 mm. long, and the seeds inside are probably not longer than 10 mm. The smallest fossil locule cast is 18 mm. long, and most of them are at least twice as large as is typical for the Odontocarya material seen. No information is available on larger fruits in other species of the genus; however, fruit size has been recorded for less than half of the 11 species which have been described. There is much range in fruit size among species in other genera of

the tribe Tinosporeae. For example, the drupes of Tinospora cordifolia (D. C.) Miers are from 6 to 8 mm. long, while those of T. macrocarpa Diels reach 40 mm. Thus size is not a conclusive factor in judging probable relationships between the fossil form and Odontocarya.

Most of the fossil locule casts are proportionately longer than corresponding parts of Odontocarya. Only for the smallest specimens (Plate V, Figs. 5, 6) is the ratio between length and width similar to that which appears to be nearly constant for the approximately 50 endocarps of Odontocarya examined. In the larger fossils, increased length is not accompanied by proportionate increases in the other dimensions (Plate V, cp. Figs. 3 and 6). Measurements of the lengths of 25 locule casts form a nearly straight line series, although the measurements of their widths and thicknesses tend to group about an intermediate figure. Length of locule (and endocarp) was evidently a variable character in the Clarno species.

One of the features of Odontocarya, and the one for which Miers named it, is the tridentate nature of the endocarp at base and apex (Plate VI, Fig. 2). In the material examined by the writer, the median apical tooth is prominent and the lateral teeth are usually much smaller. The median basal tooth is always present, though it is commonly shorter than its apical counterpart; but the lateral teeth at the basal end are often much reduced and may be entirely absent.

The external molds and nodules show that the fossil

endocarps were acute at the apex (Plate V, Fig. 7). However, because the endocarp wall formed thin, tapering extensions between the positions of the median and lateral teeth on both the dorsal and ventral sides, there were no actual projections. These "web-like" extensions, together with the thicker portions of the endocarp at the positions where teeth occur in the modern genus, bounded the hollows which molded the apical nodules of the fossil.

The possible origin of the tridentate apex from the hollowed condition is illustrated in the East African genus Desmonema Miers, tribe Tinosporeae, whose apically pointed endocarp is much like that of Odontocarya. A pair of hollows comparable to those near the apex of the fossil is similarly situated on a few specimens of D. mucronulatum Engl. var. Schweinfurthii Engl. seen at Kew Herbarium. However, on most of the specimens the endocarp is tridentate at the apex. This living form otherwise differs from the fossil in that its endocarp is considerably curved along the longitudinal axis, and its condylar cavity is covered except for a small, cruciform opening.

The blunt base of the fossil endocarp terminated as a tapering, incurved flange around a basal hollow. A median partition which occasionally divided this cavity was often greatly reduced, occurring as a short ridge on the interior surface of the portion of the flange which bounded the hollow ventrally. This ridge was widest and highest where it fused with the basal end wall and, tapering out-

ward to the margin of the flange, gave a reniform shape to the cavity and the enclosed nodule (Plate V, Fig. 4). It is possible that the median basal tooth of Odontocarya is homologous with this ridge, having been formed by the reduction of the remainder of the flange-like extension except for slight vestiges forming the lateral teeth when these are present.

From the situation in Desmonema, it is apparent that reduction of the "web-like" interdental extensions at the apex of the fossil would produce the tridentate condition typical of Odontocarya. Although the basal cavity of the fossil has no counterpart in any living genus, it suggests rather than precludes relationship to this recent genus. The endocarp of the Clarno species is comparable to that of Odontocarya, but the occurrence of hollows rather than teeth at its ends forms a constant difference from the modern genus.

Odontocarya is considered by Diels (19, p. 35) to be the most primitive of the New World genera in the tribe Tinosporeae. The genus has no previous fossil record. It is one of three closely related American genera, the others being Somphoxylon Eichl. and Synandropus A. C. Smith. Distinctions among the three genera are based chiefly on differences in the number of petals and stamens. The fruit of the monotypic Synandropus is not known, and it has been described for only one of the five species of Somphoxylon. The endocarp of this species is similar to that of Odonto-

carya, although the teeth are less prominent. It differs chiefly in that the condylar cavity, open in Odontocarya and the fossil, is covered by extensions of the endocarp which meet along a median longitudinal slit.

The Clarno species has been assigned to a new genus, Odontocaryoidea, related to Odontocarya but distinguished from it by having hollows rather than teeth at the ends of its larger, usually more elongate endocarp. It is possible that when the fruits of all species of Odontocarya, Somphoxylon, and Synandropus are known, the fossil species may be found to belong to one of these genera. However, it is more likely that Odontocaryoidea is an extinct genus from which Odontocarya, and in turn the other two genera, have been derived.

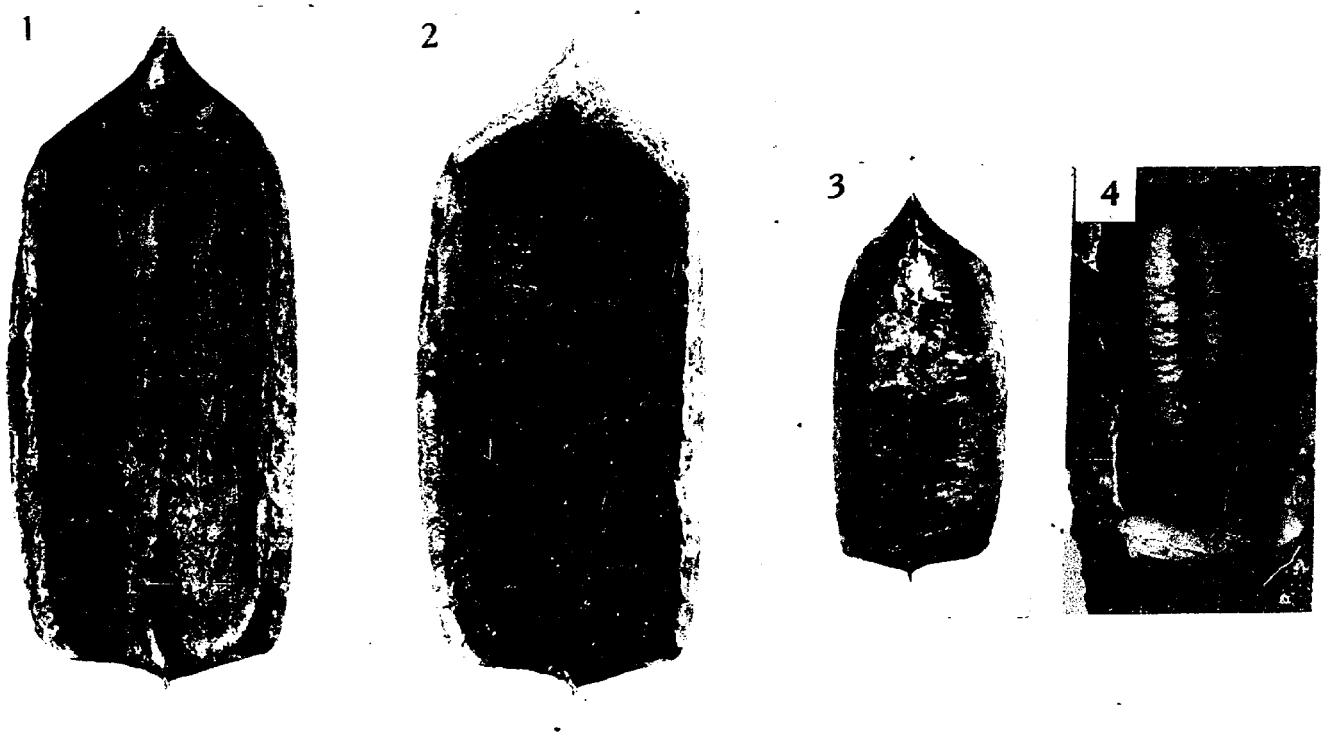
Odontocaryoidea nodulosa somewhat resembles Tinomiscoidea scaphiformis Reid & Chandler from the London Clay. The locule casts of the Clarno species are almost blunt at the base, while those of T. scaphiformis are tapered. The margins of the ventral cavity in the latter form are sharply faceted, and the ventral cavity itself is much shallower. Reid and Chandler (44, p. 162), having seen only fragments of the endocarp, concluded from the shallow ventral cavity that their species lacked a condyle, and considered it to belong to the tribe Fibraureae. Living species with prominent condyles but only shallow ventral cavities also occur in the Tinosporeae (Plate VII, Fig. 11), and there is a possibility that Tinomiscoidea is related to this tribe instead.

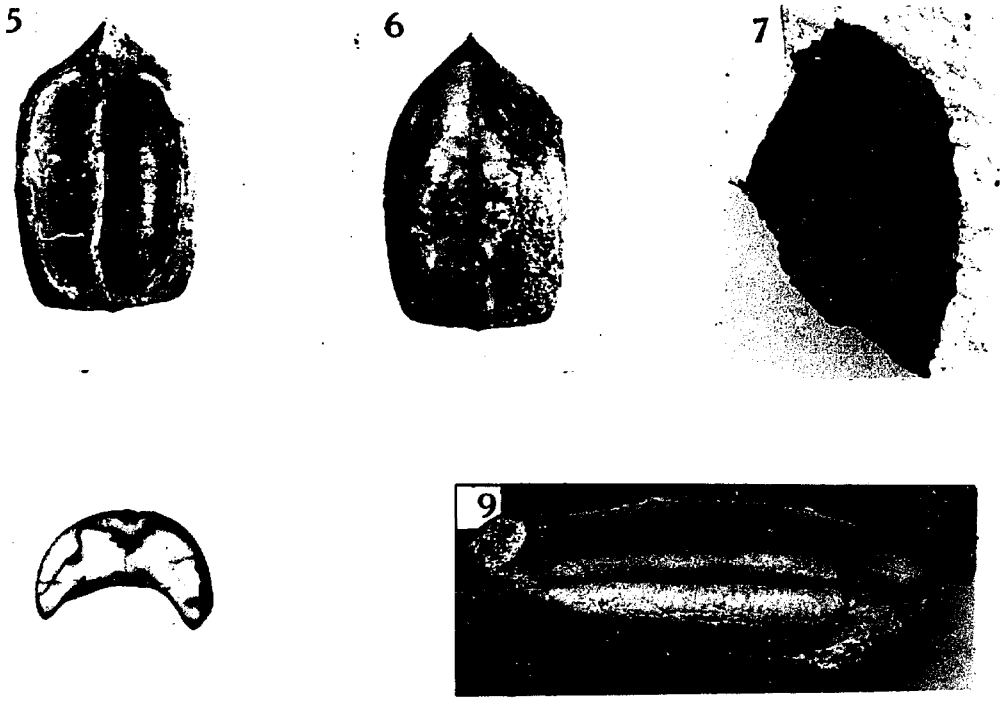
EXPLANATION OF PLATE V

Fig. *Odontocaryoidea nodulosa* gen. and sp. nov.

