SMITHSONIAN INSTITUTION
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CONTRIBUTIONS TO THE GEOLOGY AND PALEONTOLOGY OF THE CANAL ZONE, PANAMA, AND GEOLOGICALLY RELATED AREAS IN CENTRAL AMERICA AND THE WEST INDIES

THE FOSSIL HIGHER PLANTS FROM THE CANAL ZONE

By EDWARD W. BERRY
Of the Johns Hopkins University, Baltimore

Extract from Bulletin 103, pages 15–44, with Plates 12–18

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THE FOSSIL HIGHER PLANTS FROM THE CANAL ZONE.[1]

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INTRODUCTION.

It is a truism that the present floras and faunas of Central America are the result of a long series of antecedent geologic changes which might be amplified as geographic, climatic, and biologic. As the past can only be understood by means of our knowledge of the present, so, too, the present can only be understood by means of our knowledge of the past. Moreover, this can never be a local problem, and this is particularly true of the Isthmus of Panama marking as it does at times the highway of communication between the terrestrial life, both animal and plant, of North and South America; at other times marking one of the paths of communication between the marine life of the Atlantic and Pacific. Thus the history of the Central American region is of the utmost importance in any consideration of the extinct terrestrial faunas and floras of North America or the marine faunas that formerly flourished on the east and west coasts.

Our knowledge of the present flora of the isthmian region is based upon Seemann's flora[2] and Hemsley's flora of Central America, supplemented by the scattered papers by numerous authors on special topics relating to this flora. As the results of the recent Biological Survey of the Canal Zone become available, we will doubtless have a secure basis for comparisons with antecedant floras both in this region and the areas north and south of it.

The present distribution of plant associations is in its broader outlines governed almost entirely by the interrelations between

[1] R. T. Hill, who did some geological work on the Isthmus in 1895 for Alexander Agassiz, mentions lignite and fragments of fossil plants in the Culebra clays at the base of the canal cutting at Culebra station (Bull. Mus. Comp. Zool., vol. 28, No. 5, 1898), and the lignitic coal at Chiriqui Lagoon was studied by Dr. John Evans in 1857, who reported "that the fossil plants associated with the coal were endogenous and allied to or identical with those at present growing in the vicinity." (Repts. of Expl. & Surv. for the Location of Inter-oceanic ship canals, etc., by the U. S. Naval Exped., 1875, E. P. Lull, U. S. N., commanding, Washington, 1879.)

[2] Seemann, Flora Panamensis, Botany of the voyage of H. M. S. *Herald*, pp. 57–346, 1852–1857.

topography and the prevailing winds and the resulting variations in rainfall.

The climate is now moist tropical, modified by the nearness of the two oceans, and there is therefore but slight diurnal or annual variations in temperature. So far as information is available regarding the conditions during the Tertiary, there is no evidence that can be deduced from the fossil flora or the geographical history of the region to indicate that the climate was very different from what it is now at any time during the Tertiary, unless we are prepared to assent to enormous changes in the altitude of the land, for which the data does not seem to be adequate.

The prevailing winds now come from the northeast, and as the divide is near the Pacific Coast the major part of the Isthmus north of this low divide has a heavy rainfall, as, for instance, 170 inches at Porto Bello and 129 at Colon, as compared with 90 inches at Culebra or 71 inches at Ancon. There are two seasons—a short relatively dry season extending from January to April and a long and relatively wet season the balance of the year with the maximum of precipitation from September to December. Before the clearing of the French Canal Company forests covered six-tenths of the Isthmus, the remainder being broken forests and savannas. Evergreen tropical rain-forests of mixed angiosperms covered the entire northern watershed and part of the Darien region on the south side. Some of the forests of the southern watershed are what are known as monsoon forests, with many deciduous species, and at high altitudes there may be more gregarious types of forest as, for example. the oak forests which are so striking a feature in the uplands of Central America as you proceed to the northwest.

The shores are skirted with dunes abounding in Leguminosae and Euphorbiaceae with Coco palms and Hippomane. Low shores and tidal inlets are covered with mangrove swamps with Rhizophora, Avicennia, Conocarpus, etc. Less saline coastal marshes are covered with Acrostichum, Crescentia, or Paritium thickets. The evergreen forest is composed chiefly of species of Sterculiaceae, Tiliaceae, and Mimosaceae, Euphorbiaceae, Anacardiaceae, Rubiaceae, Myrtaceae, and Melastomataceae, with small palms like Chamaedorea, Trithrinax, and Bactris.

CORRELATION.

The fossil flora described in the present report is too limited for purposes of exact correlation, which may be expected to be settled by the marine faunas present at most horizons in the Isthmian region. Regarding the plants in the various formational units recognized in the Canal Zone by MacDonald a glance at the accompanying table of distribution will show that from the oldest (Bohio) to the youngest (Gatun) plant-bearing formations there is no observable difference in floral facies, and while the plants are entirely too few for positive conclusions, and while not much variation can be expected in fossil floras of the Tropics unless after the lapse of long intervals of time or the intervention of marked changes in physical conditions, I am disposed to think that this so-called Oligocene series of formations does not represent any great interval of time.

Nearly all of the fossil plants are new, the only outside occurrences being the *Hieronymia* which is common to the Tertiary of Ecuador and the *Palmoxylon* and *Taenioxylon* both of which occur in the Oligocene of the island of Antigua, and both have related types in the Oligocene (Catahoula and Vicksburg) of our Southern States In addition to the *Hieronymia* common to Ecuador there are several other elements in the Tertiary flora of the latter region that are similar to Panama forms, and it is not improbable that the coals of Loja in the Ecuadorian Andes are the same age as the so-called Oligocene series of Panama. Only one pre-Oligocene plant is recorded from Panama and the age (Eocene) rests on the stratigraphic observations of Doctor MacDonald and paleontologic determinations by C. W. Cooke. The form itself offers no intrinsic evidence of its age and might well be early Oligocene but for the fact that Doctor MacDonald collected the type stratigraphically below a bed containing a varietal form of the mollusk, *Venericardia planicosta.*

The chief question of interest in the correlation of these Panama beds is their equivalence in terms of the European section. The present flora offers no evidence on this point which must hence be determined by the accompanying marine faunas. However, in view of the traditional unscientific assumption that all of the fossiliferous beds of the Carribbean region are Oligocene in age, it is of interest to note that Douvillé[1] from a study of the foraminifera, pointed out as early as 1898, that a considerable part of the so-called Oligocene of the Isthmus was Aquitanian and Burdigalian in age; that is to say, lower Miocene according to the present conceptions of European geologists and palentologists.

In my preliminary announcement[2] of the discovery of fossil plants in the Canal Zone I stated that none of the plants recognized indicated Eocene and that they were all probably Oligocene in age. This statement was perhaps overemphasized in a desire to offset the extreme views of certain foreign paleontologists who have held that these faunas were young Miocene or even Pliocene.

The question of the exact time in the Tertiary at which connections between North and South America were replaced by marine conditions is of the utmost importance in all studies of distribution of both

[1] Douvillé, H. Bull. Soc. Géol. de France, ser. 3, vol. 26, pp. 587–600, 1898.
[2] Berry, E. W. Science, new ser., vol. 39, p. 357, 1914.

the marine faunas and the terrestrial faunas and floras. The floral evidence as previously stated is inconclusive. I should not, however, be inclined to consider any of the fossil plants, except one Eocene species, described in the present report as younger than Burdigalian nor older than Sannoisian (Lattorfian).

	Gatun formation.	Caimito formation.	Lower Oligocene Limestone.	Cucuracha formation.	Culebra formation.	Bohio formation.	Eocene.	Oligocene of Antigua.
Palmoxylon palmacites				6845 ×				×
Ficus culebrensis					6837 ×			
Guatteria culebrensis	×	6840 ×			×			
Myristocophyllum panamense					×			
Taenioxylon multiradiatum			6523 ×	6845 ×	×	×		×
Inga oligocaenica					6837 ×			
Cassia culebrensis					6837 ×			
Hiraea oligocaenica		6840 ×						
Banisteria praenuntia					×			
Hieronymia lehmanni		×						
Schmidelia bejucensis		6840 ×			×			
Mespilodaphne culebrensis					×			
Calyptranthes gatunensis	×							
Melastomites miconioides					×			
Diospyros macdonaldi							6586b ×	
Rondeletia goldmani	×							
Rubiacites ixoreoides	×							

Palm rays .... 6839 × 6837 ¼ mile S. of Empire Bridge.

Fern fragments .... 6837 *cf.* Acrostichum.

BOTANICAL CHARACTER.

The fossil flora at present known from the Canal Zone is extremely limited and entirely too small for either purposes of adequate correlation or for deductions concerning the true botanical facies or the environmental conditions. Seventeen species are determined and two or three additional forms are tentatively recognized. This paucity is especially to be regretted since it is improbable that under the existing climatic conditions as favorable opportunities for the discovery and collection of fossil plants will ever be presented as during the digging of the canal. While fossil plants were nowhere found to be abundant in the shales, nevertheless, it is very probable that an experienced collector by working over a large amount of material could have gotten together a much more representative collection.

The plants collected include ill-defined fragments of one fern, two undertermined species of palm, represented by fragments of foliage, and a third represented by petrified stems, and 16 dicotyledons, of which two are represented by fruits and the balance by leaves.

Among the Dicotyledonae there are representatives of the orders *Urticales*, *Ranales*, *Rosales*, *Geraniales*, *Sapindales*, *Thymeleales*, *Myrtales*, *Ebenales*, and *Rubiales*. Orders conspicuous in the existing flora of the Isthmian region unrepresented among the fossils are the *Arales*, *Poales*, *Cyperales*, and *Orchidales* among the Monocotyledonae, and the *Campanulales* and *Personales* among the Dicotyledonae.

The following 14 families are represented by fossils in Panama: Moraceae, Anonaceae, Myristicaceae, Mimosaceae, Caesalpiniaceae, Papilionaceae, Malpighiaceae, Euphorbiaceae, Sapindaceae, Lauraceae, Myrtaceae, Melastomataceae, Ebenaceae, and Rubiaceae. Only the last, with two species, is represented by more than a single species. When so sparse and evenly distributed a representation of the families is present in a fossil flora, it is an indication that after allowing for some accidents of preservation, those families represented may be regarded as the most abundantly represented in the Tertiary flora of the region, and in this respect there is a very great similarity to the existing flora of the Isthmian region. The present forests of Panama are made up principally of species of Arecaceae, Moraceae, Mimosaceae, Papilionaceae, Sterculiaceae, Tiliaceae, Euphorbiaceae, Anacardiaceae, Myrtaceae, Melastomataceae, and Rubiaceae. The only ones of this list not found fossil are the Sterculiaceae, Tiliaceae, and Anacardiaceae, and as these three families are all abundant in the much more complete floras from the Tertiary of the southeastern United States, it is safe to assume that they were also present in the Tertiary flora of Panama. The mainly herbaceous families abundant in the Recent flora, which are hardly to be expected in the fossil flora, are the Poaceae, Cyperaceae, Orchidaceae, Araceae, and Compositae.

The bowers of wild figs of the existing flora are represented by a small-leafed species of *Ficus* from two localities in the Culebra formation. The family Anonaceae, which has numerous species of *Anona* and *Guatteria* in the Recent flora of Central America, is represented by a fine large species of the latter genus which is not uncommon in the Gatun, Caimito, and Culebra formations. *Guatteria* contains about 50 existing species of tropical shrubs and trees of varying habitats and exclusively American, and has not been previously recognized with certainty in fossil floras. *Anona* is abundant in the Eocene and Oligocene of our Southern States, but *Guatteria* has not been recognized.

