CORNACEAE AND ALLIES IN THE MARQUESAS AND NEIGHBORING ISLANDS

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INTRODUCTION

Of the angiosperms which appear to date back to the beginning of the floral history of the islands of the South Pacific, *Cornus* and its near allies constitute a group of special interest. The members exhibit characters which not only point to a common origin of the group as a whole, but also link the living species with the early fossil floras of the continent. New lines of evidence are disclosed which indicate that the geological history of *Celastrus* and *Ilex,* found in the Marquesas and in other high islands of Polynesia, is closely linked with that of the new genus *Lautea* of the Austral Islands, *Corokia* of New Zealand, and *Cornus* of the northern hemisphere.

In comparison with the somewhat more distantly related Rubiaceae, which are well represented in the Pacific islands, the Cornaceae are a small and apparently somewhat decadent family with only two insular species east of the Chatham Islands. Hitherto, no representative had been reported in Oceanic Polynesia. Of the 11 genera of which the family is composed, *Cornus* (40 ± spp.) is the richest in species, the most widely distributed, and the one of two genera having a definite fossil record.

The existing dogwoods are widely distributed and isolated after the manner of old families, genera, and species, with their center in the cold climates of Asia, America, and Europe. Two species are circumpolar. Six mountain species are widely scattered geographically, one growing in Africa, three others in Mexico, another in Costa Rica, still another in Central America. It is a noteworthy fact, however, that *Cornus* is conspicuously absent from both South America and the region of Australia—a fact which has a bearing in tracing the early migration of the family into the Pacific. (See p. 21.)

The remaining genera of the dogwood family are widely scattered and isolated, in Eastern Asia and the Himalaya region, in the East Indies, Ceylon, Africa, and Madagascar. One genus, *Griselinia,* extends from South

America, through Antarctica, into New Zealand. With *Lautea,* however, comes the first and only record of the occurrence of the dogwood family, as revised by Wangerin,[1] in oceanic Polynesia.

A number of archaic characters new to the Cornaceae appear in *Lautea.* Their primary interest in this connection lies in the fact that they tend to separate the Cornaceae from the Umbellales, in which they are now commonly classed, together with the Umbelliferae and the Araliaceae, and to place them in the Celastrales. The inversely converging lines of evolution tend to bring the dogwoods, the climbing bittersweet (*Celastrus*), and the holly (*Ilex*), all of which are familiar plants in the woods of the northern United States, into close relationship—perhaps one family of Cretaceous time—with the isolated *Lautea* of the South Pacific. Today, however, the living representatives are greatly differentiated and bear little obvious resemblance beyond the fact that red fruits are of common occurrence in each family branch. Although the fruits of *Ilex* in the Marquesas and in Hawaii are almost black when ripe, the outer covering is red by transmitted light. The fruits of the Marquesan *Celastrus* and the allied *Perrottetia* of Hawaii are bright red.

This paper is based on studies made by the writer while a member of the Bayard Dominick Expedition of Bernice P. Bishop Museum, which afforded an opportunity to explore some 34 Pacific islands.[2] Acknowledgments are due especially to Dr. Elizabeth Brown, who voluntarily contributed to the field studies throughout the two years of the survey. During December, 1920, and January, 1921, while the writer was in Wellington en route to the Marquesas, Professor H. P. Kirk of Victoria University College and Mr. E. Philipps Turner, Secretary of the Department of Forestry gave every opportunity to observe living specimens of *Corokia* and other New Zealand plants of interest for comparison with the flora of the Marquesas and neighboring islands. Valuable materials and information from Rapa were obtained through the kindness of Mr. John F. G. Stokes and the late Mrs. A. M. Stokes.

The results of the exploration, including a complete flora of the Marquesas and important records from other islands, are in preparation.[3]

[1] Wangerin, Walther, Cornaceae: Das Pflanzenreich, vol. 41, pt. 229, 1910.

[2] Gregory, H. E., Bayard Dominick Expedition, Report of the Director for 1920: B. P. Bishop Mus., Occ. Papers, vol. 8, pp. 13-15, 1921; Report of the Director for 1922: B. P. Bishop Mus., Bull. 4, pp. 21-24, 1923.—Editor.

[3] Brown, F. B. H., Flora of the Marquesas and neighboring islands, manuscript in Bernice P. Bishop Museum.

SYSTEMATIC CLASSIFICATION

Genus LAUTEA F. Brown, New Genus[4]