1. The ventral surface of the locule cast, showing the deep hollow with the median ridge within marking the position of the raphe. x 7.
2. The same, lighted to show the sculptured surface of the ventral hollow. These markings may represent ruminations of the original seed.
3. The same, dorsal surface. x 2.
4. The same specimen, the cast of the condylar cavity from above. The basal nodule is seen below. x 2.
5. A short, broad specimen, ventral surface. Compare with Fig. 3, Plate VI. x 2.
6. The same, dorsal surface. Compare with Fig. 4, Plate VI. x 2.
7. The same specimen, the cast of the condylar cavity from above. The two apical nodules are present at the top. x 2.
8. A locule cast, fractured transversely. The testa of the seed is seen as a thin, dark line inside the margin.
9. The cavity in the matrix occupied by the fossil endocarp, seen in longitudinal section. The basal nodule is seen in transverse section on the left; one apical nodule appears on the right. The cast of the condylar cavity extends between them. The locule cast, into whose ventral hollow the cast of the condylar cavity fitted, has been removed.

PLATE V





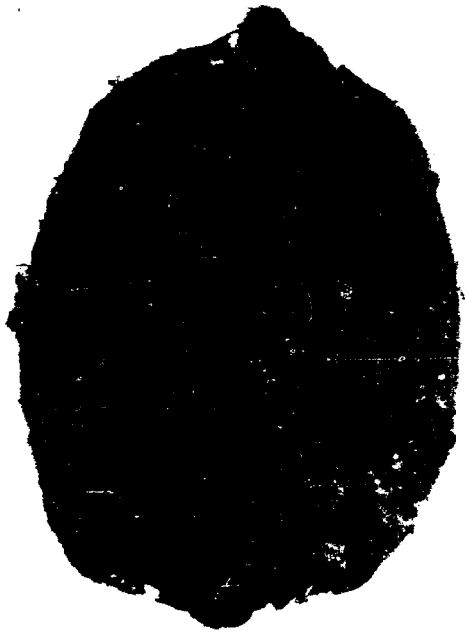
EXPLANATION OF PLATE VI

Fig. *Odontocarya tamoides* (Recent)
Herb. Brit. Mus. (Nat. Hist.), Jennian 3652

1. The ventral surface of the endocarp, showing the deep, unpartitioned condylar cavity. Note the excavations between the teeth at the ends of the endocarp. x 7.
2. The dorsal surface of the endocarp, showing the teeth. x 7.
3. The ventral surface of the seed, showing the ventral hollow, median raphe, and ruminated surface. x 7.
4. The same, dorsal surface. x 7.

PLATE VI

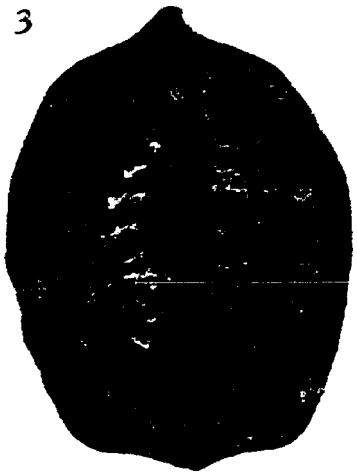
1



2



3



4



CHANDLERA gen. nov.

DIAGNOSIS: Endocarp one-loculed, one-seeded, elongate, straight from base to apex; oblong-ellipsoidal, the dorsal and ventral surfaces flattened. Interior of the endocarp wall hollowed by a system of longitudinally parallel lacunae extending from base to apex; lacunae irregularly connected laterally except across the plane of dehiscence. Condyle elongate, hollow; condylar cavity two-chambered, covered by the externally continuous endocarp wall. Locule cast shallowly boat-shaped, its margins faceted.

GENERITYPE: C. lacunosa

Chandlera lacunosa n. sp.

Plate VII

DESCRIPTION: Endocarp.--Elongate, straight from base to apex; large, length 50 mm., width 21 mm., thickness 18 mm.; oblong-ellipsoidal, the dorsal and ventral surfaces flattened. Dehiscent in a median longitudinal plane at right angles to the dorsi-ventral surfaces; bisymmetric about the plane of dehiscence. Endocarp wall smooth externally, about 5 mm. thick, extensively hollowed by a system of longitudinally parallel lacunae which extend from base to apex. Lacunae rounded in transverse section, their walls rugose, not connected across the plane of dehiscence; the three parallel lacunae in each valve irregularly con-

nected laterally; the center lacuna shortest, its ends joined sub-terminally to one or the other of the adjacent lacunae; the latter two lacunae united at their ends and extended outward, the extensions preserved in the fossil casts as four oval projections, one near each corner of the endocarp in a median plane at right angles to the plane of dehiscence. Condyle broad, elongate, hollow; condylar cavity rugose-walled, covered by the externally continuous endocarp wall; two-chambered, each chamber turning laterally at the base and connecting with the lacuna adjacent and parallel to it.

Locule cast.--Elongate, straight, shallowly boat-shaped. Strongly acute at the apex, less acute at the base. Dorsal surface strongly convex, slightly and irregularly sculptured, with a pronounced median ridge marking the suture; somewhat angular in transverse section, each straight segment of the aggregately convex profile opposite a lacuna in the endocarp wall. Ventral surface shallowly concave, the broad, elongate ventral hollow emarginate at the base, its lateral and apical margins faceted; position of the raphe indicated by a median longitudinal line in the ventral hollow; seed attached at a median subapical point at the margin of the ventral hollow. Length 30 to 37 mm., width 13 to 16 mm., thickness 10 to 12 mm.

REMARKS: This is the largest and most spectacular fruit collected at the Clarno locality, and for a long time one of the most puzzling. Of the 13 specimens at hand, 5

are locule casts only. The others, although not all complete, show various details of the endocarp structure.

The fossils of this genus are notable for the casts of the lacunal system and condylar cavity which surround the chalcedony filled locule. At first glance the casts appear to represent structural parts of the fruit or seed, but examination reveals that they are composed of matrix material that is completely surrounded by the carbonized remains of the endocarp wall (Plate VII, Fig. 10). Consequently they represent spaces which were either hollow or from which tissue has disappeared. These lacunae within the endocarp walls opened to the exterior of the endocarp at the ends, or possibly were closed by flaps of tissue. In either case they readily filled with sediment during deposition.

One transversely fractured locule cast shows the testa of the seed as a dark line near its margins (Plate VII, Fig. 9). The seed, which conformed to the shape of the locule, had shrivelled somewhat before fossilization.

AFFINITIES: The straight, elongate, boat-shaped locule cast and prominent condyle of this fossil relate it to the tribe Tinosporeae of the Menispermaceae. Its endocarp is larger than in most species in this tribe, though not of the family. The endocarp of Abuta macrocarpa Moldenke (Tribe Anomospermeae) is as large or larger than that of the fossil, and has a flattened, nearly oblong-ellipsoidal shape and exterior markings which give it a suggestive

but superficial resemblance to the Clarno species. The horseshoe shaped seed of the modern species precludes relationship to the fossil.

The combination of characters shown by Chandlera lacunosa does not occur in any living or fossil genus of the Tinosporeae. The recent monotypic Chlaenandra ovata Miq., from New Guinea, has a large endocarp ornamented by irregularly parallel rows of spines. Sometimes their branched tips coalesce laterally, roofing over the spaces between adjacent rows and thus enclosing parallel cavities, but the closure is only partial. The endocarp of this species is subglobose and the locule is sharply curved along its longitudinal axis. The condyle, although two-chambered, is deep and narrow, rather than shallow and broad as in the fossil.

The West African Rhigiocarya Miers, another monotypic genus, also possesses irregular rows of spines and plates on the exterior of the endocarp. Its locule cavity is straight and somewhat like that of the fossil in transverse section. However, the condylar cavity in this genus has only one chamber and is extremely deep; the portion of the endocarp wall which encloses it extends outward from the ventral surface to form a conspicuous bulge.

Endocarps more closely resembling the fossil are found in the genus Parabaena Miers. Those of the Philippine species P. megalocarpa Merr., seen in the Herbarium of the British Museum (Natural History), are up to 25 mm. long,

straight, and elongate. The ventral hollow of the seed is shallow and the prominent condylar cavity has a weak septum dividing it into two chambers, each of which opens laterally at the base as do those of the Clarno species (Plate VII, Fig. 11). On the exterior surface of the endocarp are numerous irregular rows of spines which are connected laterally by plates of thin tissue. The spines were not observed to join laterally at their tips.

Endocarps of Parabaena denudata Diels, also from the Philippines, have seven longitudinal rows of spines on their external surfaces. These rows correspond in number and position to the ridges between the lacunae in the fossil endocarps. Similar rows of spines occur on the endocarps of P. sagittata Miers from Burma. The endocarps of neither species are longer than 10 mm.