The Myristicaceae is represented by an infrequent species of *Myristicophyllum* in the Culebra formation, and in this connection it is of interest to note the presence of fruits and seeds of *Myristica* in the uppermost Eocene of Texas suggestive of the subgenera *Virola* and *Compsoneura*, both of which occur in the Recent flora of Central America. The Leguminosae have three fossil species. The Mimosaceae, which are very abundant in the existing forests of Panama, are represented by a fossil species of *Inga*, a large genus of tropical trees with upward of two-score species in Central America, nearly half of which are recorded from Panama. *Inga* is well represented in the abundant Eocene floras of our Southern States, and it is of interest to note the resemblance between the fossil species from Panama and a species described by Engelhardt from an unknown Tertiary horizon in Ecuador.

The Caesalpiniaceae is represented by a single species of *Cassia*, a large genus not only in the Recent equatorial floras but well represented in most fossil floras from the Upper Cretaceous to the present.

The Papilionaceae, very abundant in the existing flora of Panama, is supposed to be represented by the petrified wood of a large tree referred to the genus *Taenioxylon* and found in the Cucuracha, Culebra, and Bohio formations.

The family of Malpighiaceae is represented by the genera *Hiraea* and *Banisteria*. The former has about 30 recent species, exclusively American, ranging from Mexico and the Antilles to tropical Brazil and Peru, and it is represented by a fossil species in the Eocene of the Mississippi embayment. *Banisteria* contains about 80 existing species, mostly climbing shrubs. It is at present confined to the American tropics, but appears to have been present in Europe as well as in the southern United States during the Tertiary.

The Euphorbiaceae, abundantly represented in the present forests of Panama, is represented in the Caimito formation by a species of *Hieronymia* apparently identical with one described by Engelhardt from the Tertiary of Ecuador. *Hieronymia*, not otherwise known in the fossil state, contains about a dozen existing species which are confined to tropical America, where they range from Mexico and the West Indies to Brazil.

The Sapindaceae, abundant in all fossil floras from the Upper Cretaceous onward, and exceedingly abundant in the Tertiary floras of the Mississippi embayment, is represented in the fossil flora of Panama by a species of *Schmidelia* found in the Caimito and Culebra formations. *Schmidelia* has a large number of existing species in the equatorial regions of both hemispheres and, except for petrified material from the island of Antigua, it has not previously been recognized in the fossil state.

The family Lauraceae, so extensively represented in the Tertiary floras of the Mississippi embayment and in the Recent tropical flora of South America, is represented at Panama by a single fragmentary species which is referred to Mespilodaphne. The latter has numerous modern species in the tropics of America and Africa.

The Myrtaceae, one of the abundant families in the existing forests of tropical America, has a fossil species of *Calyptranthes* at Panama. This genus has about 70 exclusively American existing species ranging from Mexico and the West Indies to southern Brazil. Hemsley records 7 recent species from Central America, of which 2 are found on the Isthmus. It is also represented in the lower Eocene of the Mississippi embayment. The abundant, both Recent and fossil, representatives of the allied genera *Eugenia* and *Myrcia* have not been recognized in the fossil flora of the Isthmus.

The Melastomataceae, an immense tropical family in the existing flora and very abundant throughout Central America, has a single fossil species in the Culebra formation.

The family Ebenaceae, usually abundant in fossil floras from the Upper Cretaceous onward, and with a large number of species in tropical America, is represented on the Isthmus by the petrified fruits of a species of ebony (*Diospyros*) known to be from an older horizon (Eocene) than the balance of the known fossil flora.

The Rubiaceae, a prominent family in the existing flora of Central America, where according to Wallace (1911) it ranks fourth in size with 146 species, is represented by two fossil species, both found in the Gatun formation. These are referred to *Rondeletia* and *Rubiacites*.

The former has not heretofore been found fossil. It includes about 70 existing species of a variety of habitats, confined to the American tropics and chiefly massed in the Antilles and Central America. *Rubiacites* is represented by a fruit which is apparently referable to the tribe Ixoreae, now confined to the tropics of both hemispheres.

TERTIARY ECOLOGY.

The restricted variety and fragmentary condition of the fossil plants thus far collected inhibits a detailed discussion of the probable ecology of the Tertiary flora. In so far as climatic conditions are concerned the Tertiary plants indicate an abundant rainfall and relatively high equable temperatures such as prevail at the present time in the Hill country and Coastal Plain of the Isthmus. There is no indication of upland vegetation. None of the fossil plants indicate mountains sufficiently high to harbor that mixture of temperate types such as is seen at the present time in the mountains of Central America, as, for example, above 6,000 feet in Costa Rica. There was plenty of opportunity for the introduction of such types had the climate been propitious, so that I would infer that the Tertiary relief was slight, that is under 5,000 feet and probably much less than this, although there is no evidence to warrant precision of statement.

On the other hand, the collected floras do not furnish any traces of the characteristic vegetations of low muddy shores, although types like *Rhizophora*, *Avicennia*, *Conocarpus*, *Laguncularia*, etc., were already in existence in Eocene times as we know from their presence in the Mississippi embayment of that time, where they were undoubtedly derived from the south. I do not infer that these costal types were absent in the Tertiary flora of the Isthmus. On the contrary they must have been present; but no traces of them have been discovered except the traces of *Acrostichum* in the Culebra formation.

The bulk of the fossil plants clearly belong to the evergreen rain forests and they have the appearance of having been washed into the basins of sedimentation by streams. None of the lithologic specimens that I have seen from the Isthmus indicate autochonous swamp deposits either of coastal or valley situations and I picture the flora as one of a humid tropical character covering a country of low hills. This is of necessity a tentative conclusion and perhaps even such general deductions are unwarranted because of the very limited data with which I have had to deal.

FLORA OF THE CANAL ZONE.

Arecales:
- Arecaceae—
  - *Palmoxylon palmacites* (Sprengel) Stenzel.

Urticales:
- Moraceae—
  - *Ficus culebrensis*, new species.

Ranales:
- Anonaceae—
  - *Guatteria culebrensis*, new species.
- Myristicaceae—
  - *Myristicophyllum panamense*, new species.

Rosales:
- Leguminosae—
  - *Taenioxylon multiradiatum* Felix.
  - *Inga oligocaenica*, new species.
  - *Cassia culebrensis*, new species.

Geraniales:
- Malpighiaceae—
  - *Hiræa oligocaenica*, new species.
  - *Banisteria praenuntia*, new species.
- Euphorbiaceae—
  - *Hieronymia lehmanni* Engelhardt?

Sapindales:
- Sapindaceae—
  - *Schmidelia bejucensis*, new species.

Thymeleales:
- Lauraceae—
  - *Mespilodaphne culebrensis*, new species.

Myrtales:
- Myrtaceae—
  - *Calyptranthes gatunensis*, new species.
- Melastomataceae—
  - *Melastomites miconioides*, new species.

Ebenales:
- Ebenaceae—
  - *Diospyros macdonaldi*, new species.

Rubiales:
- Rubiaceae—
  - *Rondeletia goldmani*, new species.
  - *Rubiacites ixoreoides*, new species.

Fern fragments of Acrostichum.

Palm rays.

SYSTEMATIC PALEOBOTANY.

PTERIDOPHYTA.

Order FILICALES.

FERN FRAGMENTS OF ACROSTICHUM.

The material from the Culebra formation, one-fourth mile south of Empire Bridge, contains several obscure fragments of large simple fern pinnules with reticulate venation strongly suggestive of Acrostichum, but too incomplete for identification. The genus now principally represented by the cosmopolitan tropical tidal marsh species *Acrostichum aureum* is abundant in the Eocene and Oligocene of both America and Europe, and is especially characteristic in the Jackson, Catahoula, and Vicksburg of our Gulf States.

SPERMATOPHYTA.

Order ARECALES.

Family ARECACEAE.

PALM RAYS.

The broken rays of apparently two species of palms occur sparingly in the Culebra formation at the locality one-fourth mile south of Empire Bridge. These are too incomplete for even tentative generic determination.

Genus PALMOXYLON Schenk.

Group LUNARIA.

PALMOXYLON PALMACITES (Sprengel) Stenzel.

Plate 12, fig. 1.

Endogenites palmacites Sprengel, Commentatio, p. 39, figs. 6, 6*a*, 1828.

Fasciculites palmacites Cotta, Dendrol., pp. 49, 89, pl. 9, figs. 1, 2, 1832.—Unger in Martius, p. 59, tab. geol. 3, fig. 6, 1845.

Palmacites dubius Corda, Beitrage, p. 42, pl. 22, 1845.—Schimper, Pal. Végét., vol. 2, p. 513, 1870; Handbuch, Abst. 2, p. 887, 1892.

Palmacylon tenerum Felix, Foss. Hölzer Westindiens, p. 26, pl. 4, fig. 1, 1883.—Schenk in Zittel.

Palmoxylon palmacites Stengel, Foss. Palmenhölzer, p. 245, pl. 20, fig. 253, 1904.

Description.—Fibro-vascular bundles small, very numerous, closely spaced, orbicular or ovate in cross section, uniformily distributed as a rule, 0.60 mm. to 0.75 mm. in diameter, and rarely, if ever, that distance from one another. Auxiliary bundles absent.

Sclerenchyma portion excavated more or less deeply to receive the vascular portion, which is often nearly equal to it in size. Occasionally a thin zone of sclerenchyma entirely surrounds the vascular portion. Sclerenchyma fibres small, isodiametric, greatly thickened, of nearly uniform size, about 0.035 mm. in diameter. Vessels variable in size, ranging from 0.072 mm. to 0.18 mm. in diameter, usually two large vessels and either none or several small vessels on the side away from the bast in each bundle. The phloem portion in general destroyed and represented by a disorganized cavity between the vessels and the bast.

The ground mass of the stem consists of thin walled parenchyma without intercellular spaces. The cells are small, isodiametric, rounded pentagonal or hexagonal except where there are but one or two rows between closely adjacent bundles, in which case they are narrowly compressed and elongated parallel to the sides of the bundles. Their diameter varies from 0.035 mm. to 0.10 mm. Scattered through the stem parenchyma are darker cells which in polarized light appear to be gum cells. They are slightly larger than the parenchyma cells, being from 0.072 mm. to 0.108 mm. in diameter.

Occasional bundles are seen to be branching. These are the *fasciculi fibroductores* or Kreuzungsbündel.

This species was first recognized by Sprengel in 1828, who referred it to *Endogenites;* Cotta four years later transferred it to Fasciculites, and Corda in 1845 referred it to *Palmacites.* When Felix came to publish on the Antigua woods in 1883 he recognized this species, but in describing it under the genus *Palmoxylon* which had been proposed by Schenk only a year or two before he took the liberty of giving it the new name of *tenerum*, which under the rules of nomenclature has no standing as Stenzel recognized in print in 1904.

The specimen from Panama is small and may be from near the periphery of a stem, although in the group *Lunaria* there is little difference between the central and peripheral regions. In the size, outline, and crowding of the fibrovascular bundles as well as in the character of the parenchyma of the groundmass the present species greatly resembles *Palmoxylon integrum* described by Felix [1] from Cuba and considered by Stenzel [2] as merely a variety of the Antiguan species *Palmoxylon antiguense* (Unger) Felix.[3] It differs from that species in altogether lacking the numerous auxiliary sclerenchyma bundles which are so well marked in *Palmoxylon integrum.* A further difference is the presence of gum or mucilage cells which are fairly numerous in the Panama specimen of *Palmoxylon palmacites* and which might upon a merely superficial examination be mistaken for auxiliary sclerenchyma bundles. Among the Oligocene species of *Palmoxylon* from the southern United States *Palmoxylon mississippense* Stenzel [4] is very similar to the present species.