Woody arborescent plants. Leaves alternate, petiolate, entire, denticulate or serrate; secondary veins arched as in *Cornus*, but finer and more divergent near the apex of the leaf, the angle of divergence from the midrib being equal to or greater than 45° near the apex and gradually less toward the base of the leaf where the angle is less than 45°; leaf-scars crescent-shaped, with three bundle scars on the surface, and a circular inflorescence scar in the axil. Pubescence felt-like, composed of T-shaped trichomes, with a thick-walled, spindle-shaped, terminal cell forming the two arms, and a short thin-walled stalk composed of one or two cells; the terminal cell forms 6 ± oblique slit-like pits which communicate with the stalk. Inflorescence axillary, sub-racemose; flowers bisporangiate; parts of the flower variable in number, 6±, 6±, 6±, 3±; calyx turbinate, the tube adnate with the ovulary, with 5-8 valvate lobes or sepals; petals 5-7 + in number, valvate, yellow in color, pubescent outside, glabrous within, each with or without a minute fimbriate or sub entire scale at the base; stamens 5-7 +, free, shorter than the petals, inserted on the epigynous disk, alternate with the petals and commonly of the same number; filaments slender, glabrous; anthers broadly linear, 2-locular, joined to the filament slightly below the middle of the dorsal surface and above the deep sinus of the 2-lobed base, versatile; disk fleshy; ovulary 2-4-locular; style rather short, not exceeding the petals, with a fleshy 2-4-lobed stigma; ovules elongated, one in each locule. Drupe 2-4-locular, longitudinally grooved, crowned by the persistent calyx teeth, the exocarp thin, fleshy, the endocarp thick, osseous, forming a longitudinally furrowed putamen with a conspicuous cup-shaped depression at the apex, the mouth of which is decidedly over one-half the diameter of the putamen. Seeds narrowly ellipsoidal; testa membranous; embryo straight, considerably shorter than the endosperm; cotyledons minute, linear, short; endosperm abundant, oily, surrounding the embryo. Vessels of extremely small diameter, isolated or, rarely, grouped in twos, the perforations scalariform; fibers septate, thick-walled, conspicuously pitted; rays 1-5 + seriate, commonly wider than the vessels; wood-parenchyma sparingly developed or absent.

Two species, Rapa, Austral Islands, endemic.

Lautea is very closely allied to the less primitive *Corokia* of Chatham Island and New Zealand through *Lautea stokesiana*, var. γ *intergrifolia*, on one hand and *Corokia macrocarpa* of Chatham Island on the other, and is distinguished from that genus by the commonly serrate or denticulate leaves, the long axillary sub-racemose inflorescence, and the more numerous parts of the flower, the number being nearly constant in *Corokia* (5, 5, 5, 1-2) and variable in *Lautea* (6±, 6±, 6±, 3±). The versatile anther in *Lautea* is deeply lobed at the base; the filament is attached near the sinus and below the middle of the back; the anther of *Corokia* unites with the filament at the scarcely lobed base. The endocarp of *Corokia* is commonly unilocular while in *Lautea* it is commonly trilocular or even quadrilocular.

Lautea and *Corokia* form, with section *Bothrocaryum* of the genus *Cornus* of the North Temperate Zone, a closely related group of seven species. (See p. 9.) But in marked contrast to the apparently close phylogenetic

[4] Brown, F. B. H., Lautea, a new genus of the Cornaceae; its probable origin and dispersal in the Pacific: Proc. Haw. Acad. Sci., B. P. Bishop Mus., Spec. Pub. 11, p. 26, 1926.

relationship clearly indicated in the similar characters, it should be noted that the three main regions, eastern Asia, Atlantic North America, and southern Polynesia, comprising the regional distribution of the existing members of the group, are extremely isolated geographically, indicating a long and complex geological history (fig. 5, p. 20).

The native name in Rapa is *lautea* (white leaf), for all species.

KEY TO SPECIES

(1) Leaves denticulate or sub entire, densely tomentose beneath (2)
(1) Leaves coarsely serrate, glabrous or sparingly pubescent beneath........**L. serrata**
(2) Leaves sub-entire..**L. stokesiana** var. γ **integrifolia**
(2) Leaves denticulate (3)
(3) Ovulary commonly trilocular..**L. stokesiana** var. β **denticulata**
(3) Ovulary commonly quadrilocular..................................**L. stokesiana** var. α **primaeva**

1. **Lautea stokesiana** F. Brown, new species (figs. 1; 2, *a-k*).

Small tree, 3 ± meters in height, 4 ± cm. in diameter, the young branches, under side of leaves and the inflorescence covered with a dense, closely felted, yellowish white tomentum; mature twigs blackish, gray and glabrous or sub-glabrous with numerous crescent-shaped, 3-ranked leaf-scars (fig. 2, *d*), each bearing on the surface three bundle scars plainly visible with a lens, and a circular inflorescence scar in the axil; leaves approximate near the ends of the branches, lanceolate, the lamina 6.5 ± cm. long and 2.5 ± cm. wide, sub entire or with a few remote callous denticles in the median or apical portion, apiculate, coriaceous, the upper surface pubescent in young leaves, but finally glabrous or sub-glabrous and dark brown or brownish in dry specimens; under surface densely pubescent, yellowish white in color; petiole 1.5 ± cm. long, tomentose, sulcate above; trichomes (fig. 2, *a*) T-shaped, 2-3-celled; terminal cell (forming the two horizontal arms of the trichome), spindle-shaped, 300 ± μ in length, thick-walled; stalk thin-walled, short, composed of one or two cells; at the junction of the terminal cell with the stalk, there are 6 ± oblique, slit-like pits shown sectionally (fig. 2, *b*), and surface view (fig. 2, *c*); inflorescence densely pubescent throughout, sub-racemose, axillary, longer or somewhat shorter than the leaves, bearing 10 ± pedicellate flowers in the upper two-thirds, each subtended by a linear lanceolate bract as long as the pedicel or shorter; pedicels simple or branched; calyx with 5-7 + broadly triangular acute lobes 3 mm. ± in length; petals 5-7 + in number, thick, valvate, yellow, lanceolate, 7 ± mm. long, pubescent on the outer surface, glabrous within, each with or without a small minutely fimbriate or sub entire scale at the base; stamens 5-7 + in number, alternate with and shorter than the petals; filaments 2 ± mm. long, puberulous to glabrate, free; anthers broadly linear, deeply lobed at the base, 2 ± mm. long, affixed dorsally below the middle and versatile, pubescent to glabrate; style 2 ± mm. long, somewhat pubescent near the base, with a fleshy 2-4-lobed stigma; ovulary 2-4-locular, with a single ovule in each cell; drupe 2-4-locular, broadly ellipsoidal, dark red in color, 13 ± mm. long, 10 ± mm. wide, obscurely 5-7 ribbed longitudinally and commonly more or less compressed laterally, crowned with the persistent calyx teeth, the exocarp thin, fleshy; the endocarp (putamen) thick, osseous, with a deep cup-shaped depression (germinal cup) at the apex; seed narrowly ellipsoidal, 4 ± mm. long with a membranous brownish testa; embryo narrowly cylindrical, 2 mm. long, the cotyledons minute, sub-linear; endosperm abundant, oily, surrounding the embryo.