No living species in the tribe Tinosporeae has endocarps with lacunae enclosed in their walls. In several genera, however, long spines and plates are present on the exterior of the endocarp, and these are often (but not always) aligned in longitudinal rows. The tendency toward lateral coalescence of the spines noted for Chlaenandra implies that the endocarp wall was originally continuous between their tips. This, together with the longitudinal alignment, suggests that the spines in at least some members of the Tinosporeae originated by reduction. They may represent remnants of the interlacunar regions of thick endocarps whose walls contained longitudinally oriented

lacunae or masses of parenchymatous tissue, and thus were comparable to the endocarps of Chandlera lacunosa.

This Clarno genus has been named for Miss M. E. J. Chandler who, as co-author of the London Clay Flora, and author of the forthcoming volumes of the Tertiary Floras of England, has contributed greatly to the knowledge of Tertiary fruits and seeds.

EXPLANATION OF PLATE VII

Fig. — *Chandlera lacunosa* gen. & sp. nov.

1. Cast of the cavity system, ventral surface. The plane of dehiscence is vertical and at right angles to the plane of the paper. The paired extensions inside the inverted "U" shadowline represent the fillings of the condylar cavity. The point of attachment was between them at their tips. x 2.
2. The same, dorsal surface. x 2.
3. The locule cast, originally enclosed in the lacuna cast shown in Figs. 1 and 2. Note the faceted margin, open basally, and the median ridge representing the position of the raphe. x 1.
4. The same, dorsal surface. x 1.
5. Lacunal cast, apical end. x 1.
6. Lacunal cast, basal end. x 1.
7. The same, lateral view. x 1.
8. The external surface of the endocarp. This layer enclosed the lacunal cast, whose apical horns can be seen protruding through it. x 1.
9. The locule cast, transverse section. Note the angular profile and shallow ventral hollow. A portion of the testa of the seed may be seen as a thin, black line inside the margins. x 2.
10. The fruit, broken away to show the transverse section. The light-colored locule cast is surrounded by the carbonized endocarp, within which appear the individual cavities filled with matrix material. The partition of the two-chambered condyle is clearly shown. Compare this Fig. with Fig. 11. x 1.

Parabaena megalocarpa (Recent)
Herb. Brit. Mus. (Nat. Hist.), Elmer 20675.

11. Transverse section of the endocarp, showing the locule, two-chambered condyle, and spinose exterior of the endocarp. x 3.

PLATE VII


1


2


3


4

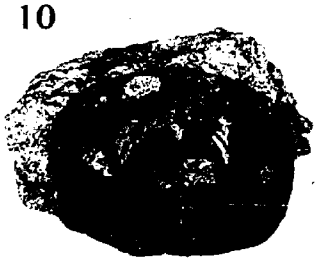

5


6


8


7


9


10


11

Family LAURACEAE (Laurel Family)

LAUROCARPUM Reid & Chandler

1933. London Clay Flora, p. 225.

Laurocarpum proteum Reid & Chandler

Plate VIII

1933. Laurocarpum proteum Reid & Chandler, pp. 230-231, Plate VII, Figs. 39-43.

REMARKS: This species is represented by a single specimen from the Clarno locality. It is a locule cast with a few adhering fragments of the endocarp. Although little of the endocarp remains, observations at the time of collection indicate that the fruit was one-loculed and one-seeded. The locule cast is irregularly ovoid, being 11 mm. long and 9 mm. in diameter. At the hilar end there is a large beak which is bounded laterally by a depression whose margins form an arcuate triangle. On the side opposite the depression, a slight groove indicating the course of the raphe or the line of junction of the faces of the cotyledons extends from the beak to the chalazal end (Plate VIII, Fig. 1). The chalaza is large, being 4.5 mm. in diameter, and occupies most of the area of the flattened end of the locule cast.

AFFINITIES: The genus Laurocarpum was founded by Reid and Chandler to contain one-loculed, one-seeded fruits

showing more than one diagnostic characteristic of the Lauraceae, but which cannot be assigned to a living genus. Fruits and seeds of lauraceous genera are difficult to separate, their distinctions often depending on such features as the occurrence of cupules and peculiarities in the structure of the carpellary coats. Such details are lacking on the Clarno specimen.

The lauraceous affinities of the specimen are indicated primarily by the large, circular chalaza occupying almost the entire basal end of the locule cast which formed in an unilocular fruit. Among the numerous species assigned to Laurocarpum by Reid and Chandler, L. proteum is unique in showing a large, subtriangular depression below the hilar end. These authors state that a similar depression occurs on the seed of the Recent Persea gratissima Gaertn. (incorrectly called Phoebe gratissima Gaertn. by Reid and Chandler), but suggest that it may be due in part to shrinkage. The Clarno specimen possesses this distinctive depression and appears otherwise to be identical with the London Clay material of the species except for its slightly smaller size. (Compare Plate VIII, Fig. 1, with Plate VII, Fig. 42 in The London Clay Flora.) The existence of such an unusual feature in fossils from two such widely separated localities suggests that it probably has morphological significance and is not accidental.

Members of the Lauraceae are common in the Clarno flora. Chaney has identified three lauraceous genera,

including *Persea*, from the fossil leaves.

EXPLANATION OF PLATE VIII

Fig. *Laurocarpum proteum* Reid & Chandler

1. A locule cast, showing the large, sub-triangular depression. The line leading from the apex to the base on the right probably indicates the course of the raphe. The chalaza occupied the base. x 3.

PLATE VIII

1



Family ICACINACEAE

Tribe Phytocreneae Engler

PALEOPHYTOCRENE Reid & Chandler

1933. London Clay Flora, p. 333

The genus Paleophytocrene was founded by Reid and Chandler to include fossil forms related to living members of the tribe Phytocreneae, but generically distinct from them. Their diagnosis of the genus is as follows (44, p. 333):

> Endocarp oval, compressed or slightly inflated, obscurely pitted externally, the closed inner ends of the pits forming parallel-sided protuberances projecting into the locule; locule lining not papillate, formed of small polygonal cells.

Members of the tribe Phytocreneae are distinguished by the possession of numerous straight canals in the walls of their unilocular endocarps. These canals are perpendicular to the surface of the endocarp and appear on its exterior as pits. The endocarp is not perforated as the canals terminate in an inner layer of its wall. In most genera of the tribe this inner layer is modified into numerous protuberances or tubercles which extend into the locule cavity. Each tubercle is at the base of a canal and is hollow, its cavity being continuous with, and forming a part of, the canal. The tubercles, projecting into the locule, appear as pits on the surface of the fossil locule cast. These

pits are larger than the pits on the external surfaces of the endocarp, but correspond in position to them.

The relationship of the fossil genus to living genera of the tribe is shown principally by the internal protuberances of its endocarps. Reid and Chandler state that characteristics relating to the shape and arrangement of the protuberances, now found separately in the modern genera Phytocrene Wall., Chlamydocarya Baill., and Miquelia Meissn. are combined in Paleophytocrene. In Phytocrene the pits which appear on the exterior of the endocarp are similar in arrangement to those which occur on the fossil. However, unlike the fossil, their bases are not extended into the locule; but they appear on the inner surface only as slight mounds or not at all. Chlamydocarya has internal protuberances with parallel sides which differ from those of Paleophytocrene by being elongated longitudinally rather than circular in transverse section, and by being arranged in more regular rows. The tubercles of Miquelia are funnel shaped, with conical rather than straight sides. In addition, the external surface of its endocarp is ridged and ornamented while that of Paleophytocrene is smooth. Reid and Chandler (44, pp. 334-335) conclude regarding P. foveolata, the generitype, that "in the disposition of the tubercles or protuberances it comes nearest to Phytocrene, and in their form and character to Chlamydocarya.". An additional species with conical protuberances, P. ambigua Reid & Chandler, is more like Miquela.

Re-examination of the London Clay specimens and the endocarps of modern members of the tribe by the writer supports the correctness of the relationships pointed out by Reid and Chandler. Only a brief further note can be added to their observations.

In most species of Chlamydocarya the tubercles are elongate longitudinally, as Reid and Chandler state. In material of C. capittata Baill. including the type specimen, however, they are circular in transverse section and tend to occur in pairs. The derivation of the elongate condition is suggested by the appearance of some of the tubercles; occasional pairs are fused at their bases and part way along their lengths. Casts of locules with such tubercles would show pits with intersecting circumferences. Such coalescent pits occur in Paleophytocrene foveolata from the London Clay (44, Plate XV, Fig. 29) and also in material of the genus from the Clarno locality (Plate IX, Figs. 6, 8).

In addition to interspecific variation in the shape of the tubercles, the regularity of their arrangement into longitudinal rows can also differ within a single genus. Again in Chlamydocarya, the type specimen of C. Thompsoniana Baill. has tubercles distributed quite as irregularly as those of many fossil specimens although their supposed regular alignment in this modern genus distinguishes it from Paleophytocrene.

In discussing the relations of Paleophytocrene Reid

and Chandler consider only the genera mentioned above. Although material of all seven Recent genera in the tribe was not available to the writer, two additional genera, Pyrenocantha Wight and Polycephalium Engl., were examined. Both have internally tubercled endocarps which are much like Paleophytocrene. In Polycephalium the tubercles also occur in pairs, although no fusion was observed.

Although the relationships of Paleophytocrene as set forth by Reid and Chandler are not under discussion, it should be pointed out that some of the characteristics they regard as of generic value vary somewhat within a single genus, and that essentially similar endocarps occur in at least five genera of the tribe. Study of a much greater amount of modern material than is presently available would be necessary, in the opinion of the writer, before the generic value of the characteristics of the tubercles could be positively set forth. Although it is possible that the characteristics combined in Paleophytocrene have become segregated in separate genera since the Eocene, it is also possible that the characteristics in question are not reliable for generic distinctions.