Other described fossil species which show more or less resemblances are *Palmoxylon stellatum*, *aschersoni*, *variabile*, and *ceylanicum.* The nearest affinity among recent palms is not determinable in the present state of our knowledge of the anatomy of the latter. The present type of structure is commonly known as the Cocos-like type.

For some unknown reason the upper Eocene and lower Oligocene in southeastern North America abounds in silicified palm wood. Palm leaves are often very abundant in the Wilcox and Claiborne Eocene and in the Apalachicola Oligocene; but all of the petrified

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[1] Felix, Foss. Hölz. Westindiens, p. 24, pl. 5, fig. 2, 1883.
[2] Stenzel, Foss. Palmenhölzer, p. 154, pl. 1, figs. 1–10, 1904.
[3] Felix, Foss. Hölz. Westindiens, p. 22, pl. 4, fig. 5.
[4] Stenzel, Foss. Palmenhölzer, p. 248, pl. 21, figs. 254–265.

palm wood in our Gulf region is confined to the Jackson or Vicksburg groups.

The island of Antigua, celebrated for at least a century for its petrified woods, has furnished at least seven species of petrified palms, five of which were known to Unger as early as 1850, and one was figured by Witham in 1833. These also are of Oligocene age. There are two additional Oligocene species described from the West Indies without definite information as to exact locality, and there is also a species from Trinidad and another from Cuba. The Oligocene species at present known from the southern United States are seven in number, four of which have not been found outside of that region, while one or possibly two are common to Antigua, and a third has been reported by Felix from Southern Mexico.

Occurrence.—Cucuracha formation, green clays, Gaillard Cut (loc. 6586). Collected by D. F. MacDonald.

Collection.—U. S. National Museum. Cat. No. 35310.

Order URTICALES.

Family MORACEAE.

Genus FICUS Linnaeus.

FICUS CULEBRENSIS, new species.

Plate 13, fig. 1.

Description.—Leaves of relatively small size, broadly oblong-lanceolate in general outline, apex acute but not extended or cuspidate. Base bluntly pointed. Margins evenly rounded. Texture coriaceous. Length about 8 cm. Maximum width, in the middle part of the leaf, about 2.15 cm. Petiole short, stout, and curved. Midrib stout and prominent on the under surface of the leaf. Secondaries thin, very numerous, evenly spaced, subparallel; they diverge from the midrib at wide angles averaging about 75 degrees, pursue an almost straight outward course, their ends being connected well within the margins by regular flat arches formed by their abrupt camptodrome endings. Tertiaries obsolete.

This is an especially well-marked species of the lanceolate leafed section of *Ficus*, and it may be matched by a number of still existing species found in the American tropics. Among such a large number of both existing and fossil forms detailed comparisons are not especially pertinent. Two comparisons that seem significant are the resemblance of the present form to *Ficus newtonensis* Berry of the Upper Claiborne of the Mississippi embayment and to the forms from the Sannoisian of Haering in the Tyrol which Ettingshausen[1] refers

[1] Ettingshausen, Tert. Fl. von Haering, p. 41, pl. 10, figs. 6, 8, 1853.

to *Ficus jynx* Unger, but which appear to me to be decidedly different from Unger's type.

Occurrence.—Culebra formation, upper part. East wall of the Gaillard cut just north of Canal Commission station 1760 (collected by M. I. Goldman).

Order RANALES.

Family ANONACEAE.

Genus GUATTERIA Ruiz and Pavon.

GUATTERIA CULEBRENSIS, new species.

Plate 13, fig. 2.

Description.—Leaves of large size, broadly ovate in general outline, with a narrowed slightly decurrent base and a narrowed and extended acuminate tip. Length about 20 cm. Maximum width, approximately midway between the apex and the base, between 6 cm. and 7 cm. Margins entire. Texture coriaceous. Petiole short and stout, enlarged proximad, about 2.25 cm. in length. Midrib stout and promient. Secondaries mediumly stout and prominent, about ten opposite to alternate pairs diverge from the midrib at angles ranging from 45° to 60°, sweeping upward in regular ascending subparallel curves, camptodrome in the marginal region. Tertiaries, where visible, percurrent.

The present is one of the more abundant and better preserved forms from the Canal Zone, but the large size of the leaves usually results in fragmentary specimens, the tip being almost invariably missing. The species shows great similarity with various existing forms of Anonaceae. It is very close to *Anona marcgravii* Martius of Venezuela, French and Dutch Guiana, and Brazil (Bahia and Pernambuco). It is, however, among the various species of *Guatteria* that the closest homologies are found. The latter genus contains about fifty species of shrubs and trees, exclusively American[1] and found in Mexico, Central America, tropical South America, and in the northern Andes. The fossil may be compared with a large number of the existing species, as for example *Guatteria ouregon* Dunal, a large tree of the Carribbean islands and equatorial South America. *Guatteria dolichopoda* De Candolle or *G. grandiflora* De Candolle of Central America.

The family Anonaceae contains about 700 existing species, distributed among about 48 genera, only two of which are present in North America. The family is practically confined to the Tropics,

[1] The Asiatic species of various authors are referred to the genus *Polyalthia*.

a single Australian species, and the North American genus *Asimina*, with 6 or 7 species being the only conspicuously extratropical forms. The area of maximum representation is southeastern Asia and the adjoining region of Malaysia, for while only 16 genera are confined to this region it contains over 350 species, and six additional genera (*Miliusa*, *Uvaria*, *Polyalthia*, *Oxymitra*, *Melodorum*, and *Poporvia*), with a total of over 250 species have the bulk of their species in this area. Only a single genus is confined to Australia, and the bulk of the Australian species are to be regarded as migrants from the preceding area. There are upwards of 100 species and 6 peculiar genera in tropical Africa; and America has about 200 species and 10 peculiar genera. These are all confined to the Tropics, except for a species of *Anona*, which reaches the coast of peninsular Florida, and for the genus *Asimina*, with six or seven species of shrubs and small trees of the south Atlantic and Gulf States. One of these, *Asimina triloba* Dunal, is hardy as far north as New York, and has the distinction of growing the farthest distance from the Equator of any existing member of the family. The fossil record of the Anonaceae is very incomplete, only the genera *Anona* Linneaus and *Asimina* Adanson, being known with certainty. Both of these genera are present in the flora of the Wilcox group of the Mississippi embayment.

The genus *Guatteria* has not, so far as I know, been heretofore found fossil, except for a doubtful species described by Hollick from the Upper Gretaceous of Marthas Vineyard and Long Island. The genus *Uvaria* Linnaeus has a Pliocene and three Pleistocene species on the Island of Java, and the genera *Melodorum* Dunal and *Mitrephora* Blume are both represented in the Pleistocene of that island.

The genus *Anona* has from fifteen to twenty fossil species, five of which are also represented by seeds. The oldest is a species described from the Dakota sandstone. There is a second species in the late Cretaceous or Early Eocene of the Rocky Mountain province. The flora of the Wilcox affords a glimpse into the true stage of evolution of Tertiary floras in that expanded belt of the American equatorial region which was the center of radiation of so many recent types. There were three exceedingly well-marked species of Anona along the Wilcox coast and their leaves are very common at some localities, although no seeds have as yet been discovered. I assume that these Wilcox forms had habits similar to those of the majority of the existing species, exemplified by our Florida *Anona glabra* Linnaeus, or pond apple, which frequents shallow fresh-water swamps, low shady hammocks, or stream borders near the coast. Other species occur in the low coppice association or on edges of brackish swamps on the Bahamas. The cultivated species, as, for example, the American *Anona reticulata* Linnaeus, which is planted in Guam, often spreads naturally along the inner beaches, while attempts to introduce others of the most highly esteemed American species in the Orient have failed. From its prevalence among the existing species the habit of growing in wet, shaded soils is evidently an old one, and since the Wilcox *Anonas* are associated with a strand flora the assumption that they grew on the inner beaches or the shaded and more swampy edges of lagoons possesses every degree of probability.

In the pipe clays of Alum Bay which were contemporaneous with the Wilcox there are two species of *Anona*, and Engelhardt has described two species from the Eocene or Oligocene of Chili. The Oligocene record shows a species in France and a second in Saxony. In the Miocene there are two species each in England, Styria, and Croatia, and one each in Bohemia, Colorado, and Transylvania. There is one each in the Pliocene of France and Italy, showing how modern was their extinction in the south of Europe.

The genus *Asimina* has only four or five recorded fossil species. These are all American except for a form from the Pliocene of Italy which has been referred to this genus, although I suspect that it represents *Anona*, since *Asimina* appears to have originated and been confined to the Western Hemisphere. The oldest known species is based on foliage which is found in the basal Eocene of the Rocky Mountains (Denver formation) and of the embayment (Midway Group). There is a single species based on a seed from the basal Wilcox and no other records except a form close to the modern from the late Miocene of New Jersey (Bridgeton sandstone) and the occurrence of the existing *Asimina triloba* Dunal in the interglacial beds of the Don valley in Ontario. There are 17 existing species of Anona recorded from Central America, six of which are known from Panama. Hemsley records 11 species of *Guatteria* from Central America, at least two of which occur in Panama.

Occurrence.—Culebra formation, upper part. East wall of Gaillard Cut just north of Canal Commission station 1760 (collected by M. I. Goldman). Gatun formation. Gatun borrow pits (collected by M. I. Goldman). 7 miles northeast of Bejuca near Chame (=Caimito formation) (collected by MacDonald).

Family MYRISTICACEAE.

Genus MYRISTICOPHYLLUM Geyler.

MYRISTICOPHYLLUM PANAMENSE, new species.

Plate 13, fig. 3.

Description.—Leaves ovate or ovate lanceolate in outline with pointed apex and base, entire, evenly rounded margins, subcoriaceous in texture. Length about 9 cm. Maximum width, midway between the apex and the base, about 3.3 cm. Petiole slender, about 8 mm. long. Midrib slender. Secondaries thin, about 8 subopposite ascending subparallel pairs; they diverge from the midrib at acute angles and are subparallel with the lower lateral margins, eventually camptodrome. Tertiaries obsolete.

This species is unfortunately represented by fragmentary remains inadequate for conclusive identification. The genus *Myristica* Linnaeus contains about two score existing species, rather more than half being American tropical forms, now often segregated into several genera. Many are insular and coastal forms, Schimper recording 4 species in the Indomalayan strand flora and several species ranging eastward in the Pacific to the Fiji, Tonga, and Samoan Islands, and their fruits are recorded by both Gaudichaud and Guppy in the sea drift, although the oriental species are normally distributed by fruit pigeons (Mosley, Hemsley, Guppy).

De Candolle and Miquel both considered the foliage, especially the venation, as offering the best criteria for differentiation, but in the absence of comparative material and the incomplete character of the Panama fossil it is not possible to apply these criteria. The American Recent species number about 25, and these are mainly South American in their distribution, although the sections or genera *Virola* Aublet and *Compsoneura* De Candolle both occur in Central America.

The distribution of the Recent species in tropical America, Asia, and Africa is conclusive evidence of a Tertiary history, although this evidence is practically unknown. Geyer[1] described two forms of leaf fragments from the Miocene of Labuan (Borneo) and Engelhardt[2] a third from the Tertiary of Ecuador and Chile. The most conclusive evidence of their Tertiary radiation is furnished by the characteristic fruits described recently by the writer[3] and preserved in the windblown sands of the uppermost Eocene of Texas.