Var. α **primaeva** F. Brown.

Leaves sub-entire or sparingly denticulate in the upper central portion, the upper surface dull dark green in color or finally dark brown when dry, lanceolate or obovate, 8 ± cm. long, 3.5 ± cm. wide, mucronate, cuneate at the base; petiole 1.5 ± cm. long; inflorescence approximately as long as the leaves; flowers with as many as 7 + sepals, 7 + petals, and 7 + stamens; filaments puberulent; anthers glabrate or pubescent with scattered appressed hairs; stigma commonly 4-lobed; ovulary commonly 4-locular; fruit commonly 4-locular.

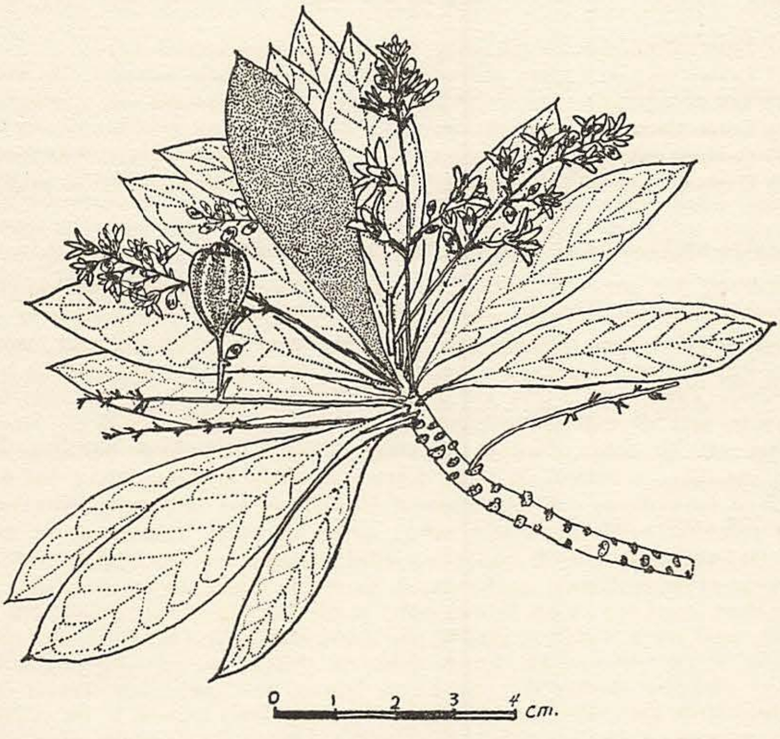

FIGURE 1.—*Lautea stokesiana* F. Brown; var. γ; leaves, inflorescence, and mature fruit.

Type, Stokes No. 367 A., Rapa, B. P. Bishop Museum; type of the genus. The most primitive variety or species collected.

Rapa; endemic.

Var. β **denticulata.**

Small tree 6 ± m. in height, 8 ± cm. in diameter; bark dark brown, rough, of medium thickness, the inner tissues dark reddish brown; leaves commonly lanceolate, up to 10 ± cm. long, remotely denticulate in the upper central portion; ovulary and fruit commonly trilocular, less commonly bi- or quadri-locular.

Type, A. M. Stokes No. 37, Ororangi, Rapa, elevation 300 feet, B. P. Bishop Museum. Stokes No. 225, from base of Lauea peak, Rapa, elevation 1050 feet.

Var. γ **integrifolia.**

Leaves commonly lanceolate, sub-entire, the upper surface dark brown when dry; ovulary and fruit commonly trilocular, less commonly bi- or quadri-locular; small tree 3 ± m. high.

Type, Stokes No. 348, Maungaaeae, Rapa, elevation 900 feet, B. P. Bishop Museum.

2. **Lautea serrata** F. Brown, new species.

Small tree 3 ± meters in height, the young branches clothed with fine, closely felted tomentum; leaves not crowded, lanceolate, 15 ± cm. long, 4 ± cm. wide, acute, mucronate, cuneate at the base, sharply and rather coarsely serrate, the teeth conspicuously mucronate, thin, pubescent in the early stages of growth but soon glabrous or sub-glabrous except on the under surface of the mid-vein which is clothed with a fine white tomentum of two-armed hairs; petiole short, 1 ± cm. long, tomentose; trichomes T-shaped and similar to those of *L. stokesiana* except on the young leaves which bear T-shaped trichomes with a long terminal cell; flowers and fruit unknown.