Paleophytocrene foveolata Reid & Chandler

Plate IX, Figs. 1-4

1933. Paleophytocrene foveolata Reid & Chandler, pp. 333-334, Plate XXV, Figs. 24-32.

The diagnosis of this species is as follows (44, p. 333):

Endocarp with surface pits about twelve in the length of the nut and eight in the width. Length 15 to 27 mm.; breadth 14 to 17 mm.; thickness 5.5 to 13 mm. Seed with testa cells inflated 0.05 to 0.15 mm. in diameter.

REMARKS: Six specimens of this species and numerous endocarp fragments marked with the characteristic pitting were found at the Clarno locality. Three of the specimens are nearly complete and show the locule cast and adhering portions of the carbonaceous endocarp; one of these has been fractured and shows the pitchy remains of the seed (Plate IX, Fig. 4). The nature of the testa cells cannot be determined.

The pits on the locule casts of the specimens are cylindrical and mostly about 1 mm. in diameter. There are usually about 80 pits on each side of the cast, although the largest specimen has a few more (Plate IX, Fig. 1). The endocarp is pitted on its outer surface, the pits representing the hollows in the tubercles. The hollow nature of the tubercles, described below in detail for Paleophytocrene pseudopersica n. sp., is observable on these specimens. The outer surface of the endocarp is without ridges or ornamentation. The complete locule casts have the following dimensions: length 26 to 32 mm.; width 19 to 22 mm.; thickness 7 to 16 mm. They vary from flattened to subrounded.

AFFINITIES: The presence of protuberances in these specimens is diagnostic for Paleophytocrene. They were compared with the twenty five specimens of P. foveolata in the London Clay collection in the British Museum (Natural Hist-

ory), and fall within the range of variation exhibited by this material in the diameter, cylindrical shape, and arrangement of the pits. The Clarno specimens are larger than many of the London Clay specimens; their maximum dimensions slightly exceed those given in the species diagnosis. The largest Clarno locule casts have more rows of pits and thus a larger total number of pits than do the London Clay fossils, although the arrangement of the pits into rows in the species is only approximate.

Reid and Chandler have distinguished a smaller form with 6 or 7 pits in its length and 5 or 6 pits in its width as Paleophytocrene foveolata var. minima. The inclusion in the species of this form with its pits fewer than defined in the species diagnosis illustrates the range of variation recognized by the original authors. The Clarno specimens, although slightly larger rather than smaller, may also be considered as belonging to P. foveolata.

Paleophytocrene foveolata is distinct from P. ambigua Reid & Chandler, which has fewer and larger pits with sides that are conical rather than cylindrical. Its differences from P. pseudopersica n. sp. and P. hancockii n. sp. will be given in the discussion of these species.

Paleophytocrene pseudopersica n. sp.

Plate IX, Figs. 5-8

DESCRIPTION: Endocarp.--Woody, oval to ovate, flattened or slightly inflated. Inner surface non-papillate,

bearing numerous thin walled, hollow tubercles which project into the locule. External surface pitted, the pits continuous with the hollows of the tubercles. Thickness of the endocarp wall 2 mm.

Locule cast.--Oval to ovate, sometimes slightly extended at the apex. Surface bearing prominent pits formed by the protuberances of the endocarp wall. Pits deep, cylindrical, mostly about 2 mm. in diameter with a few marginal pits smaller; about 50 in number on each side, arranged into 6 or 7 irregular, longitudinal rows; circumferences of adjacent pits sometimes coalescing. Length 25 to 30 mm., width 18 to 22 mm., thickness 5 to 11 mm.

REMARKS: This species is based on three locule casts, one of which was donated by Mr. A. W. Hancock. Two of the specimens have fragments of the endocarps remaining on their surfaces.

Examination of the pits on the locule casts reveals the nature of the structures which formed them. Each pit is lined with a thin, carbonaceous layer which extends down the sides and is continuous across the bottom. This layer is the remains of the hollow tubercle. It surrounds a core of ashy matrix sometimes altered to clay, or of chalcedony. Some cavities, perhaps protected by a now absent exocarp, were not filled by sediment at the time of deposition; but chalcedony was later deposited in the empty spaces. Regardless of the nature of their filling, the hollow tubercles characteristic of the Phytocreneae are demonstrated.



AFFINITIES: Paleophytocrene pseudopersica has only about 50 pits on each side of the locule cast instead of 80 or more, as found in P. foveolata. The pits, except for a few smaller ones along the margins, are approximately twice the diameter of those in P. foveolata. The pits of P. ambigua from the London Clay, although similar in size and number to this Clarno species, are conical rather than cylindrical. Because size of the tubercles and the slope of their sides were observed to be consistent in modern species of the tribe Phytocreneae, the combination of characteristics shown by P. pseudopersica warrants its designation as a separate species.

Locule casts of P. pseudopersica look somewhat like the "stones" of the cultivated peach, Prunus persica L. They are called "peach pits" by the amateur collectors who have found them at the locality. The species is named for this resemblance.

Paleophytocrene hancockii n. sp.

Plate IX, Figs. 9, 10

DESCRIPTION: Endocarp woody, ovoid but somewhat flattened; large, length 65 mm., width 35 mm., thickness 26 mm. External surface bearing numerous pits whose number and arrangement are obscured. Inner surface lined by numerous protuberances extending a short distance into the locule. Thickness of endocarp 2 mm.; diameter of protuberances 1.5 mm. (equivalent to diameter of the locule cast pits).

REMARKS: This species is known from a single specimen donated by Mr. A. W. Hancock. The endocarp has been preserved almost uncarbonized. It is filled with calcite rather than chalcedony as are the other Clarno specimens. The pits on the exterior of the endocarp have been filled by matrix material, and many of them are difficult to locate; hence their number and arrangement are not clear. Mr. Hancock sectioned the specimen, revealing the characteristic protuberances (Plate IX, Fig. 10).

AFFINITIES: The protuberances visible in section on the edges of its endocarp relate this specimen to the genus Paleophytocrene. It is notable for its large size and for the fact that, in proportion to its size, the tubercles project only a short distance into the locule in comparison to the other species of the genus. In both respects it more closely resembles Phytocrene than the other modern genera in the tribe. Although the largest modern fruits known for the tribe occur in this genus, the fossil is over twice as large as any endocarp belonging to species of Paleophytocrene. Such large fruits are not unknown in the family, for the endocarp of Poraqueiba sericea Tuslane, described by Howard (26), is 80 mm. long and 55 mm. in diameter. Both the inside and outside surfaces of the endocarp, however, are smooth in this New World species.

The species is named for Mr. A. W. Hancock, who found the specimen at the Clarno locality.

EXPLANATION OF PLATE IX

Fig. *Paleophytocrene foveolata* Reid and Chandler

1. A locule cast. x 2.
2. Another specimen. x 2.
3. A fractured locule cast upon which the endocarp still remains. x 2.
4. The same, lateral view. The internal tubercles of the endocarp can be seen extending into the locule. The central black mass is apparently the pitchy remains of the seed. x 2.

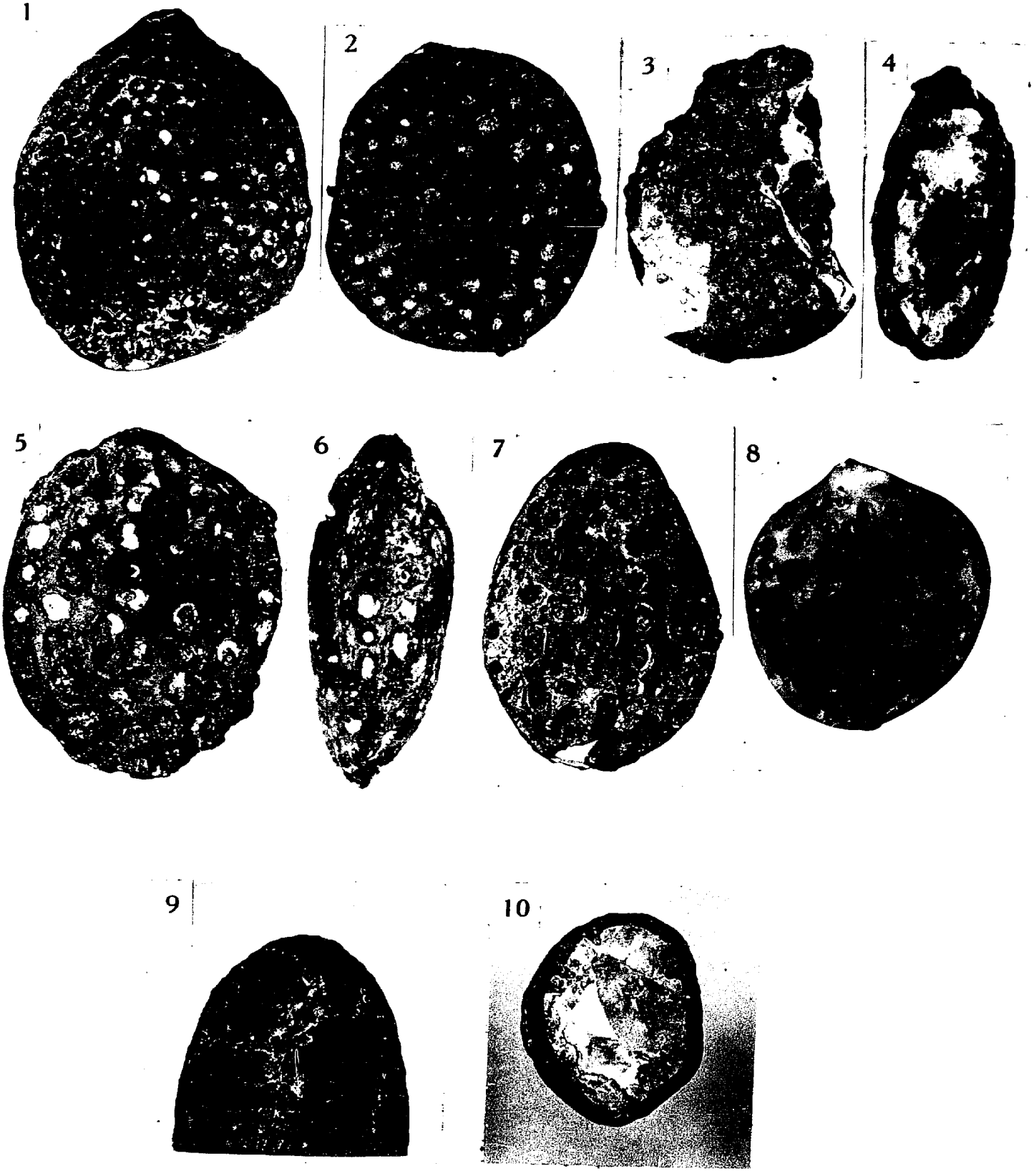
Paleophytocrene pseudopersica n. sp.