Occurrence.—Culebra formation (upper part). East wall of Gaillard Cut just north of Canal Commission station 1760 (collected by M. I. Goldman).

Order ROSALES.

Superfamily LEGUMINOSAE.

Genus TAENIOXYLON Felix.

TAENIOXYLON MULTIRADIATUM Felix.

Plates 14 and 15.

Taenioxylon multiradiatum Felix, Die fossilen Hölzer Westindiens. Samml. palaeont. Abh., ser. 1, Heft 1, p. 11. pl. 1, figs. 10, 11; pl. 2, fig. 10, 1883.

Transverse section.—In a radial distance of 5 cm. there are no definite annual or seasonal rings. In certain zones the vessels are

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[1] Geyler, H. T., *Vega* Expedition, vol. 4, p. 498, pl. 33, figs. 3–6, 1887.

[2] Engelhardt, H., Abh. Senck. Naturf. Gesellsch., vol. 16, p. 663, pl. 6, fig. 9; pl. 7, fig. 12, 1891; vol. 19, p. 13, pl. 1, fig. 21, 1895.

[3] Berry, E. W., Amer. Journ. Sci., ser. 4, vol. 42, pp. 241–245, figs. 1–6, 1916.

larger, more generally compound, and closer together, and in other zones they are more distant, slightly smaller, and prevailingly single. No changes are observable in the other elements and there is no regular alteration of vessel rich and vessel poor areas nor any change from so-called summer to spring wood such as characterizes the trees of the temperate zone.

Vessels single or two, three, or four together in radial rows (an anomalous group of five vessels in juxtaposition is shown in the detailed drawing). Outline of single vessels elliptical, those in groups flattened on one or both sides by mutual compression; their tangential diameter ranging from 0.10 mm. to 0.14 mm.; their radial diameter ranging from 0.12 mm. to 0.16 mm., exceptionally large ones up to 0.22 mm.; their walls thick, 0.0067 mm. to 0.01 mm. in thickness, clearly showing the numerous small pits in section. Vessels frequently filled with gum. Vessels usually surrounded by one to three layers of rounded or more or less compressed thin-walled wood parenchyma, somewhat variable in amount in different parts of the stem and tending to form tangential bands. Prosenchyma very abundant, the elements polygonal, small, somewhat smaller than those of the wood parenchyma, and thick walled. Rays very numerous, one or two cells wide as seen in transverse sections, flexuous in their courses since they are bowed out around the large vessels and approach more or less in the radial intervals between vessels; from 0.10 mm. to 0.20 mm. apart, averaging nearer the former than the latter figure. The ray cells toward the ends of the rays which appear to be those usually seen in the several sections examined are not elongated radially but are nearly isodiametric and about 0.02 mm. in diameter.

Radial section.—The radial section shows the close set, fine, transversely elongated pits of the vessels which have simple perforations. The wood parenchyma is septate, the cells being about 3½ times as long as wide with large simple pits. The rays are of variable height, from 9 to 17 cells. They are seen in radial view to consist of a central series of radially elongated cells with numerous fine simple pits, above and below which is a series of longitudinally elongated cells, beyond which are one or two rows of isodiametric cells which are regularly hexagonal in this view.

Tangential section.—The tangential section shows the uniform close set fine pitting on all the walls of the vessels, the relative short length and the large simple pits of the adjoining septate wood parenchyma. The rays are seen to be very numerous, and separated by but few rows of flexuous prosenchyma; they are lenticular in outline and of variable height, one or two rays of terminal cells (those which are hexagonal in outline in the radial view) are single; then come one to three biseriate rows (those longitudinally elongated in the radial view); toward the median region the rays are three or four cells broad (the radially elongated cells in the radial view).

Felix states that in the Antigua material the rays were usually biseriate, while uniseriate and triseriate rays were rare. I do not know the extent of his material, but in the case of that from Panama I had but few radial sections cut. Ray cells frequently filled to a greater or less degree with gum.

Remarks.—Fragments of the wood of this species are very common in the collections from Panama, but a good deal was rather badly decayed before petrification. That which has formed the chief basis for the foregoing description and all of the photographs and drawings is beautifully preserved. The species is clearly identical with the type, as very insufficiently described and illustrated by Felix. One highly ferruginized and fairly well preserved quadrant of a trunk indicates a large tree, with a diameter of at least 25 cm.

The genus *Taenioxylon* was established by Felix in 1882 with *T. varians* from Antigua as the type. He has since described 7 additional species including 2 additional from Antigua, 1 from southern Brazil, 1 from East Indies, 1 from Philippines, 1 from Caucasus, and 1 from the Swabian Alps. All are of Tertiary age and show resemblances to various members of the 3 Leguminous families, Caesalpiniaceae, Miomosaceae, and Papilionaceae. Felix considers the present species to be a member of the Papilionaceae, and it agrees entirely with Solereders account of the anatomy of this family. The two kinds of ray cells described have, according to Saupe, been shown to occur in the following tribes in this family, namely the Podalyrieae, Genisteae, Galegeae, Hedysareae, and Sophoreae. Without much recent comparative material, which is unavailable, it is impossible to allocate the present species more definitely within this extensive family.

Occurrences.—Bohio formation, middle Bohio Ridge (poorly preserved) quadrant of a large trunk indicating a tree with trunk at least 25 cm. in diameter. Cucuracha formation, upper part. Green clays of Gaillard Cut (locality 6845) Oligocene limestone. Orbitoidal limestone, 2 miles north of David (locality 6523) (all above collected by D. F. MacDonald). Culebra formation, upper part. Near top of big slide, just north of Culebra. Collected by M. I. Goldman (figured material).

Collections.—U. S. National Museum, Johns Hopkins University.

Family MIMOSACEAE.

Genus INGA Willdenow.

INGA OLIGOCAENICA, new species.

Plate 16, fig. 2.

Description.—Leaflets rather above medium size, elliptical-ovate and very inequilateral in general outline. Apex abruptly acute, not extended. Base very inequilateral, truncate or ascending on one side and wide and cordate on the other. Margins entire, full. Texture subcoriaceous. Length about 8 cm. or 9 cm. Maximum width, at or slightly above the middle, about 4 cm. Petiolule curved, short and stout, about 3 mm. long. Midrib stout, greatly curved. Secondaries thin, five or six pairs, angles of divergence and courses various, all ultimately camptodrome; lower pair opposite, from the top of petiolule; they diverge from the midrib at angles of about 45 degrees, curving slightly outward and then ascending, parallel with the respective margins; the one in the narrow side of the lamina arches along the margin in a brochiodrome manner; the one in the wide side of the lamina sends off on the outside a series of regularly spaced camptodrome tertiaries. Tertiary venation for the most part obsolete.

This characteristic species may be compared with *Inga densiflora* Bentham,[1] *Inga edulis* Martius,[2] *Inga marginata* Willdenow,[3] or *Inga speciosa* Spruce[4] and with various other of the larger-leafed species of Inga in the American Tropics to which region the 212 of its existing species of shrubs and trees are confined. It may also be compared with a number of tropical American species of *Cassia*, as, for example, *Cassia ruseifolia* Jacquin.

About fiften fossil species have been referred to *Inga*. These include three from the Upper Cretaceous, two European, and one North American. There are also two or three species in the Oligocene of Europe, one in the Pliocene of Bolivia, two in the Tertiary of Ecuador, and one in the Tertiary of Colombia, four well-marked species in the Lower Eocene of the Mississippi embayment (Wilcox Group) and one in the middle Eocene of that region (Claiborne Group). The Panama species is not especially close to any of the foregoing. It is nearest, however, to *Inga latifolia*, described by Engelhardt[5] from the Tertiary of Ecuador, differing in its broader form and more inequilateral base.

Pittier records 14 existing species of *Inga*, from Panama.[6] Hemsley lists 35 species in his flora of Central America, or which number 18 are recorded from Panama.

Occurrence.—Lower part of Culebra beds one-fourth mile south of Empire Bridge. (Collected by D. F. MacDonald.) U.S.G.S. 6837.

Type.—Cat. No. 35311, U.S.N.M.

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[1] Bentham, Trans. Linn. Soc. Lond., vol. 30, p. 617, 1875 (Peru).
[2] Martius, Flora, vol. 20, Beibl., p. 113, 1837 (Brazil).
[3] Willdenow, Sp. Pl., vol. 4, p. 1015, 1806 (Venezuela).
[4] Spruce, in Bentham, Trans. Linn. Soc. Lond., vol. 30, p. 620 (Brazil).
[5] Engelhardt, H., Abh. Senck. Naturfor. Gesell., vol. 19, 1895, p. 20, pl. 2, figs. 11, 12.
[6] Pittier, H., Cont. U. S. Natl. Herb., vol. 18, pt. 5, pp. 218–223, 1916.

Family CAESALPINIACEAE.

Genus CASSIA Linnaeus.

CASSIA CULEBRENSIS, new species.

Plate 16, fig. 1.

Description.—Leaves obviously pinnately compound. Leaflets ovate, slightly inequilateral and falcate, with an obliquely acuminate, practically equilateral tip, and an acuminate markedly inequilateral base. Length about 6.25 cm. Maximum width, about midway between the apex and the base, 2.75 cm.; one side of the lamina 15 mm. wide, the other 12.5 mm. wide. Texture mediumly coriaceous. Petiolule reduced to a thickened proximal part of the midrib extending but 1 mm. below the point of junction of one margin and about 2.5 mm. below the point of junction of the opposite margin. Margins entire, evenly rounded and full. Midrib relatively thin, not prominent, curved. Secondaries thin, numerous, about 10 subopposite to alternate pairs; they diverge from the midrib at wide angles, about 70° in the middle part of the leaflet, are nearly straight regularly spaced and subparallel in their outward course for two-thirds of the distance to the margin where the principal ones fork to join in rounded arches the similar branches of adjacent secondaries; the secondaries in the apical and basal portions of the leaflet are regularly camptodrome; those toward the tip of the leaflet more closely spaced. Marginal tertiaries camptodrome, internal tertiaries mostly obsolete.

This type in its general form and the character of its base and petiolule indicates that it is a leaflet of a pinnate leguminous leaf. Its general appearance suggests comparisons with the genera *Sweetia*, *Myrocarpus*, *Toluifera*, *Cassia*, and *Sophora*—the first three confined to tropical South America and the last two cosmopolitan in the existing flora. While the evidence is not conclusive, I prefer to consider it more closely allied to *Cassia* than to the other genera mentioned, particularly as the venation characters are such as I have considered referable to *Cassia* in my studies of the fossil floras of the southern United States. No species related to the Panama form is known from the Oligocene of the United States.

The modern species of *Cassia* are very numerous, upwards of 400 having been described. They comprise herbs, shrubs, and trees of varied habitats in the warmer parts of both hemispheres, particularly tropical America. The fossil species are also numerous and the generic history goes back to near the base of the Upper Cretaceous. The genus has been continuously represented in the warmer parts of

America from the time of deposition of the Tuscaloosa sediments of Alabama to the present.

Occurrence.—Culebra formation, lower part, one-fourth mile south of Empire Bridge (collected by D. F. MacDonald) U.S.G.S. 6837:

Type.—Cat. No. 35312, U.S.N.M.

Order GERANIALES.

Family MALPIGHIACEAE.

Genus HIRAEA Jacquin.

HIRAEA OLIGOCAENICA, new species.

Plate 17, fig. 1.