Only a single young branch with a stem 5 ± mm. in diameter, without flowers or fruit, is available for microscopic examination; but all observed structural characters of the stem are consistent with the genus.

Type, A. M. Stokes No. 57, Morongota, Rapa, elevation 800 feet, B. P. Bishop Museum.

Native name, *lautea.*

Rapa; endemic.

COMPARATIVE MORPHOLOGY

Lautea, Corokia, and Section *Bothrocaryum* Koehne of the genus *Cornus* form a closely related group of seven species, characterized by (1) alternate leaves, (2) fruits having a stony 1-4-locular putamen with a jagged edged, cup-like cavity at the apex (fig. 2, *i*), (3) pubescence composed of two-armed hairs, (4) vessels with scalariform perforations.

The two-armed trichome of *Lautea* and *Corokia* is highly peculiar in structure, being composed of an elongated, thick-walled, fiber-shaped terminal cell, and a short thin-walled stalk of one or two cells. At the junction of the terminal cell with the stalk, there are formed 2-9 + oblique slit-like pits, which are plainly visible, under moderate magnification, in the thick walls of detached fiber-like terminal cells. The presence of this remarkably specialized trichome in *Lautea* and *Corokia* indicates the close phylogenetic relationship of the two genera. Two-armed hairs occur in *Cornus,* but they are composed of a single cell in which the stalk-cells and slit-like pits are lacking, and the surface is crusted with calcium carbonate. The genus *Cornus,* therefore, stands somewhat apart.

It is of interest to note, in this connection, that two-armed hairs of somewhat different form and structure have been found in both the Umbellales (Araliaceae) and the Celastrales (*Myginda ilicifolia*), but are uncommon. Existing species of *Ilex* and *Celastrus* are glabrous, as a rule. In fact, all primitive species in Australia, with which fossils have been compared, are described as glabrous. Hence the presence of abundant two-armed trichomes, which are closely felted together and tend to obscure the venation somewhat on the under surface, may serve as a useful character in the identification of fossil Cornaceae. The fact that two-armed trichomes occur in both *Cornus* and *Lautea* leads to the belief that they were also present and very likely abundant in the primitive antecedent.

The germinal cup in the apex of the putamen of *Lautea* (fig. 2, *i*) approaches that of *Corokia,* but is deeper. In both genera, the mouth of the cup is decidedly over one-half the cross-diameter of the putamen, in which respect the fruit characters approach *Cornus alternifolia* of North America, rather than the closely related *C. controversa* of eastern Asia. Another fruit character which approaches *Cornus alternifolia* more closely than any other of the Cornaceae with which comparisons have been made, consists of the few low, rounded, longitudinal ridges which characterize the fruits of *Lautea.*

The extreme primitiveness of *Lautea* in comparison with other genera of the Cornaceae is indicated in several characters. For example, in *Lautea* there are as many as 4 fertile locules in the endocarp; in *Corokia* and *Cornus*