5. A locule cast. x 2.
6. The same, lateral view. x 2.
7. Another specimen. x 2.
8. Another specimen. x 2.

Paleophytocrene hancockii n. sp.

9. The exterior of one half of the endocarp. x 1.
10. The same specimen, transverse section. The internal tubercles of the endocarp are shown. x 1.

PLATE IX



Family VITACEAE (Grape Family)

PARTHENOCISSUS Planchon

1887. In DeCandolle, Monog. Phan. v., p. 447

Parthenocissus angustisulcata n. sp.

Plate X, Fig. 1

DESCRIPTION: Seed obovate, with a slight notch at the apex marking the course of the raphe. Ventral surface sharply faceted, its faces meeting at an angle of approximately 90 degrees, suggesting 4 seeds to a berry. Raphe ridge narrow below, broadening in the upper third of its length, the shallow groove of the raphe visible upon its surface. Ventral infolds narrow, long, extending from the base almost to the apex, adjacent and parallel to the raphe ridge at the base, but diverging conspicuously in the upper third of their length. Dorsal surface not known with certainty. Length of seed 6.5 mm., width 4 mm.

REMARKS: This species is represented by a single specimen which is imbedded in the matrix so that only its ventral surface is visible. Although a piece has been broken from the raphe ridge, the groove of the raphe is present on the remainder.

AFFINITIES: While examining the London Clay material belonging to the Vitaceae, the writer noted a similarity between the specimens described by Reid and Chandler (44, pp. 387-388), as "Cayratia ? monasteriensis" and the Clarno seed.

In their discussion they cite "Cayratia Thomsoni Laws," as the the most similar modern species.

While examining modern seeds at Kew Herbarium the writer discovered that "Cayratia" Thomsoni is not a species of Cayratia, but belongs instead to the genus Parthenocissus. The confusion arose because sheets of P. Thomsoni, labelled Vitis, were erroneously placed in the same cabinet with Cayratia in Kew Herbarium at the time Reid and Chandler studied them. The species was originally described by Lawson (31) as Vitis Thomsoni, and was subsequently transferred to Parthenocissus (with a question) by Planchon (45). This transfer was upheld by Metcalf (39), who had seen the isotype specimen. The proper name for the species is P. Thomsoni (Laws.) Planch., and the name "Cayratia Thomsoni" used by Reid and Chandler is an accidental invalid combination.

After discovering this mistake, the writer examined the seeds of available species of Cayratia and Parthenocissus. The genus Cayratia has been divided into two groups on the basis of seed structure by Gagnepain, (24), who monographed it. In one group the seeds are semi-lunar in transverse section; in the other they are T-shaped. The former group bears little resemblance to either the London Clay or Clarno forms, but the T-shaped seeds do resemble the fossils to some extent. However, as Reid and Chandler noted, the Recent seeds are more angular, and in addition, (omitting the misplaced species "Cayratia Thomsoni"), have elongate chalazas and are markedly ridged and furrowed on the dorsal surface. The chalaza is

round in the London Clay species, and the dorsal surface is smooth or but slightly fluted around the chalaza. The ventral infolds are long and narrow, but do not approach the margins. They are approximately straight throughout their length, and are inclined to the raphe ridge. In the fossils the ventral infolds extend almost to the margins, and are parallel to the raphe ridge at the base and diverge apically. In Cayratia seeds the raphe ridge does not widen apically as it does in the fossils.

The seeds of other species of Parthenocissus are much like those of P. Thomsoni, and may resemble the fossil "Cayratia monasteriensis" even more closely in certain respects. Reid and Chandler pointed out that P. Thomsoni differs from the fossil species by having a slightly elongate chalaza; the chalaza of P. tricuspidata Planch. agrees in being round. All species examined are smooth or show only the slightest ruminations immediately surrounding the chalaza, and have much less angular contours than do the Cayratia species. On the ventral side, the raphe ridge is narrow and broadens apically. The ventral infolds are narrow and long, often extending virtually to the margins. They are parallel to the raphe ridge at its base, and diverge in the apical third of its length. Examination of seeds of the other genera of the Vitaceae shows that ventral infolds of this nature are limited to Parthenocissus, and thus are diagnostic for seeds of the genus.

The features of the seeds of Parthenocissus Thomsoni show that its assignment to this genus is correct. The

characters of "Cayratia ? monasteriensis" are also in complete agreement with those of Parthenocissus, and the doubt formerly associated with the generic position of the species can be eliminated by transferring it to this genus. Miss M. E. J. Chandler agrees with these conclusions.[1]

The Clarno specimen has the long, narrow, apically divergent ventral infolds and the raphe ridge characteristic of Parthenocissus. It differs from modern species and from Parthenocissus monasteriensis (Reid & Chandler) nov. comb. by its larger size. The ventral infolds are also conspicuously narrower than those of the London Clay species, the feature suggesting the specific name.

Fossil seeds of Parthenocissus are rare. Aside from the London Clay and Clarno species, the only other is a form described from the upper Eocene of Hordle, Hants, as Parthenocissus sp. by Chandler (9).

PARTHENOCISSUS ? sp.

Plate X, Fig. 2

DESCRIPTION: Seed broadly oval to oblate in outline; chalaza subcircular, forming a central depression on the dorsal face, surface of the testa around the chalaza smooth; groove of the raphe deep, extending from the chalaza over the apex and forming a prominent apical notch; with a slight groove extending between the base of the seed and the chalaza, together with the raphal groove giving the seed a bilobed

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[1]Letter dated Feb. 15, 1952.

appearance; length 6 to 8 mm., width 5 to 7 mm.; ventral surface not known with certainty.

REMARKS: Only the dorsal surface is visible on each of the six specimens. One seed has been broken transversely, showing that the ventral surface has been removed. Kirchheimer has reported vitaceous seeds from the Pliocene of the Netherlands similarly divided into dorsal and ventral "valves." The Clarno fossils are silicified dorsal "valves" together with internal casts and the carbonized pericarps of the berries.

AFFINITIES: Although only the dorsal side has been preserved, the characters show that these seeds belong to the Vitaceae. The form of the seed, the nature and location of its chalaza, and the raphal groove with its apical notch are typical of this family.

Kirchheimer (30) has found the dorsal surface to be of more constant diagnostic value than the ventral surface for identifying vitaceous seeds. He distinguishes two types of seeds in the family based primarily on the nature of the region surrounding the chalaza. In the (Vitis) teutonica type the dorsal surface is almost smooth or smooth; in the (Vitis) Ludwigii type it is rugose or furrowed. Both types are based upon representative fossil species of Vitis from the German Braunkohle beds. Among living members of the Vitaceae possessing seeds of the (Vitis) Ludwigii type are the species of Vitis in the subgenus Muscadinia, and the species of Ampelocissus and Tetrastigma. Kirchheimer states (Vitis) teutonica type fossils belong to Vitis or a closely

allied group. Parthenocissus and some species of Ampelopsis are included in this type whose seeds are characterized by a smooth dorsal surface.

Because their dorsal surfaces are not furrowed, the Clarno specimens are of the (Vitis) teutonica type. As such, their generic assignment cannot be certain. Since the ventral portion of Parthenocissus angustisulcata has been found in intimate association, there is some basis for considering that these detached dorsal sides belong to this genus. The separate dorsal and ventral sides agree in their large size, although the specimen of P. artosulcata is somewhat narrower. The fossil dorsal sides show a slightly deeper raphal groove than has been observed by the writer in living species of Parthenocissus. Their observable features are also conformable with those of Vitis, although the fossil seeds are larger and less pyriform than is typical for this genus.

Because there is a good possibility that these specimens are the dorsal sides of the seeds of Parthenocissus angustisulcata, they have been tentatively placed in this genus. Their final assignment must await the collection of complete seeds.

EXPLANATION OF PLATE X

Fig.

Parthenocissus artosulcata n. sp.

1. The seed, ventral surface. A piece has been broken from the narrow raphe ridge. x 10.

Parthenocissus ? sp.

2. The seed, dorsal surface. The carbonized remains of the berry are shown at the edges. x 10.

PLATE X

1



2



Family NYSSACEAE

PALEONYSSA Reid & Chandler

1933. London Clay Flora, p. 431

Palaeonyssa spatulata n. sp.

Plate XI

DESCRIPTION: Endocarp.-- Ovoid, woody, 3-loculed; the locules 1-seeded, extending from the base to the apex of the endocarp, dehiscing by means of oval valves which are half or slightly more than half the length of the locules, reniform in median transverse section, the dorsal (outer) side concave. Exterior surface smooth or but slightly furrowed. Length 23 mm., diameter 16 mm.

Locule cast.-- Straight, elongate; spatulate, broadened and flattened at the upper end and narrowed at the lower; reniform in median transverse section, the dorsal side concave. Length 17 mm., width 7 mm.