Description.—Leaves relatively large, ovate-lanceolate in outline, falcate, with an equally cuneatly pointed apex and base. Margins entire, evenly curved. Texture subcoriaceous. Length about 9.5 cm. Maximum width, at or somewhat below the middle, about 3.5 cm. Petiole short, stout, about 3 mm. in length. Midrib stout, flexuous. Secondaries thin, regularly spaced, about 9 pairs, prevailingly alternate; they diverge from the midrib at angles of about 45° and sweep upward in regular subparallel slight curves, and are camptodrome in the marginal region. Tertiaries obsolete.

This genus, which has well characterized leaves, has seldom been recognized in the fossil state. One species [1] is not uncommon in the lower Eocene of the Mississippi embayment, and Ettingshausen [2] has recorded, but not described, a second species from the Ypresian of Alum Bay, England.

The existing species number between 25 and 30 and are exclusively American, ranging from Mexico and the Antilles throughout Central and northern South America to the Peruvian tropics.

The present fossil species is not unlike *Hiraea wilcoxiana* Berry [3] from the lower Eocene of Tennessee and is closely comparable with the existing *Hiraea chrysophylla* Jussieu of the northern coastal region of South America.

Occurrence.—Caimito formation 7 miles northeast of Bejuca (U.S.G.S. station 6840). Collected by D. F. MacDonald.

Type.—Cat. No. 35313, U.S.N.M.

Genus BANISTERIA Linnaeus.

BANISTERIA PRAENUNTIA, new species.

Plate 17, fig. 2.

Description.—Leaves of medium size, broadly ovate in general outline, with an abruptly acuminate tip and a broad rounded or cuneate base. Length about 8 cm. Maximum width, at or slightly above the

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[1] Berry, E. W., U. S. Geol. Survey Prof. Paper 91, p. 257, pl. 57, fig. 8; pl. 109, fig. 6, 1916.

[2] Ettingshausen, C. von, Roy. Soc. London Proc., vol. 30, p. 235, 1880.

[3] U. S. Geol. Survey Prof. Paper 91, p. 257.

middle, about 5 cm. Margins entire, full and rather evenly rounded. Petiolar character unknown. Midrib of medium size, uncharacteristic. Secondaries thin, seven or eight opposite to alternate pairs diverge from the midrib at regular intervals at angles varying from 45° in the upper part of the leaf to 55° in the basal part; they ascend in slight but subparallel curves increasing in intensity as they proceed toward the margins with which they become subparallel and eventually camptodrome. Tertiaries thin, mostly obsolete. Leaf substance thin but apparently of a somewhat coriaceous texture.

The present species receives its name from its supposed praenuntial relationship to the existing *Banisteria sinemariensis* De Candolle, a form ranging from the West Indies to Brazil and whose somewhat variable leaves may be exactly matched by the fossil.

The genus contains upward of eighty existing species, mostly climbing shrubs, confined to the American tropics and largely developed in northern South America. Its geological history goes back to the Lower Eocene, a species having been described by Watelet from the Ypresian of the Paris basin and four homotaxial species, one based on seeds, having been described by the writer from the Wilcox group of the Mississippi embayment in Western Tennessee and Kentucky. Several additional fossil species have been described from the European Tertiary, from all of which the Panama fossil is conspicuously different, its major differential character being its relatively short and broad outline.

A species based upon fruits has been described by Engelhardt[1] from the Tertiary of Ecuador.

There are 5 species of *Banisteria* recorded by Hemsley from Central America, 3 of these in Panama, *B. billbergiana* Beurling on the seashore of the island of Manzañillo. Two additional Panama species of *Banisteria* are referred to the allied genus *Heteropterys* Kunth by Hemsley.

Occurrence.—Culebra formation. West wall of Gaillard Cut below Miraflores locks (collected by M. I. Goldman). Culebra formation (lower). West wall of Canal opposite Culebra Railroad station. (Collected by D. F. MacDonald).

Family EUPHORBIACEAE.

Genus HIERONYMIA Allem.

HIERONYMIA LEHMANNI Engelhardt (?).

Plate 16, fig. 3.

Hieronymia lehmanni ENGELHARDT, Über neue Tertiärpflanzen Süd-Amerikas, Abh. Senck. Naturf. Gesell., vol. 19, p. 11, pl. 2, figs. 1, 2, 1895.

Description.—Leaves broadly elliptical or somewhat deltoid and inequilateral in outline, with a shortly acuminate tip and broadly

[1] Engelhardt, H., Über neue Tertiärpflanzen Süd-Amerikas, Abh. Senck. Naturf. Gesellsch., vol. 19, p. 14, pl. 2, figs. 18, 19, 1895.

rounded full lower lateral margins and a very wide, somewhat obliquely truncated base. Length about 12 cm. Maximum width, in the lower half of the leaf, about 10 cm. Margins entire, full, and rounded. Texture thin but coriaceous. Midrib stout, curved, prominent on the lower surface of the leaf. Secondaries stout, 10 or 11 irregularly spaced pairs, prominent on the lower surface of the leaf; they diverge from the midrib at wide angles which become more acute in the apical part of the leaf, those on the narrower side are more ascending and somewhat straighter than those on the wide side, all are conspicuously camptodrome at some distance from the margin. Tertiaries thin, mostly percurrent. Areolation of small, isodiametric polygonal meshes, well marked on the under side of the leaf.

This large leaf is unfortunately represented by fragmentary material from a single locality in the Caimito formation. In some respects its characters suggest a broad *Ficus*, but it seems clearly identical with the species described by Engelhardt[1] in 1895 from the Tertiary of Ecuador. I have, however, queried the determination because of the broken character of the Panama material. In the illustration I have reconstructed a leaf from a combination of the Panama material with the more complete specimens figured by Engelhardt from Ecuador. The two largest fragments from Panama are indicated on the drawing by tinting. It is unfortunate for purposes of correlation that the present determination can not be conclusive, although in view of other similarities shown between the Oligocene plants of Panama and those from the Tertiary of Ecuador, I am disposed to regard the present determination as fairly satisfactory.

The genus *Hieronymia* comprises about a dozen existing species of shrubs and trees confined to tropical America and rather widely distributed from Mexico to Brazil as well as in the West Indies.

Occurrence.—Caimito formation, 7 miles northeast of Bejuca (U.S.G.S. station No. 6840). (Collected by D. F. MacDonald.)

Collection.—U. S. National Museum, Cat. No. 35314.

Order SAPINDALES.

Family SAPINDACEAE.

Genus SCHMIDELIA Linnaeus.

SCHMIDELIA BEJUCENSIS, new species.

Plate 17, fig. 4.

Description.—Leaf or leaflet elongate elliptic in outline, inequilateral. Apex and tip equally and bluntly pointed inequilateral. Margins entire. Texture coriaceous. Length about 11 cm. Maxi-

[1] Über neue Tertiärpflanzen Süd-Amerikas, vol. 19, p. 11, 1895.

mum width, midway between the apex and the base, about 4.5 cm. Width on one side of the midrib 21.5 mm., on opposite side 24 mm. Petiole missing. Midrib flexuous, stout, and prominent. Secondaries stout, regularly spaced, mostly immersed, about 7 alternate pairs diverge from the midrib at angles of about 50°, curving upward subparallel and camptodrome in the marginal region. Tertiaries mostly obsolete, a few percurrent ones seen.

This large and striking leaf is referred to the sapindaceous genus *Schmidelia*, which comprises about 100 existing species of the equatorial regions of both hemispheres with unifoliate or palmately compound leaves. About half of the species are American where they are confined to the Antilles, Central, and tropical South America. They are sometimes referred to the genus *Allophylus* Linnaeus (as by Radlkofer) and with the exception of this genus all of the members of the tribe Thouinieae are confined to America. Fossil representatives have been unknown except for the petrified wood from the Oligocene of the island of Antigua which Felix described as Schmideliopsis.[1]

Occurrence.—Culebra formation. East wall of Gaillard Cut just north of station 1760 (collected by M. I. Goldman).

Caimito formation, 7 miles northeast of Bejuca (U.S.G.S. 6840). Collected by D. F. MacDonald.)

Type.—Cat. No. 35315, U.S.N.M.

Order THYMELEALES.

Family LAURACEAE.

Genus MESPILODAPHNE Nees.

MESPILODAPHNE CULEBRENSIS, new species.

Plate 17, fig. 3.

Description.—Leaves lanceolate-falcate in general outline, with acuminate apex and base. Margins entire. Texture subcoriaceous. Length about 10 cm. Maximum width, in the middle part of the leaf, about 2.5 cm. Petiole missing. Midrib stout, curved, prominent on the under surface of the leaf. Secondaries stout, remote, regularly spaced, nine or ten subopposite to alternate pairs, they diverge from the midrib at angles of about 65 degrees and are conspicuously camptodrome close to the margins. Tertiaries obscured by the poor preservation of the material.

The present species resembles numerous existing and fossil species of Lauraceae, from all of which, however, it appears distinct. It is similar to *Mespilodaphne columbiana* Berry of the Upper Claiborne of the Mississippi embayment, but is a stouter, more falcate, shorter, and less acuminate form.

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[1] Felix, J., Die fossile Hölzer Westindiens, p. 16, pl. 2, figs. 6, 8, 1883.

The modern species of *Mespilodaphne* are numerous, inhabiting Africa and tropical America, and are often united with *Oreodaphne* and *Strychnodaphne* to form the composite genus *Ocotea* of Aublet. Their fossil history is almost entirely lost in the multitude of species that have been referred to the form genera *Laurus* and *Laurophyllum*. *Mespilodaphne* is abundant and varied throughout the Eocene and Oligocene of the Mississippi embayment area.

Occurrence.—Culebra formation, upper part. East wall of the Gaillard Cut just north of Canal Zone station 1760. (Collected by M. I. Goldman.)

Order MYRTALES.

Family MYRTACEAE.

Genus CALYPTRANTHES Swartz.

CALYPTRANTHES GATUNENSIS, new species.

Plate 18, fig. 1.

Description.—Leaves broadly oblong-elliptic in general outline, widest in the middle and tapering equally in both directions to the abruptly acute apex and base. Margins entire. Texture subcoriaceous. Length between 7 cm. and 8 cm. Maximum width between 3.5 cm. and 4 cm. Petiole missing. Midrib stout, somewhat curved, prominent on the lower surface of the leaf. Secondaries thin, very numerous, and close set, often inosculating by forking; they diverge from the midrib at angles averaging about 70 degrees, at intervals of 1 mm. to 3 mm., pursue a but slightly curved outwardly ascending course and have their ends united by an acrodrome vein on each edge of the lamina parallel with and from 1 mm. to 2 mm. within the margin. Tertiaries forming open isodiametric polygonal meshes.

The present well-marked species closely resembles the only other named fossil form *Calyptranthes eocenica* Berry from the lower Eocene of the Mississippi embayment (Wilcox Group). It may also be compared with the slightly smaller *Myrtus rectinervis* described by Saporta[1] from the Sannoisian of southeastern France.

The genus *Calyptranthes*, which is exclusively American in the existing flora, has about seventy species ranging from Mexico and the West Indies to southern Brazil. There is a strong generic likeness between the leaves of all of the species. *Calyptranthes zyzygium* De Candolle may be mentioned, among others, as a form with leaves almost exactly like the fossil. There is also a marked family resemblance to some of the existing tropical American species of *Eugenia*, and more especially *Myrcia*, *Myrcia multiflora* De Candolle from the Guianas being very similar to the present species.

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[1] Saporta, Études, vol. 1, p. 251, pl. 11, fig. 5, 1863.