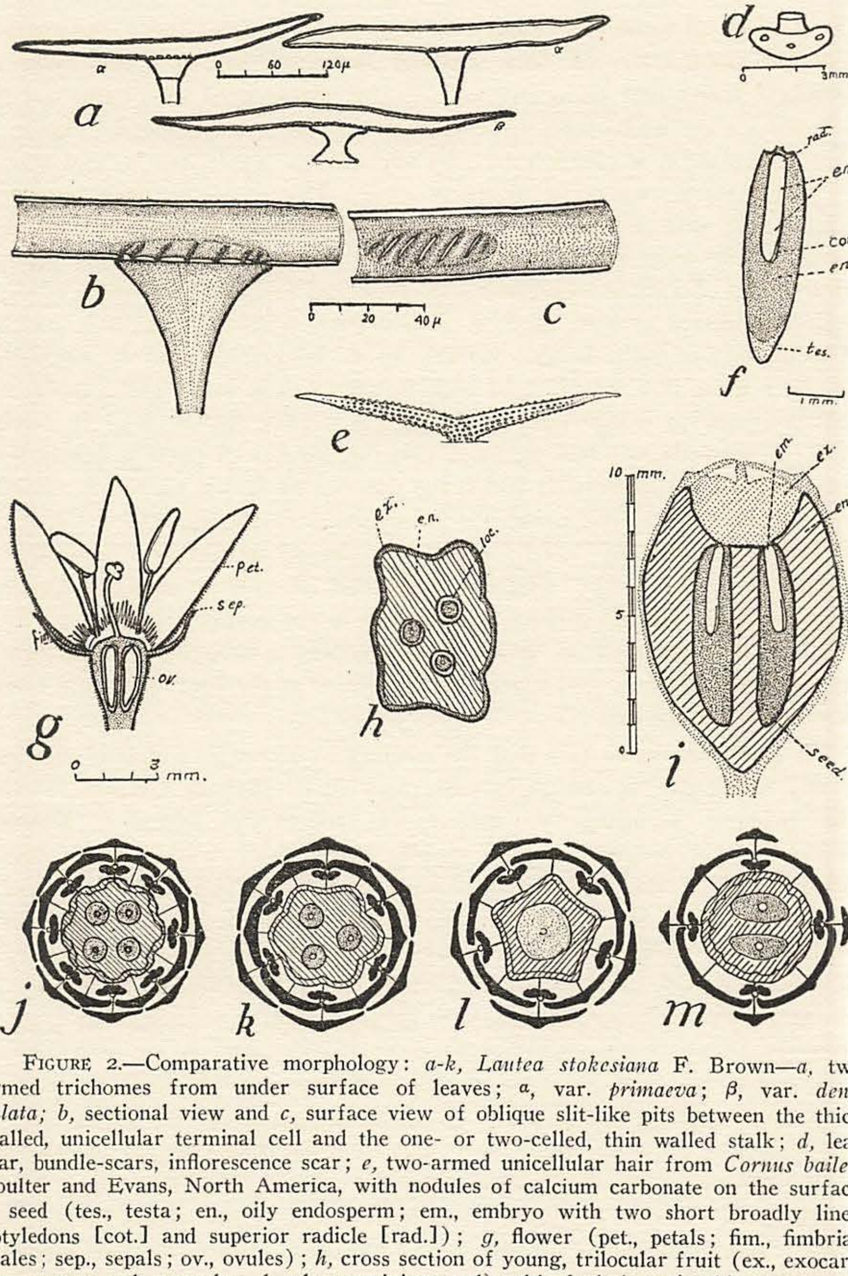

FIGURE 2.—Comparative morphology: *a-k, Lautea stokesiana* F. Brown—*a*, two-armed trichomes from under surface of leaves; α, var. *primaeva*; β, var. *denticulata*; *b*, sectional view and *c*, surface view of oblique slit-like pits between the thick-walled, unicellular terminal cell and the one- or two-celled, thin walled stalk; *d*, leaf-scar, bundle-scars, inflorescence scar; *e*, two-armed unicellular hair from *Cornus baileyi*, Coulter and Evans, North America, with nodules of calcium carbonate on the surface; *f*, seed (tes., testa; en., oily endosperm; em., embryo with two short broadly linear cotyledons [cot.] and superior radicle [rad.]); *g*, flower (pet., petals; fim., fimbriate scales; sep., sepals; ov., ovules); *h*, cross section of young, trilocular fruit (ex., exocarp; en., osseous endocarp; loc., locule containing seed); this fruit is noticeably compressed, but the outline is commonly more nearly circular; *i*, longitudinal section of fruit, showing fleshy exocarp (ex.), hard endocarp (en.) with germinal cup at the apex in which the radicle of the embryo is near the surface; *j-m*, floral diagrams illustrating progressive simplification of the flower; *j, Lautea stokesiana*, var. α, *primaeva*; *k, Lautea stokesiana*, var. γ, *integrifolia*; *l, Corokia buddleoides*; *m, Cornus alternifolia*.

the number of locules is reduced to 1 or 2; in fact, of the 5 endocarps of *Corokia buddleioides* of New Zealand examined, all were unilocular and Mueller[5] states that endocarps of *Corokia macrocarpa* of Chatham Island are unilocular—a character of foremost systematic importance. Again, the flower of *Lautea* is characterized by superfluous sepals, petals, and stamens of which there may occur as many as 8. This is an extreme number in comparison with any other genus of the Cornaceae as restricted by Wangerin.[6] The most primitive flower found in any member of the group is clearly that of *Lautea stokesiana*, var. *primaeva* (fig. 2, *j*) in which a numerical composition as high as 8, 8, 8, 4 occurs, while 7, 7, 7, 4 is common. The number of parts is also variable in *L. integrifolia* and *L. denticulata*, but here there is a reduction of superfluous parts in every cycle, the numerical composition being 6±, 6±, 6±, 3±. (See fig. 2, *k*.) In *Corokia* still further reduction has occurred, and the number of parts is nearly stable except in the gynoecium in which the number of fertile carpels is stated to vary from 1 to 2; the numerical composition in the flower of *Corokia* is 5, 5, 5, 1-2. (See fig. 2, *l*.) The genus *Cornus* represents a final stage of reduction in the flower, which is composed of only 4 sepals, 4 petals, 4 stamens, and 2 fertile carpels, represented in the formula 4, 4, 4, 2 (fig. 2, *m*). In each stage of the series, there has been a progressive simplification of the flower with *L. stokesiana*, var. *primaeva* at the beginning, and *Cornus alternifolia* at the end.

It is a remarkable fact that the ovulary of *Corokia*, which is very commonly unilocular, is seemingly more specialized than in *Cornus*, in which the ovulary, according to authors, is constantly 2-locular. Evolution seems to have progressed more rapidly in the ovulary of *Corokia* than in other parts of the flower which have undergone less reduction than in *Cornus*, resulting in a slight divergence in the otherwise homogeneous series. Although the reduced ovulary is one of the distinguishing characters of *Corokia*, correctly observed by Cheeseman,[7] it was overlooked by Wangerin.[8]

Mueller's[9] observations in which he states that the number of sepals in *C. macrocarpa* of Chatham Island is "5, occasionally 6 or 7" is of vital importance, for, in this respect as well as the habit of growth (5 to 7 meters in height) and the axillary sub-racemose inflorescence, the characters are, on the whole, more like those of *Lautea* of Rapa than *Corokia* of New Zealand. However, Mueller's observation, if correct, that the ovary is two-celled while the ripe endocarp (putamen) is one-celled, places the Chatham Island species definitely in the genus *Corokia*, rather than in *Lautea* in

[5] Mueller, Ferdinand, The vegetation of the Chatham Islands, p. 16, Melbourne, 1864.
[6] Wangerin, Walther, Cornaceae: Das Pflanzenreich, vol. 41, pt. 229, 1910.
[7] Cheeseman, T. F., Manual of the New Zealand flora, p. 685, Wellington, 1925.
[8] Wangerin, Walther, Cornaceae: Das Pflanzenreich, vol. 41, pt. 229, p. 92, 1910.
[9] Mueller, Ferdinand, The vegetation of the Chatham Islands, p. 16, Melbourne, 1864.

which a unilocular endocarp has never been found. If, on further observation, it is found that the number of locules is 3 ± and the number of sepals, petals, and stamens 6 ±, then the Chatham Island representative cannot be admitted to *Corokia* and should be transferred to *Lautea*.