REMARKS: This species is represented by four specimens, one of which (Plate XI, Figs. 4, 5, 6) is in the United States National Museum. This specimen best shows the shape of the valves. The outer part of the carbonized endocarp has crumbled away, exposing the edges of the locule casts. One of the other specimens shows valves extending about half the length of the endocarp, but since the outer surface has been cracked and later cemented, the surface

features can be made out only with difficulty. This endocarp has been fractured to show the locule casts inside (Plate XI, Fig. 2). In another specimen the carbonized endocarp has been largely lost although the locule casts remain in their original positions (Plate XI, Fig. 1). The outer surface of the endocarp, partially visible in irregular transverse section, shows that the form was at most slightly ridged.

AFFINITIES: Multilocular fruits with woody endocarps occur in several families, among them the Nyssaceae, Cornaceae, Burseraceae, Symplocaceae, and some of the palms. The distinctive characters of the fruits of the Nyssaceae are listed by Reid and Chandler (44, pp. 428-429). These authors established the genus Paleonyssa, with one species, P. multilocularis, for London Clay material in which the endocarp is three- to four-loculed, but otherwise comparable to the chiefly unilocular Recent genus Nyssa except for germination valves narrowed at the base. All the characters listed by Reid and Chandler for nyssaceous fruits cannot be observed in the Clarno material due to the nature of its preservation. However, the large ovoid form of the endocarp combined with its relatively short valves and especially the shape of the seeds-- expanded above and narrowed below-- indicate that these fossils belong to the Nyssaceae. They have been assigned to Paleonyssa after comparison with the London Clay material of the genus. So far as can be determined on the basis of the material at hand, P. spatulata n. sp. differs from the London Clay species chiefly by its larger size, being 23 mm. long compared with 15 mm. for the latter

species.

Although *Paleonyssa* has been described previously only from the London Clay, Barghoorn and Spackman (5), in a preliminary paper on the Brandon lignite flora, report that among the abundant nyssoid endocarps present several of the three-carpellate forms are comparable to this genus. The age of the Brandon lignite is still in doubt.

EXPLANATION OF PLATE XI

Fig. *Laurocarpum proteum* Reid & Chandler

1. A poorly preserved endocarp, end view. The 3 locule casts are still in place. x 2.
2. An endocarp fractured to expose 2 of the locule casts. x 2.
3. The same specimen; the median transverse section of the carpel which was removed. Note the U-shaped locule cast. x 2.
4. A well preserved endocarp (U. S. Nat. Mus. specimen 40543) showing the shape of the valves. x 2.
5. The same, lateral view. x 2.
6. The same, end view. x 2.

PLATE XI


1


2


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6

Family CORNACEAE (Dogwood Family)

Subfamily Mastixioideae

MASTIXIOIDIOCARPUM gen. nov.

DIAGNOSIS: A genus which includes endocarps and locule casts referrable to the subfamily Mastixioideae of the Cornaceae, but whose generic affinities cannot be determined more accurately.

Mastixioidicarpum oregonense n. sp.

Plate XII

DESCRIPTION: Endocarp.-- One-loculed, ovoid, woody. External surface with 9 or more rows of sharp, irregular ridges alternating with deep hollows. Dorsal surface of the endocarp wall with a deep, longitudinal infold which extends into the locule; the space between adjacent walls of the infold forming a deep, narrow, parallel-sided groove which is open to the exterior along the length of the dorsal surface. Thickness of endocarp wall 2 to 3 mm.; other dimensions probably 4 to 6 mm. larger in each case than those given below for the locule cast.

Locule cast.-- Narrowly saddle-shaped; the ventral face convex, the dorsal face concave. U-shaped in transverse section, the arms proximate. Lateral margins rounded, but thinning towards the ends and acute at base and apex. Traces of

a strand representing the raphe visible medianly on the ventral surface. Length 14 to 17 mm.; width 6 mm.; thickness (across the infold) 7 mm.

REMARKS: The material consists of three saddle-shaped locule casts. The dorsal infold of the endocarp, its groove filled with sediment, is present in each. One locule cast is otherwise completely separated from its carbonized endocarp; the incomplete remains of the endocarps of the other specimens are sufficient to show the thickness of the wall and its ridged exterior (Plate XII, Fig. 1). No traces of valves or of lines of dehiscence have been preserved.

AFFINITIES: The subfamily Mastixioideae is represented in the modern flora by a single genus, Mastixia Blume. Its fruit has been described in detail by Kirchheimer (27). The thick, woody endocarp is ovoid, one- or uncommonly two-loculed, and frequently finely rugose or somewhat sculptured. On the dorsal surface there is a longitudinal groove formed by the adjacent sides of the infolded endocarp wall. This infold projects into the locule, and together with the ventral side of the endocarp, gives the cavity a horseshoe-shaped transverse profile. Dehiscence occurs by means of an elongate valve which is located on the dorsal side of the endocarp so that the infold projects medianly from its inner surface. The raphe is located on the ventral surface of the seed. Kirchheimer states that the most distinctive morphological feature of the fruits, the longitudinal infold of the dorsal endocarp wall does not occur in additional members of the Cornaceae or in other families, but is confined to the subfamily Mastixioideae.

Although histological details and valve structure have not been preserved in the Clarno specimens, the association of the unique dorsal infold and U-shaped locule cavity, the thick, ridged, woody endocarp, and the ventral raphe are sufficient to authenticate its reference to the Mastixioideae.

Although only a single genus is now extant, the subfamily Mastixioideae was much larger in the past. Kirchheimer (29), in his monograph of the fossil Cornaceae, recognizes twelve extinct genera in addition to the still living Mastixia. He has founded eight of these twelve genera on material from the European Tertiary Braunkohlenformation, two were described by Chandler from the upper Eocene of Hordle, Hants, and two are from the London Clay. Another London Clay genus, Langtonia Reid & Chandler, has been excluded from the subfamily by Kirchheimer.

The characters upon which these genera have been differentiated include cellular structure, the nature of the dorsal infold and its external groove, the number of locules, the sculpture of the exterior of the endocarp, occurrence of secretion cavities in the tissues of the fruit, and the nature of the valve and the dehiscence which forms it. By using the available information the Clarno form can be separated from eleven of the twelve extinct genera. However, it is impossible to determine whether it should be assigned to Mastixia, Ganitrocera Kirchheimer, or some undescribed extinct genus. Plate XII, Figs. 4, 5, 6, 7, 8, illustrate the resemblances among the transverse sections of the endocarps of these two genera and the Clarno fossil. Other species of both genera are more

strongly ridged than those shown.

All of the previously named genera of Mastixioideae have been described from material which enabled them to be characterized in detail. No name exists for fruits definitely belonging to the Mastixioideae, but not more precisely assignable. The proposal of a new genus for such fossils seems preferable to merely referring them to the Mastixioideae without any name. Accordingly, the genus Mastixioidiocarpum is set up for the Clarno fruits.

The oldest known fruits of the Mastixioideae occur in the lower Eocene London Clay. Remains of members of the subfamily are abundant in the middle and upper Oligocene Braunkohlenformation of Germany, but have not been found in younger beds. The occurrence of the Mastixioideae in the New World has not previously been demonstrated with certainty, although Kirchheimer (29) lists as doubtful and unproved forms the following American species: Myristica catahoulensis Berry, Nyssa Jonesi Perkins, N. texana Berry, and Phoenicites occidentalis Berry.

EXPLANATION OF PLATE XII

Fig. *Mastixioidicarpum oregonense* gen. & sp. nov.

1. The locule cast and endocarp, from above. The filling of the dorsal infold is seen between the arms of the locule cast. x 2. The endocarp appears in transverse section.
2. The same, dorsal surface. The filling of the dorsal infold appears as a white line. x 2.
3. An isolated locule cast. The white line marks the position of the dorsal raphe. x 2.

Diagrammatic transverse sections of members of the Mastixioideae

4. The endocarp of *Mastixia* sp. (Recent). (After Kirchheimer).
5. The endocarp of *Mastixia pistacina* (Unger) Kirchheimer. (After Kirchheimer).
6. The endocarp of *Mastixia menzeli* Kirchheimer. (After Kirchheimer).
7. The endocarp of *Ganitrocera halzapfeli* (Menzel) Kirchheimer. (After Kirchheimer).
8. The endocarp of *Mastixioidicarpum oregonense* n. sp.

PLATE XII

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RELATIONSHIPS TO MODERN PLANTS

Ten species of dicotyledonous fruits and seeds representing eight genera and seven families are described from the Clarno formation. Four of the genera are extinct and the status of a fifth, Mastixioidicarpum, is uncertain. Eight of the species and three of the genera have not previously been described. In addition, there are at least seven more forms not well enough preserved for identification.

Systematic List of Species

Angiospermae
- Juglandaceae
  - *Juglans clarnensis* n. sp.

Menispermaceae
- *Odontocaryoidea nodulosa* gen. & sp. nov.
- *Chandlera lacunosa* gen. & sp. nov.

Lauraceae
- *Laurocarpum proteum* Reid & Chandler

Icacinaceae
- *Paleophytocrene foveolata* Reid & Chandler
- *Paleophytocrene pseudopersica* n. sp.
- *Paleophytocrene hancockii* n. sp.

Vitaceae
- *Parthenocissus angustisulcata* n. sp.
- *Parthenocissus* ? sp.

Nyssaceae
- *Paleonyssa spatulata* n. sp.

Cornaceae
- *Mastixioidiocarpum oregonense* gen. & sp. nov.

The living species of Juglans (Juglandaceae) are widely distributed, occurring in the United States, Central and South America, and southeastern Asia. Except for J. nigra in eastern United States, the members of the section Rhysocaryon range from southwestern United States into South America. J. major, which the Clarno walnut most closely resembles of the species in this section of the genus, extends from western New Mexico and Arizona southward into northern Mexico. This species and the closely related J. microcarpa and J. californica require a considerable amount of moisture and typically occur along streams and in canyons. Asiatic species of the section Cardiocaryon also occur beside streams and in moist river bottoms. Because of its position between these two sections of the genus, the Clarno walnut cannot be considered as equivalent to one particular modern species. Nevertheless, it was probably a riparian form.