Hemsley records 7 existing species of *Calyptranthes* from Central America, two of which occur in Panama.

Occurrence.—Gatun formation, Gatun Borrow Pits. (Collected by M. I. Goldman.)

Family MELASTOMATACEAE.

Genus MELASTOMITES Unger.

MELASTOMITES MICONIOIDES, new species.

Plate 18, fig. 2.

Description.—Leaf oblong-elliptic in outline, of relatively small size, with an equally and bluntly pointed apex and base. Length about 6 cm. Maximum width, in the middle part, about 2.25 cm. Margins entire. Texture subcoriaceous. Petiole short and stout. Midrib stout and prominent. Lateral primaries stout, prominent, diverging from the midrib at an acute angle just above the base and acrodrome. From the disposition of the outwardly directed nervilles from the primaries it is probable that subordinate acrodrome primaries constitute an infra marginal vein on each side, but these can not be made out. Close-set subparallel nervilles run transversely between the midrib and the primaries.

This species is represented by a small amount of fragmentary material, too poor to permit definite generic determination. It is, therefore, referred to the form-genus *Malastomites* proposed by Unger for generically undeterminable leaves of the Melastomataceae. While the fossil somewhat suggests the leaves of various Lauraceous genera, such as *Cinnamomum*, *Camphoromaea*, *Goeppertia*, and *Cryptocarya*, its characters are clearly those of the Melastomataceae. It particularly suggests the genus *Tibouchina* Aublet, which has upward of 200 species of shrubs and undershrubs in tropical America.

The family Melastomataceae is a relatively large one, with about 150 genera and over three thousand species. It is almost strictly tropical, although some members range southward to 40° south latitude. This great family is typically American, seven of the fifteen tribes into which it is divided being confined to tropical America, and about 2,500 of the existing species being also endemic in this region. While the geologic history of this vast assemblage of forms is practically unknown, there is no evidence to disprove the theory that it, like the allied families Combretaceae and Myrtaceae, had its origin in that most prolific region—the American tropics.

The few fossil forms that have been found, including leaves, flowers, and calices, have been referred to the form-genus *Melastomites* first proposed by Unger. A doubtfully determined species, which probably belongs to the Lauraceae, has been recorded from the Upper Cretaceous of Westphalia. The only known Eocene species is the well-marked form present in the lower Eocene of the Mississippi embayment region (Wilcox Group.) Four Oligocene species have been described from Bohemia, Styria, and Egypt; four Miocene species from Switzerland, Prussia, and Croatia; and a Pliocene species from Italy.

Occurrence.—Culebra formation, upper part. East wall of Gaillard Cut just north of Canal Zone station 1760. (Collected by M. I. Goldman.)

Order EBENALES.

Family EBENACEAE.

Genus DISOPYROS Linnaeus.

DIOSPYROS MACDONALDI, new species.

Plate 18, figs. 4–8.

Description.—Globose berry-like fruits of small size and considerable consistency, possibly preserved in an unripe state since the flesh is stringy and with a great many tannin cells. The great abundance of these fruits in the andesitic tuffs makes it seem more probable, however, that they are mature, particularly as some are greatly flattened. The numerous elongated pendulous seeds and the amount of vascular fibers in the flesh would tend to prevent much compression in a certain number of cases. Diameter 12 to 15 mm. Flesh hard, very tanniferous, and with numerous fibers. Seeds 8 to 10 in number, oblong, elliptical, compressed, with a hard seed coat. The interior of the seeds is filled with amorphous silica and fails to show any structure. Seeds about 7.5 mm. long, averaging 3 mm. high and 1 mm. to 2 mm. thick, very unequally developed, one to three usually more or less abortive. Peduncle not preserved, nor do any of the specimens show the calyx.

These seeds are exceedingly abundant and more or less perfectly silicified, the flesh being dark brown and the seeds white, making very striking objects. They are clearly referable to *Diospyros* and so far as I know represent the only known petrified fruits of this genus, although the persistent calices are not uncommon as impressions from the Upper Cretaceous onward. The modern species have from 4 to 12 compressed seeds which tend to become less numerous with the increase in the fleshy part of the fruit, so that possibly these more consistent and prevailingly 10-seeded fossil fruits may represent an earlier stage in their evolution, although this seems doubtful since the calyx of a very large fruited form is known from the Upper Eocene of southwestern Texas.

Diospyros is cosmopolitan in the existing flora with about 180 species in the warmer regions of both hemispheres. Mostly Oriental, but not uncommon in the southern United States, Antilles, and from Mexico through tropical South America. Upward of 100 fossil species are known ranging in age from the Upper Cretaceous to the present.

Occurrence.—Section near mouth of Tonosi River, in deposits of Eocene age (MacDonald).

Type.—Cat. No. 35316, U.S.N.M.

Order RUBIALES.

Family RUBIACEAE.

Genus RONDELETIA Plumier.

RONDELETIA GOLDMANI, new species.

Plate 18, fig. 3.

Description.—Leaves lanceolate in outline, somewhat falcate and inequilateral, with an equally acuminate apex and base. Length between 12 cm. and 13 cm. Maximum width, midway between the apex and the base, about 3 cm., 13.5 mm. on the concave side and 15.5 mm. on the convex side. Margins entire. Texture coriaceous. Petiole short and stout, expanded proximad, about 5 mm. long. Midrib curved, stout, and prominent. Secondaries thin, numerous, subopposite to alternate, rather regularly spaced; about 15 pairs diverge from the midrib at angles of about 45° and ascend in rather flat but regular and subparallel curves and are camptodrome in the marginal region. Tertiaries obsolete.

This well-marked species is referred to the subfamily Cinchonoideae and tribe Rondeletieae and seems to indicate an Oligocene species of *Rondeletia*, a genus of shrubs and trees confined to tropical America and not heretofore found fossil. Rondeletia has about 70 existing species, a few of which occur in northern South America, but the majority are confined to the Antilles (45 species) and Central America (24 species).[1] The present species may be compared with the existing *Rondeletia racemosa* Swartz of Jamaica, and with other Antillean and Central American forms. More remote comparisons may be made with certain species of *Psychotria*, as, for example, *Psychotria barbiflora* De Candolle of Brazil, and with the genus *Tapiria* Jussieu of the Anacardiaceae, a fossil species of which, *Tapiria lanceolata*, has been described by Engelhardt[2] from the Tertiary of Ecua-

[1] Britton records 35 species from Cuba. Bull. Torrey Bot. Club, vol. 44, pp. 20–30, 1917.

[2] Engelhardt, H., Über neue Tertiärpflanzen Süd-Amerikas, Abh. Senck. Naturf. Gesell., vol. 19, p. 15, pl. 9, fig. 4, 1895.

dor. Another fossil species somewhat resembling the Panama form is *Cinchonidium multinerve* described by Ettingshausen[1] from the Tertiary of Priesen, Bohemia.

Named in honor of Dr. Marcus I. Goldman, who collected it while a Fellow at the Johns Hopkins University.

Occurrence.—Gatun formation, Gatun Borrow Pits. (Collected by M. I. Goldman.)

Genus RUBIACITES Weber.

RUBIACITES IXOREOIDES, new species.

Plate 18, figs. 9–12.

Description.—Fruit bilocular, indehiscent or tardily dehiscent, ligneous, capsular-like. Form a prolate spheroid 2.7 cm. long and 2 cm. in diameter. The surface roughened by small tuberculations and pits. Walls about 2 mm. thick. Median partition thin. Seeds one in each cell, suspended, elliptical in both transverse and longitudinal sections, compressed along the central partition. Surface striate. Endosperm not ruminating. One seed is more fully developed than the other. The larger is about 2 cm. long, 1.4 cm. wide and 9 mm. thick.

This well marked form is unfortunately represented by but a single specimen which however shows most of the cavity occupied by the fruit, the two contained seeds partially petrified and the lignified wall and part of the partition. The accompanying illustrations show the external appearance of the fruit (fig. 9) and a side view showing the relative development of the two seeds (fig. 10). Figure 12 shows a lignified end of the fruit with the median partition and figure 11 is a side view with the smaller seed in front and the larger forming the background. So far as I know nothing like it has previously been found fossil.

There seems to be no question but that the present fruit represents some Oligocene species of Rubiaceae and it is consequently referred to the form-genus *Rubiacites* proposed by Weber, although probably not congeneric with the previously described fossil species of *Rubiacites*. The fruits of this large family exhibit considerable variety being either capsular, achene-like or drupaceous. Without a much larger amount of recent comparative material than is available it is not possible to definitely fix the botanical relation of the present species which, however, appears to be referable to the tribe Ixoreae or the Psychotrieae. The specific name chosen suggests a resemblance to the fruits of *Ixora* Linnaeus, a genus with over 100 species of

[1] Ettingshausen, C. von, Die Fossile Flora des Tertiär-Beckens von Bilin, Theil 2, p. 208, pl. 36, fig. 5, 1868.

shrubs and small trees found in the tropics of both hemispheres but chiefly Asiatic.

Occurrence.—Gatun formation. Gatun Borrow Pits. (Collected by M. I. Goldman.)

EXPLANATION OF PLATES.

PLATE 12.

Palmoxylon palmacites (Sprengel) Stenzel. Cucuracha formation.

FIG. 1. Showing abundance of fibrovascular bundles and gum cells. ×20.

PLATE 13.

FIG. 1. *Ficus culebrensis* Berry. Culebra formation.
2. *Guatteria culebrensis* Berry. Culebra formation.
3. *Myristicophyllum panamense* Berry. Culebra formation.

PLATE 14.

Taenioxylon multiradiatum Felix. Culebra formation.

FIG. 1. Transverse section. ×25.
2. Same. ×200.

PLATE 15.

Taenioxylon multiradiatum Felix. Culebra formation.

FIG. 1. Radial section. ×200.
2. Tangential section. ×200.

PLATE 16.

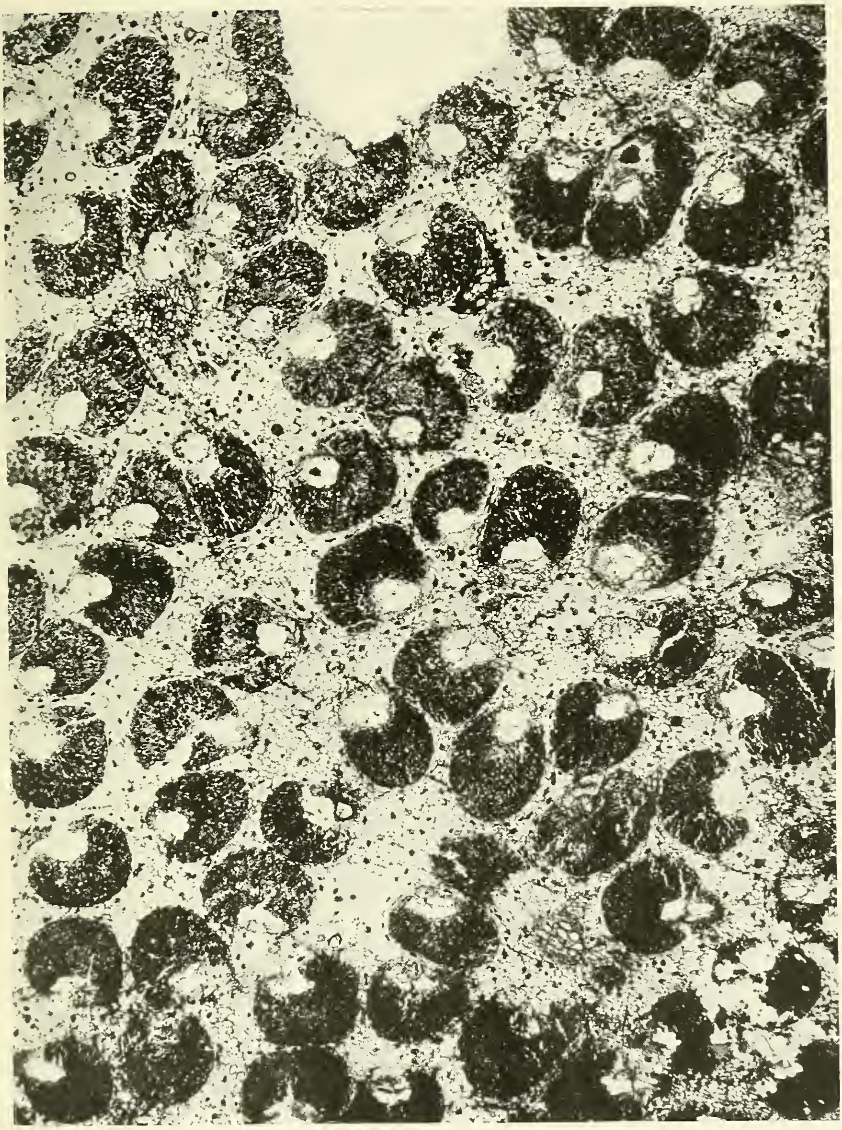
FIG. 1. *Cassia culebrensis* Berry. Culebra formation.
2. *Inga oligocaenica* Berry. Culebra formation.
3. *Hieronymia lehmanni* Engelhardt (?). Caimito formation.