The wood of *Lautea* is characterized by vessels of remarkably small diameter (average 31 μ), which is only slightly larger than that of the fibers (26 μ). Vessels of nearly the same average diameter (32 μ) occur in the closely related *Corokia*. According to the writer's measurements, however, taken from a stem of *C. buddleioides* 4 cm. in diameter, the vessels are not as small, on the average, as stated by Solereder,[10] who gives a vessel diameter of only 13 μ for *Corokia*. The fibers are of the same diameter as in *Lautea*. In continental species of *Cornus*, the vessels are considerably larger than this, even in twigs of herbarium sheets, but do not acquire the large diameter of certain continental species such as the oaks of the North Temperate Zone.

[10] Solereder, Hans, Systematic anatomy of the Dicotyledons, p. 437, Oxford, 1908.

VENATION

The midvein is rather prominent, straight, depressed in the upper surface and raised below where the veins are somewhat obscured by the thick felt-like pubescence. The secondaries vary in number from 6 to 15 pairs, are slender, are opposite or alternate, diverge from the midrib at an average angle of 45°, and arch inward near the margin of the leaf. The tertiaries,

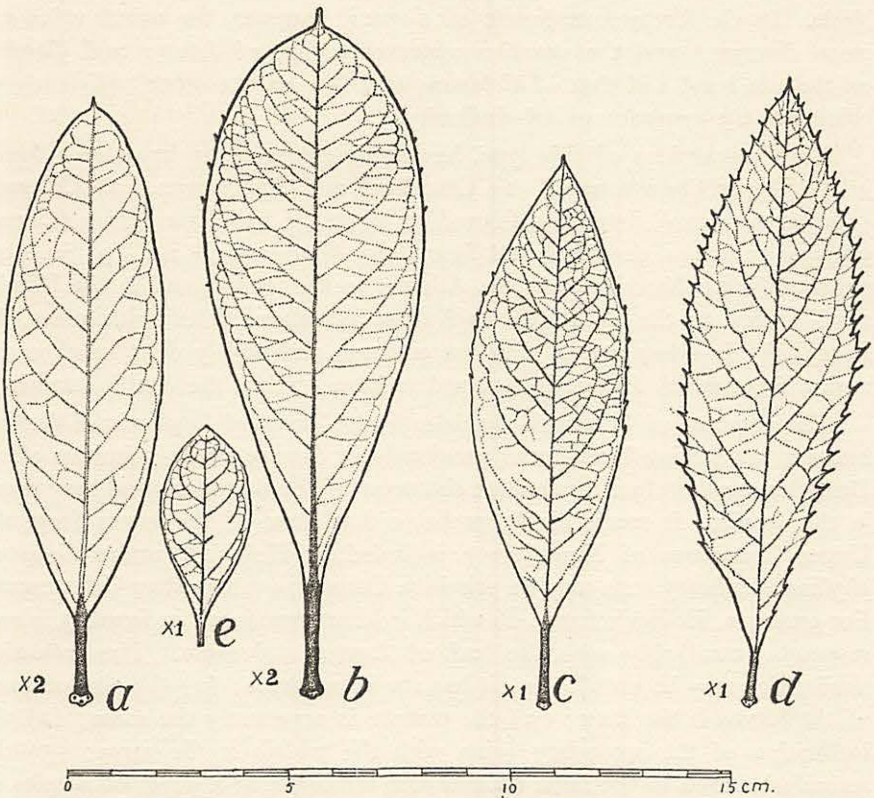

FIGURE 3.—Venation: *a, Lautea stokesiana* var. *γ integrifolia; b, L. stokesiana* var. *α primaeva; c, L. stokesiana* var. *β denticulata; d, L. serrata; e, Lautea newberryana* (Hollick) new name, of the Cretaceous of North America.

(X1, X2, represent dimensions in relation to scale.)

visible with a lens, are somewhat reticulately branched, and join the arched secondaries in a series of loops.

The venation of the Cretaceous fossil (fig. 3, *e*) and the existing *L. stokesiana*, var. *primaeva* (fig. 3, *b*) is typical and remarkably similar. In *Corokia macrocarpa* of Chatham Island and *C. cotoneaster* of New Zealand, the secondaries are fewer, more distant, straighter near the base and more abruptly arched at the end. The tertiaries are somewhat obscure. The *Corokia* type of venation may be regarded as a moderately specialized derivative of that of *Lautea,* indicating a close phylogenetic relationship of the two genera.