The species of the menispermaceous tribe Tinosporeae are chiefly lianas, although a few are erect shrubs and small trees. They occur in the tropical and subtropical regions of both hemispheres. Of the American representatives of the tribe, Calycocarpum lyoni (Pursh.) Gray is the only species found north of Mexico. The recent New World genus Odontocarya, the nearest relative of the fossil genus Odontocaryoidea, and the closely related genera Somphoxylon and Synandropus, also limited to the New World, are all climbing vines. Odontocarya has the widest distribution of

the three, ranging from Panama and Columbia to the West Indies, Brazil, Paraguay, and Ecuador. Its species have been collected from situations ranging from riverbanks to dry forests, and varying in altitude from nearly sea level to about 5000 feet. O. nodulosa is most closely related to American genera.

The resemblances of the extinct menispermaceous genus Chandlera are to Old World genera of the Tinosporeae. Although it cannot be considered as ancestral to one particular genus, the greatest similarity of the fossil is with Parabaena, a liana from the Malayan region, the Phillippines, China, New Guinea, and Australia.

The approximately 1000 living species of the Lauraceae are widely distributed in tropical and subtropical regions, and include a few temperate forms. The Clarno representative, referable only to Laurocarpum, a genus for fruits belonging to the family, furnishes no habitat or distributional information.

The Icacinaceae is a pantropical family which in America does not range north of Mexico. The tribe Phytocreneae, to which the three Clarno species of Paleophytocrene belong, is limited to the Old World. Of the Recent genera of this tribe sharing relationship to Paleophytocrene, Miquelia is Indo-Malayan, Phytocrene is widely distributed in tropical southeast Asia, Chlamydocarya and Polycephalium are found in tropical Africa, and Pyrenocantha occurs both in eastern Asia and in Africa. All living

members of this tribe are forest lianas, and according to Reid and Chandler (44, p. 335), Chlamydocarya and Phytocrene are chiefly aquatic.

Parthenocissus (Vitaceae) is a chiefly temperate genus of climbing vines often found along stream banks. It includes about 10 species in North America and south and east Asia. In America it ranges from Canada to Mexico. One North American species, P. quinquefolia (L.) Planch., is also an endemic in the mountains of southern Guatemala, where, along with several other genera, it is regarded by Steyermark (46) as an apparent relic of early Tertiary types now found at least several hundred miles to the north.

The Nyssaceae is a warm-temperate and tropical family which is found in southeastern United States and southeastern Asia. The Clarno representative, Paleonyssa, is most closely related to the Recent genus Nyssa, which includes about one hundred and twenty tropical and subtropical species. The species of Nyssa, which are mostly large trees, usually are found in moist, low situations such as the flood plains of rivers or coastal plains.

Mastixia, the only living genus of the subfamily Mastixioideae (Cornaceae), consists of 25 to 30 species distributed throughout the tropical and subtropical regions of southeastern Asia. Its members are trees and shrubs growing in habitats which vary from tropical rain forests to mountain woods at an altitude of 7500 feet. Mastixioidiocarpum oregonense is the first certain evidence

for the existance of the subfamily in the New World.

The diverse geographical affinities of the relatively small number of Clarno species precludes their comparison with a single association of modern plants. The nuts of Juglans clarnensis are the most abundant fossils, and far outnumber all others. However, it should not be concluded from this fact that J. clarnensis was necessarily the dominant species. The number of fruits which would be fossilized of any given species would depend upon several factors, including the season in which deposition took place, the distance from the water, and the type of plant. A majority of the Clarno species appear to have been scandent vines, and a single vine probably produced fewer fruits than one walnut tree. A few walnut trees growing at the edge of a stream would contribute large numbers of nuts. The preponderance of walnuts, the small number of specimens of most other species, and the high proportion of unidentifiable forms all combine to make meaningless any determination of the percentage composition of the florule.

It has been stated earlier in this paper that the plants which produced these fruits and seeds probably lived adjacent to a stream or on a flood plain. This assumption is borne out by the habitat preferences which have been given above for the nearest living relatives of the Clarno species, especially those concerning the numerically prominent Juglans clarnensis whose relationships to modern species can be more closely established than those of the

other fossil forms. Six of the other nine species were probably lianas whose closest living equivalents would be at home in this habitat, although not necessarily confined to it. Paleonyssa spatulata was also probably a riparian form. The habitats of Laurocarpum proteum and Mastixioidiocarpum oregonense are unknown.

TABLE 1.

GEOGRAPHICAL DISTRIBUTION OF THE NEAREST MODERN EQUIVALENTS OF THE CLARNO FRUIT AND SEED GENERA

Fossil Genus	Nearest Modern Equiv.	Southwestern United States	Mexico & Central America	Central & South China	Indomalaya	Philippines	Tropical Africa
Juglans	Juglans spp.	X	X	X			
Odontocaryoidea	Odontocarya spp.		X				
Chandlera	Old World Members of Tribe Tinosporeae				X	X	X
Laurocarpum	Lauraceae	X	X	X	X	X	X
Paleophytocrene	Tribe Phytocreneae				X	X	X
Parthenocissus	Parthenocissus spp.		X	X	X		
Paleonyssa	Nyssa spp.			X	X		
Mastixioidiocarpum	Mastixia spp.			X	X	X	

RELATIONSHIPS TO FOSSIL FLORAS

In recent years a number of early Tertiary floras from western United States have been studied by Chaney and his associates, utilizing in part a detailed ecological and associational method in the identification of fossil leaves. These floras, among them the Clarno, Comstock, and Goshen floras from Oregon; and the Chalk Bluffs, LaPorte, and Weaverville floras from northern California, indicate humid, subtropical conditions for northwestern United States during Eocene and lower Oligocene time. Most of the plants were members of the Neotropical or Paleotropical Floras whose modern relatives are either characteristic of low latitudes or range into them. Chaney (12) regards these western floras as indicating the sort of climate now found approximately 20 degrees of latitude farther south.

There exists much skepticism among botanists regarding the reliability of identifications based on leaves alone. Fossil fruits and seeds, when available, furnish independent and presumably more accurate information regarding the affinities of the plants in the geologic record. The Clarno formation, containing leaves, fruits, and seeds, offers a limited opportunity for the comparison of the two types of evidence.

As was mentioned in the introduction of this paper, Chaney has identified numerous leaf remains from the Clarno formation although he has not yet published the results of his study in complete form. Although Chaney obtained a few leaves from the nut locality, most of the best material came from West Branch Creek, 3½ miles west of the bridge across Bridge Creek, which is 6 miles north of Mitchell, Oregon. This location is approximately 18 airline miles southeast of the nut locality. In order that the known generic composition of the Clarno flora might be assembled, Professor Chaney has furnished the following preliminary list of Clarno genera:[1]

Schizaeaceae
Lygodium

Cycadaceae
Dioon

Anacardiaceae
Astronium
Rhus

Bignoniaceae
Catalpa

Boraginaceae
Cordia

Celastraceae
Celastrus

Euphorbiaceae
Alchornea

Flacourtiaceae
Casearia

Lauraceae
Cinnamomum
Nectandra
Persea

Menispermaceae
Abuta

Moraceae
Ficus

Nyssaceae
Alangiophyllum

Platanaceae
Platanophyllum

Rhamnaceae
Gouania

Sabiaceae
Meliosma

Vitaceae
Vitis

---

[1]Letter dated April 3, 1952.

Although details of this assemblage must await publication, Chaney has briefly discussed the Clarno plants in several papers from which the following excerpts are taken:

1. (12, p. 383)

> The Comstock flora of western Oregon, and the Clarno flora of eastern Oregon, both of Eocene age, contain a relatively large proportion of Lauraceae, Leguminoseae, and Euphorbiaceae, as does the somewhat younger LaPorte flora of northern California. It is interesting to note that the Clarno flora, although as yet incompletely known, is so similar to the Comstock flora on the opposite side of the Cascade range as to indicate that this modern climatic barrier was not then in existance. In fact, all of the older Tertiary floras of this province indicate lowland conditions such as are now found adjacent to the seacoast in low latitudes.

2. (13, pp. 10-15)

> The Clarno flora: Turning first to the kinds of trees which made up the forests of the John Day Basin sixty million years ago, we find members of the laurel family among the most numerous. This family, the Lauraceae, is now largely restricted to the warmer parts of the world, although a temperate member, the pepperwood (Umbellularia californica) is a common tree in southwestern Oregon.... The tropical family the Sabiaceae, is most characteristic of Asia; one of its genera, Meliosma,...has been recorded from the Eocene of North America at a number of localities, including the Clarno deposits on West Branch Creek.... A large, thick fossil leaf is referred to the genus Ficus, or fig,...and there are numerous large leaves with lobes which appear to represent the ancestors of the sycamore and are assigned the name Platanophyllum. Ferns of tropical types are more numerous than in any other Eocene flora from western North America as yet studied. At most localities, notably Pilot Rock, there are abundant leaves of palm. A few miles east of the Clarno Bridge I collected, some years ago, a large leaf of a cycad which is provisionally referred to the genus Dioon.... I was guided to the cycad locality by two enthusiastic and competent fossil collectors, A. W. Hancock and A. D. Vance... These men were also responsible for my visit to a nearby cliff where abundant fruits are preserved, in some cases with their walnut-

like seeds replaced by quartz. There are few places in the world where fossil fruits are equally numerous, and future studies will add critical information regarding their relationships. Identification of these fruits may also serve to confirm the determination of many of the leaves of the Clarno flora, although their assignment to genera now living in the tropics seems well established.