PLATE 17.

FIG. 1. *Hiraea oligocaenica* Berry. Caimito formation.
2. *Banisteria praenuntia* Berry. Culebra formation.
3. *Mespilodaphne culebrensis* Berry. Culebra formation.
4. *Schmidelia bejucensis* Berry. Caimito formation.

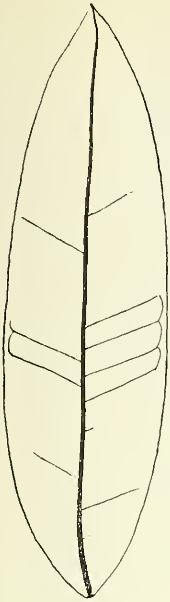
PLATE 18.

FIG. 1. *Calyptranthes gatunensis* Berry. Gatun formation.
2. *Melastomites miconioides* Berry. Culebra formation.
3. *Rondeletia goldmani* Berry. Gatun formation.
4–8. *Diosypros macdonaldi* Berry. Eocene (?).
4. Showing abundance of fruits in tuffs.
5, 7, 8. Transverse median sections of fruits.
6. Longitudinal median section of fruit.
9–12. *Rubiacites ixoreoides* Berry. Gatun formation.
9. External appearance.
10. Median longitudinal section showing unequally developed seeds.
11. Side view of seeds.
12. Lignified fragment showing end walls and partition.



PALMOXYLON PALMACITES (SPRENGEL) STENZEL.

FOR EXPLANATION OF PLATE SEE PAGE 44.



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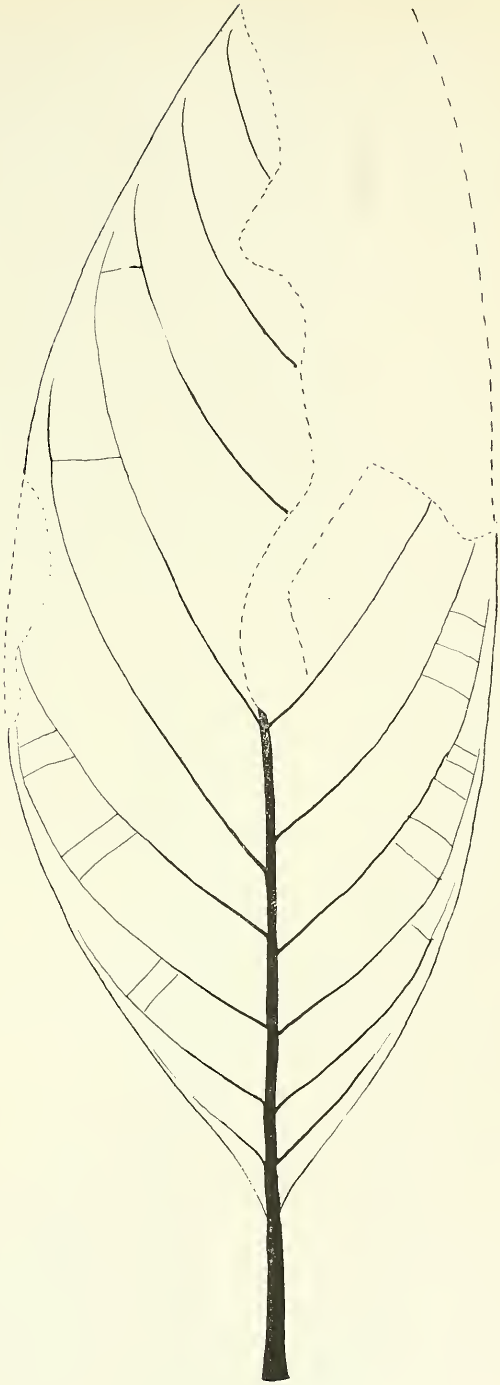

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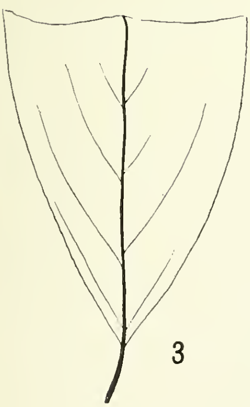
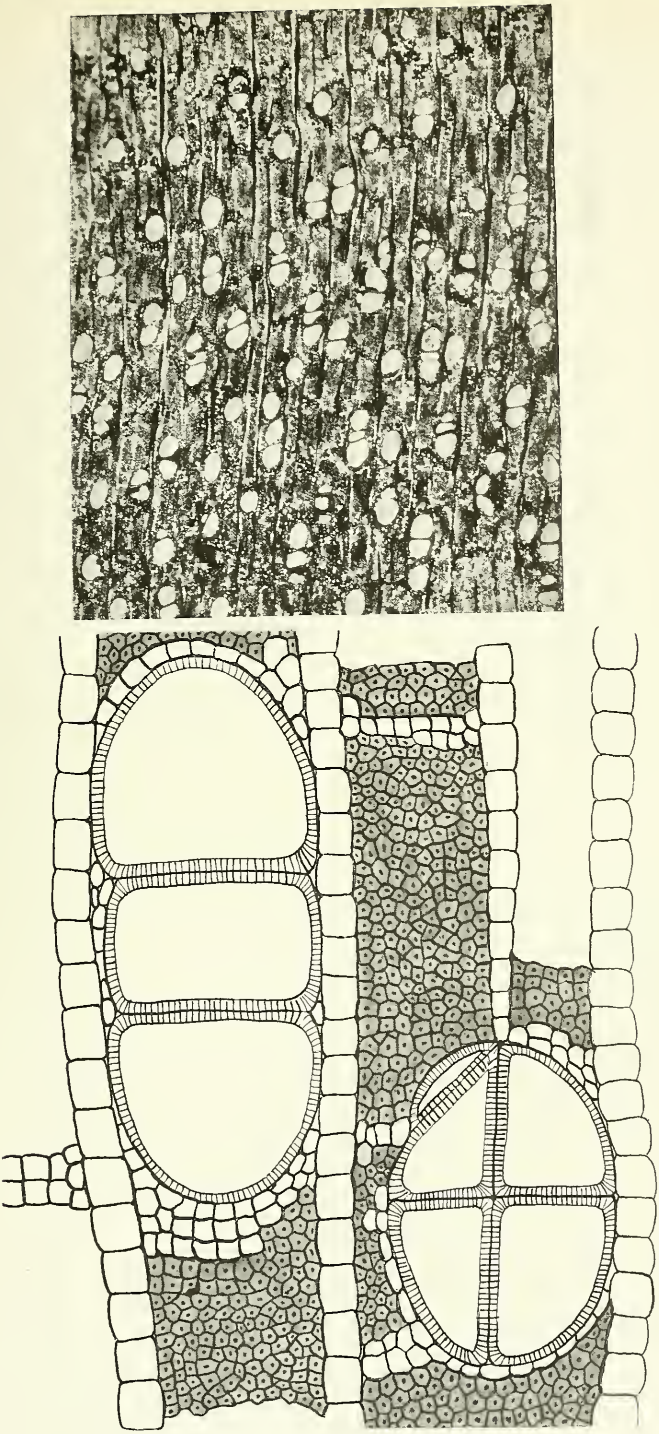


3

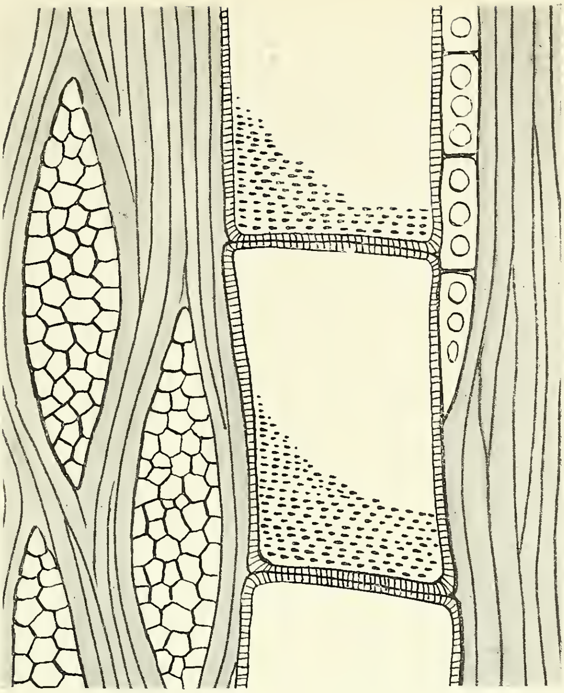
FOSSIL DICOTYLEDONOUS LEAVES.

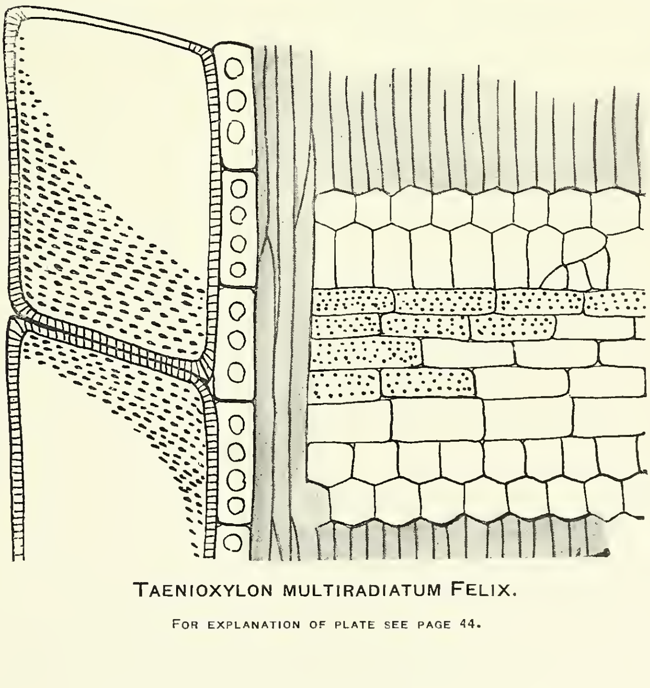
FOR EXPLANATION OF PLATE SEE PAGE 44.