In existing species of *Cornus,* the venation differs considerably from that of the *Lautea-Corokia* type. The apical secondaries converge acutely and run out in an approximately parallel direction toward the apex of the blade. In the Cretaceous fossils of *Cornus,* however, the apical veins are more divergent and the venation approaches that of *Lautea* and *Corokia* on the one hand and that of *Celastrus* and *Ilex* on the other sufficiently to bring out the general marked similarity.

Leaf impressions of this type, having divergent veins, have been found in the Upper Cretaceous of (1) Greenland and Spitzbergen, (2) Colorado (*Cornus emmonsii,* listed and figured by Ward),[11] (3) New Jersey (*Cornophyllum vetustum,* described and figured by Newberry),[12] and (4) in other parts of North America from the Atlantic to the Pacific, and in the Mississippi Valley to the Gulf (*Cornophyllum vetustum,* listed with notes, by Berry).[13] In other words, they are common and widely distributed in the region from which *Lautea* is assumed to have reached the Pacific islands.

The presence of Celastroid denticles in the leaves of *Lautea* is of decided interest, not having been found previously in *Cornus* or its primitive allies. Denticles are therefore a primitive character of the dogwoods and may occur in the fossils. It seems highly probable that some of the leaves from the Upper Cretaceous of New Jersey, included by Hollick[14] under *Celastrophyllum newberryanum* may be primitive Cornaceae rather than Celastraceae. For example, Hollick's figure 16 which is here reproduced in figure 3, *e* corresponds remarkably with the leaf of *Lautea stokesiana.* The following similarities may be noted: (1) it has the same shape; (2) the size of some of the leaves is the same; (3) the texture is apparently the same; (4) the inclination of the secondary veins with the midrib is the same; (5) the secondaries arch in the same manner and terminate in a series of aeroles of diminishing size near the margin, the apical pair forming in the apex of the leaf low broad arches; (6) a few, remote, appressed denticles may be present in the margin of the upper central portion of the blade, clearly shown in Hollick's[15] figure 27, but indicated in his figure 16, or the margin may be entire;

[11] Ward, L. F., Flora of the Laramie group: U. S. Geol. Survey, Sixth Ann. Rept., p. 553, pl. 48, fig. 2, 1884-85.

[12] Newberry, J. S. and Hollick, A., Flora of the Amboy clays: U. S. Geol. Survey, Mono., vol. 26, p. 119, pl. 19, fig. 10, 1895.

[13] Berry, E. W., Upper Cretaceous flora of the eastern Gulf region in Tennessee, Mississippi, Alabama, and Georgia: U. S. Geol. Survey, Prof. Papers no. 112, p. 129, 1919.

[14] Newberry, J. S. and Hollick, A., Flora of the Amboy clays: U. S. Geol. Survey, Mono., vol. 26, p. 101-102, pl. 49, 1895.

[15] op. cit., pl. 49, fig. 27.

(7) the base of the leaf tapers gradually and is slightly decurrent on the short, rather stout petiole; (8) the basal secondaries branch from the midrib at an angle somewhat less than the average of 45°, but the apical veins diverge at an angle equal to or somewhat greater than the average. It is therefore probable that the specimen, illustrated in the paper by Newberry and Hollick [16] as *Celastrophyllum newberryanum* Hollick, should be transferred to the Cornaceae under *Lautea newberryana* (Hollick), new name. In their plate 49, figures 5, 23, and 27, are probably other Cretaceous Cornaceae.

The shape, size, venation, and marginal characters of existing and fossil leaves indicate a marked convergence of families and genera in the Cretaceous. The genera *Cornus* and *Lautea* were apparently less divergent then than at present. Furthermore, the leaf impressions of some of the Cornaceae are hardly distinct from those of the Celastraceae, Aquifoliaceae, and related families of the Celastrales. Very likely it would not be far from the truth to infer that the Cretaceous antecedents of *Ilex, Celastrus, Cornus, Corokia, Lautea* and related genera were members of one and the same family. Wettstein's [17] suggestions, pointing to several evidences which indicate that the Cornaceae may have had a different origin from the Araliaceae or Umbelliferae, seem well founded. Other characters which tend to unite the Cornaceae with the Celastrales are: (1) septate fibers; (2) scalariform perforations, and (3) spiral thickenings in the vessels; (4) sparingly developed wood-parenchyma. Prominent artificial characters, such as the complete fusion of the calyx tube with the walls of the ovulary, are not inconsistent with those of a group (Celastrales) in which partial fusion has occurred.

The serrations of the leaves of *L. serrata* are wide at the base and terminate in a long mucro, somewhat as in *Torricellia* of eastern Asia; but only a comparatively distant alliance to this genus is indicated in the venation and significant structural characters. The trichomes, vessels, fibers, and medullary rays have the characters of *Lautea.*

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[16] op. cit.

[17] Wettstein, Richard. Handbuch der systematischen Botanik, p. 744, Leipzig, 1924.

WOOD CHARACTERS

Lautea stokesiana var. **denticulata** F. Brown (fig. 4).

Wood rather hard, of fine uniform texture, without growth-rings, light red in color, with a thin pinkish-white sapwood.

Cross Section

Gross: Vessels extremely small, visible with a strong lens, isolated or rarely grouped in twos; rays plainly visible with a lens, several times broader than the vessels.

Minute: Vessels mainly isolated, a few in radial groups of two, mostly less than 40 μ in diameter (average 31 $\pm$ μ), slightly (31:26) larger than the fibers; rays up to 6 + cells wide, the cells short, of nearly the same radial length as the diameter of the vessels, the lumina filled with dark brown contents; wood-parenchyma absent or sparingly developed; fibers with rather thick walls, 4-6-sided, 26 $\pm$ μ in diameter.