3. (14, pp. 358-359)

For a number of years we have known of a mixture of subtropical with temperate trees in the Eocene Clarno flora of the John Day Basin of Oregon.... This is the best known occurrence of an altitudinal ecotone, and again its most conspicuous member is Metasequoia....
Metasequoia has long been a member of the forest of the temperate zone, and has commonly ranged southward into latitudinal ecotones with the forests of the subtropical zone. During the Eocene epoch this conifer extended still further south in the uplands, where it lived in an altitudinal ecotone bordering the Clarno flora of the John Day Basin. It has survived in the high valleys of central China under conditions which seem to resemble closely its Tertiary environment in Oregon.

Comparison of Professor Chaney's list of Clarno plants with those based on fruits and seeds (listed at the beginning of the previous section) shows that although 15 dicotyledonous families are recognized by leaves, only four of the seven families represented by fruits are among them. These are the Menispermaceae, Lauraceae, Vitaceae, and Nyssaceae. No genus is represented by both leaves and fruits. This lack of similarity is probably due to the fact that the leaves and fruits came from places several miles apart and probably from different horizons in the Clarno formation. The relatively small number of genera represented in this instance most certainly includes only a portion of the plants which grew in the region.

TABLE 2.

DISTRIBUTION OF CLARNO FRUIT AND SEED FAMILIES IN OTHER EARLY TERTIARY FLORAS

Family	Clarno Flora (leaves)	Comstock Flora	Goshen Flora	Chalk Bluffs Flora	LaPorte Flora	Weaverville Flora
Juglandaceae				X		X
Menispermaceae	X			X	X	
Lauraceae	X	X	X	X	X	X
Icacinaceae				X		
Vitaceae	X			X		
Nyssaceae	X			X		
Cornaceae				X	X	

The distribution of the Clarno fruit and seed families in the western floras mentioned at the beginning of this section are shown in Table 2. The only flora which contains over half of the families is the middle Eocene Chalk Bluffs, and this contains all of them. This correspondence may be due to the fact that the Chalk Bluffs flora

is the largest and contains almost twice as many genera as any of the others. All the families are also represented in the London Clay flora, and all except the Icacinaceae have been recorded from the upper Cretaceous.

Juglans is the only genus represented at Clarno by fruits that is present in any of the leaf floras listed in Table 2. A single species, J. orientalis, occurs in the lower Oligocene Weaverville flora. The former existence in western United States of the now exclusively Paleotropical icacinaceous tribe Phytocreneae is known only from leaves of Phytocrene in the Chalk Bluffs flora. This distribution is now confirmed by the fruits of Paleophytocrene in the Clarno.

Because of the difficulties in comparing fossil floras made up of different plant parts, it is not surprising that fewer Clarno forms are recognized in the western leaf floras than in the London Clay. There are four genera common to these two fruit and seed deposits, Parthenocissus, Paleonyssa, Laurocarpum, and Paleophytocrene; the latter two include species in common. The only American deposit of fruits and seeds worthy of note is in the Brandon lignite. This flora was not described in sufficient detail to permit comparison, and is presently being revised by Barghoorn and Spackman (5).

Of much greater significance than agreement in detail is the bearing of the affinities of the fruit and seed forms upon the climatic and distributional relationships

which have been ascribed to the Clarno and other western Eocene floras. The fruit and seed genera illustrate the Paleotropical, Neotropical, and temperate to warm-temperate floral elements which have been recognized in the early Tertiary leaf floras of northwestern United States. Omitting the indeterminate Laurocarpum, the affinities of three of the remaining seven genera are Paleotropical, one is Neotropical, and three are temperate to warm temperate forms whose modern relatives range southward from the temperate regions of both hemispheres. One of the families, the Icacinaceae, is exclusively tropical at the present time, and another, the Menispermaceae, is almost exclusively tropical. Their occurrence along with that of the first certain New World member of the Mastixioideae, substantiates the existance of much warmer and more humid conditions in north-central Oregon during the Eocene.

Although Parthenocissus has not been identified from leaves, the occurrence of a few incomplete seeds belonging to the genus is of interest in the light of Chaney's statement (quoted above) regarding the existence of Metasequoia in the uplands bordering the Clarno Flora. Chu and Cooper (17) list Parthenocissus as one of the prominent vines associated with the living Metasequoia glyptostroboides Hu and Cheng in its present limited range in central China.

The evidence from the Clarno fruits and seeds is in complete agreement with the climatic and distributional re-

lationships which have been established for the early Tertiary leaf floras from western United States.

EVOLUTIONARY CONSIDERATIONS

A part of the interest in fossil fruits and seeds arises from the prospect that, as modern plants are differentiated primarily by means of their reproductive structures, these ancient remains may indicate developmental trends. In practice, however, such information is seldom forthcoming unless successive members of a taxonomic category can be collected from a stratigraphic sequence. Because the Clarno fruits and seeds occur in a single geologic horizon, they are of only limited value in this respect.

Four of the Clarno species may indicate the direction of subsequent morphological change in the fruits of their respective groups. As was shown earlier in this paper, Juglans clarnensis combines characters found separately in two modern sections of the genus. Until more walnuts of Eocene or earlier age have been described, it is not possible to state whether this species is ancestral to members of the two sections or whether it is an extinct, intermediate species which was a member of a once more continuous series. Odontocaryoidea nodulosa suggests the derivation of certain endocarp features of the Recent genus Odontocarya, but the relationship cannot be stated exactly

until the fruits of all the living species are known. Chandlera lacunosa also suggests a possible mode of origin for certain endocarp characters in the menispermaceous tribe Tinosporeae, but its affinities cannot be restricted to any one Recent genus. The relationship between the chiefly unilocular Recent genus Nyssa and the trilocular extinct genus Paleonyssa has been considered by Reid and Chandler (44, p. 42) as evidence for a trend toward reduction in number of locules.

The occurrence of Juglans clarnensis in rocks as old as the Eocene has a bearing on the evidence for an aspect of the evolutionary development of the angiosperms stated by Chaney (15, p. 199) in a paper in a recent symposium. After a carefully qualified discussion of the London Clay genus Juglandicarya, which he regards as intermediate between and possibly ancestral to Juglans and Carya, Chaney summarizes his viewpoint as follows:

> Fruits of the Juglandaceae from the London Clay indicate that the walnut (Juglans) and hickory (Carya) were not generically differentiated during the Eocene, although their leaves have been recognized as distinct in floras of that age. Clearly we may expect earlier development and stabilization in some organs of a plant than in others.

There is little basis for considering Juglandicarya to be intermediate between Juglans and Carya, as has been pointed out in the present paper in the discussion of the affinities of Juglans clarnensis. Even if the intermediate status of Juglandicarya had been correctly surmised, the existence of a true walnut in the Clarno forma-

tion demonstrates that Juglans and Carya were differentiated during the Eocene.

The theory of differential rates of development among different plant organs stated by Chaney in the above quotation is probably correct although Juglandicarya can no longer be considered as evidence for it. An example which supports it is now available from the Eocene of western United States. The leaves of Phytocrene sordida (Lesquereux) MacGinitie from the middle Eocene Chalk Bluffs flora are described by the latter author (35) as corresponding to the modern species P. blancoi (Azaola) Merrill in every detail. Paleophytocrene, well represented in the upper Eocene Clarno formation as well as in the lower Eocene London Clay, is an extinct genus with endocarp features now found in several genera composing the tribe Phytocreneae, including Phytocrene. Although the present author has questioned the constancy of some of the endocarp characters of these modern genera in his discussion of Paleophytocrene, he agrees with Reid and Chandler that the genus is an intermediate and possibly ancestral one. It definitely is not equivalent to the Recent genus Phytocrene, as MacGinitie regarded it in his discussion of P. sordida.

The high proportion of extinct genera among the Eocene plants identified from reproductive structures seems to be better evidence for this principle than isolated and vulnerable examples like those above. Excluding the genera Laurocarpum and Mastixioidiocarpum, whose status in this re-

spect is doubtful, four of the six remaining genera to which the Clarno fruits and seeds belong, or 67%, are extinct. This is a small number of genera, but the indicated high proportion is in agreement with that found in the London Clay flora. Of ninety genera whose affinities were definitely determined by Reid and Chandler, sixty five, or 72%, were found to be extinct.

Barghoorn (4) has combined into a single category the extinct, unidentified, and "form" genera from each of a number of American Upper Cretaceous and Tertiary floras, and has computed the percentage of this category in the total number of angiosperm genera composing each flora. Of the Paleocene Raton genera 32% fall into this category. The Eocene floras included range from 4% from the Comstock flora to 52% from the Green River flora, and average 29% as computed by the present writer. The LaPorte flora with 27% contains the largest proportion of this category among the early Tertiary floras listed in Table 2 of the present paper. (Barghoorn did not compute figures for the Chalk Bluffs and Clarno floras, but Macginitie (34) lists only 9.2% extinct or doubtful species for the former flora. The list of Clarno leaf genera furnished by Chaney contains two extinct or form genera among the seventeen angiosperms listed, or 12%.)

It is apparent that the percentages given above for the floras known principally from leaves are increased in comparison to those for the floras known from fruits and

seeds by the inclusion in the former of unidentified and "form" genera as well as extinct genera. Nevertheless, the proportion of extinct genera alone among the Clarno fruits and seeds, 66%, is about double the highest combined percentage among the early Tertiary leaf floras from the same botanic province. The figures for the Clarno and London Clay fruits and seeds agree better with those given by Barghoorn for the upper Cretaceous floras, which range from 28% to 75%, and average 49%.

The higher proportion of extinct genera among the Eocene Clarno and London Clay fruit and seed assemblages than among the Eocene floras based on leaves is in accordance with Chaney's suggestion that the leaves of some early plants may have differentiated along modern generic lines before their reproductive organs. Although the evidence is as yet scanty, it at least hints that when a greater number of fossil plants are known from reproductive structures, the prevalent concept of the largely modern generic composition of the early Tertiary floras may be partially modified.

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