TAENIOXYLON MULTIRADIATUM FELIX.

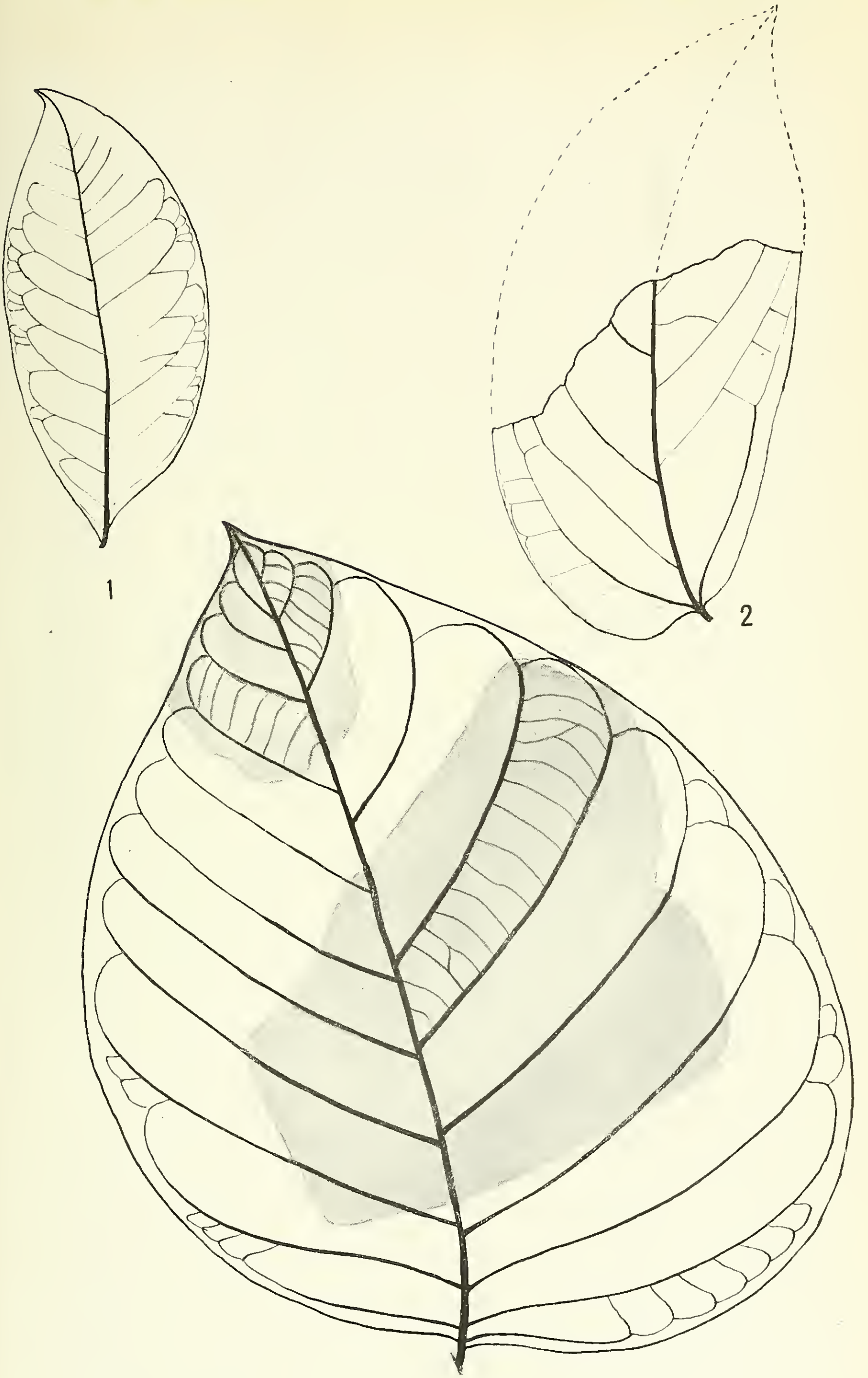
FOR EXPLANATION OF PLATE SEE PAGE 44.





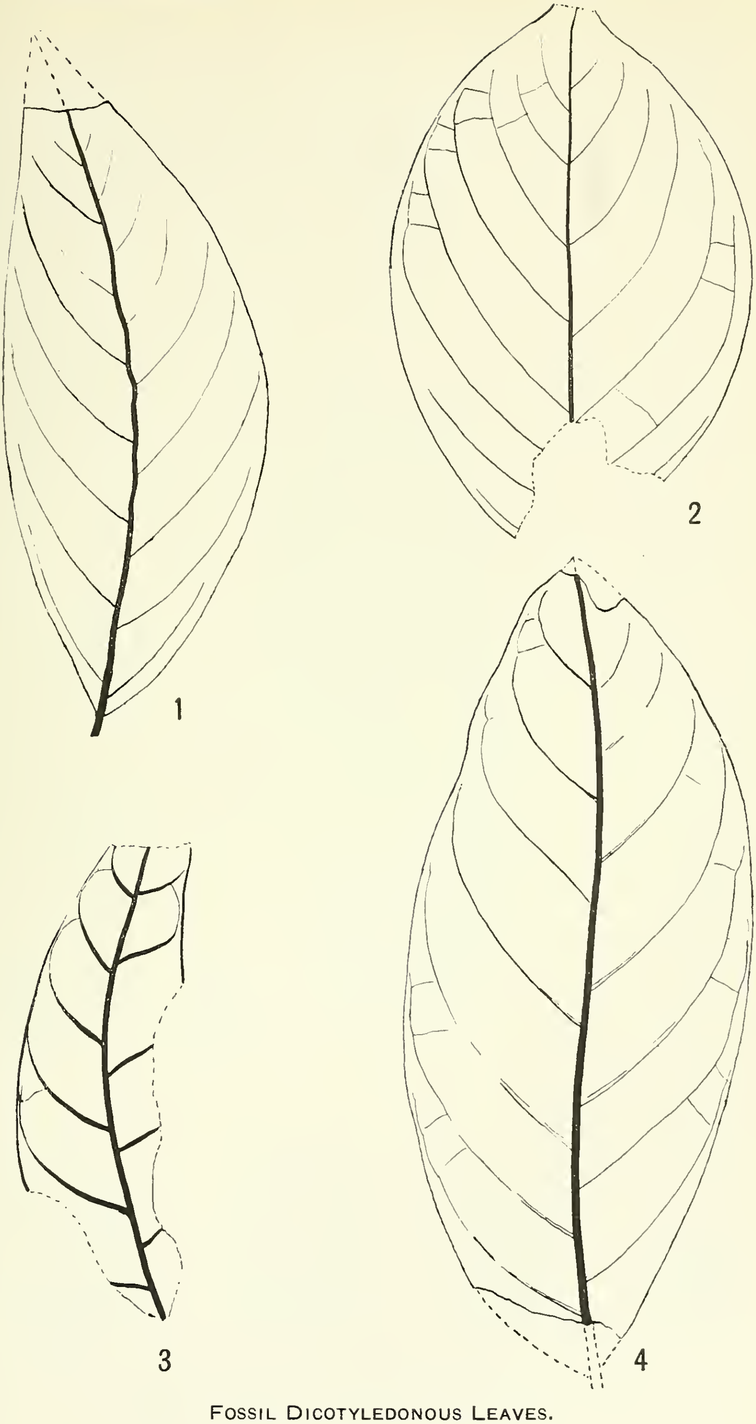
TAENIOXYLON MULTIRADIATUM FELIX.

FOR EXPLANATION OF PLATE SEE PAGE 44.



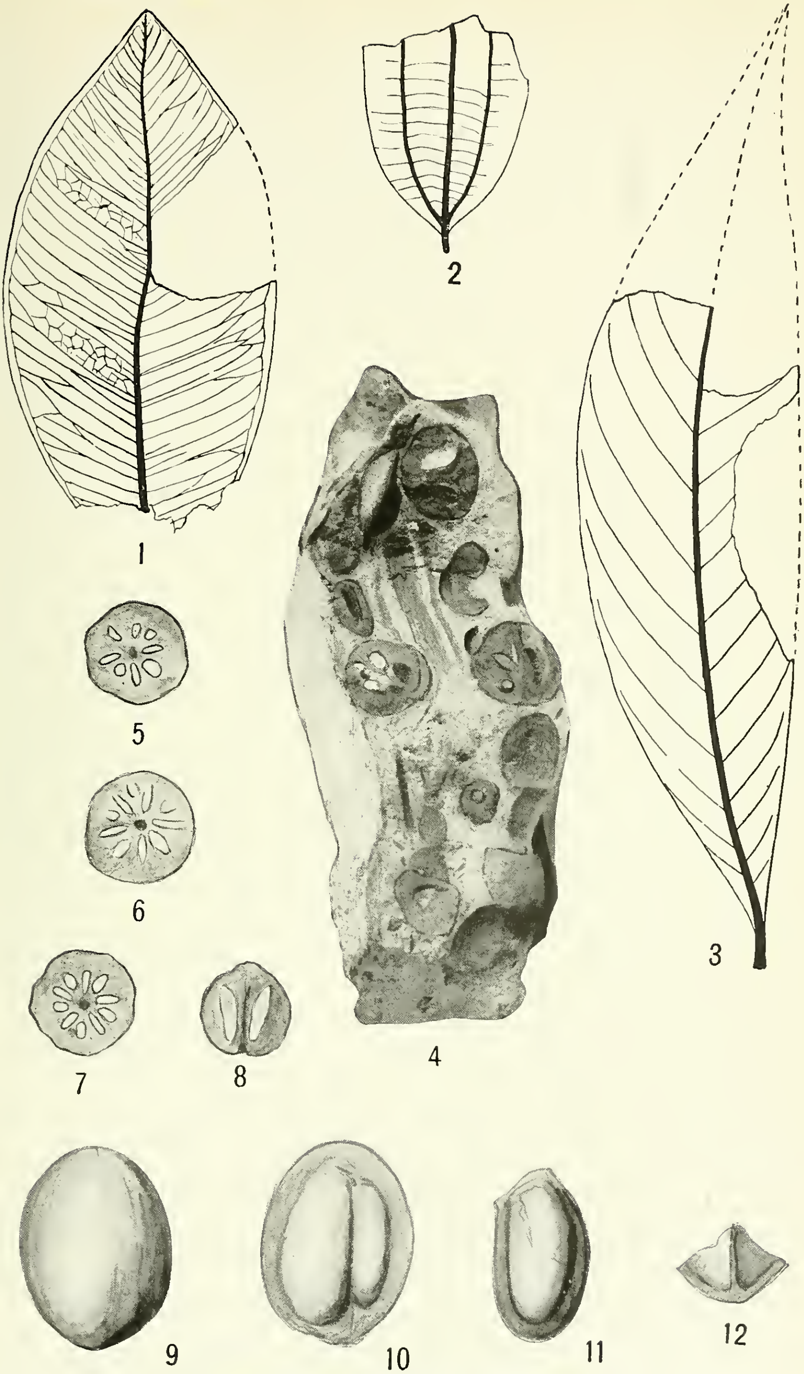
FOSSIL DICOTYLEDONOUS LEAVES.

FOR EXPLANATION OF PLATE SEE PAGE 44.



Fossil Dicotyledonous Leaves.

For explanat.on of plate see page 44.



Fossil Leaves, Fruits, and Seeds.

For explanation of plate see page 44.

INDEX.