Radial Section

Gross: Rays plainly visible without a lens, deep red in color; texture fine, uniform; no distinct ripple marks.

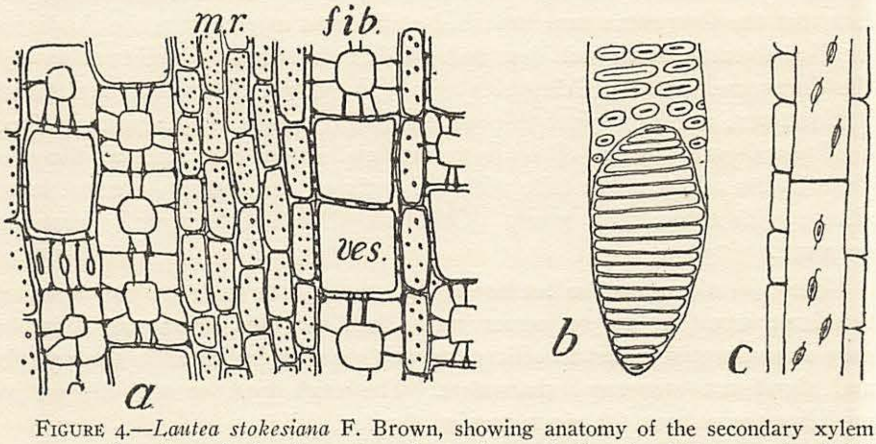

Figure 4.—*Lautea stokesiana* F. Brown, showing anatomy of the secondary xylem: *a*, cross section of wood, showing extremely small vessels (ves.), which are only slightly larger than the thick-walled fibers (fib.), and smaller than the multiseriate rays (mr.); *b*, scalariform perforations of the vessels; *c*, septate fiber with conspicuous bordered pits.

Minute: Elements serried; vessels with scalariform perforations with numerous bars of which there are up to 18 + in large stems or 32 + near the primary xylem; rays composed of square or moderately elongated cells with elliptical or sub-scalariform semi-bordered pits communicating with the vessels; ray-cells conspicuously pitted; vessel-pits, elliptical, in alternate or transverse arrangement.

Tangential Section

Gross: Texture fine, uniform; rays plainly visible under a lens, lanceolate in outline, red in color.

Minute: Rays 1-6 + cells wide, up to 20 + cells high, elliptical in outline, acute; fibers septate, with numerous bordered, oblique, slit-like pits in the radial and tangential walls; vessels with spiral thickenings and circular elliptical or scalariform bordered pits in alternate or transverse arrangement.

Maceration

Vessel-segments 600 ± μ long; prosenchyma septate, conspicuously pitted; wood-parenchyma not abundant, apparently absent; no crystal-parenchyma.

Distinguishing Characters

Wood without growth-rings, reddish in color, of medium hardness and fine uniform texture; elements serried but without distinct ripple effect; vessels isolated or, rarely, grouped in twos, extremely small in diameter; perforations scalariform; vessel-pits rather large, circular, elliptical or elongated in outline, and opposite, alternate or sub-scalariform in arrangement; walls spirally thickened; rays considerably broader than the vessels, plainly visible in radial section; fibers septate, with oblique, slit-like bordered pits; wood-parenchyma absent or sparingly developed.

Type, wood specimen, Stokes No. 37, 5 cm. diameter, Rapa, B. P. Bishop Museum.

Lautea stokesiana var. α and var. γ: *Lautea serrata.*

Only young stems not over 1 cm. diameter of *L. serrata* and varieties *primaeva* and *integrifolia* of *L. stokesiana* were available; but all exhibit vessels of extremely small diameter (32 ± μ), perforations with numerous (30 ±) scalariform bars, septate thick-walled fibers, and 1-2 + seriate rays. The young wood of *L. serrata,* however, is relatively light in color, and the rays are perhaps slightly narrower than in *L. stokesiana.*

Structural Characters of Historical Interest

The remarkably small vessel diameter in *Lautea* may be regarded as an indication of a long geological history in a humid insular environment, more likely, however, in the region of Rapa than in Rapa itself. All diameter measurements fall within the curve of values which the writer[18] has described and found in subsequent researches to characterize the wood of the supposedly most ancient element of the Hawaiian flora. Species which have apparently had a long history in the region of Hawaii and other parts of Polynesia are characterized by vessels of extremely small diameter, ranging from -20 to 180 + μ. In *Lautea,* the vessel diameter (31 μ) falls near the very minimum values of the curve, characteristic of species assumed to date back to Cretaceous time.

Smallness of vessels in *Lautea* may be, to a greater or less extent, a primitive character in itself rather than entirely the result of gradual reduction in response to a humid insular climate, such as probably occurred in other species of less primitive structural organization. In *Lautea* the vessel-segments are not greatly differentiated from the fibers in diameter, shape,

[18] Brown, Forest B. H., Origin of the Hawaiian flora: B. P. Bishop Mus., Special Pub. no. 7, p. 138, 1921.

or arrangement. The obliquely pointed tracheid-like ending of the vessel-segments, together with the small size and isolation of the vessels are suggestive of the early stages in the evolution of vessels and fibers from tracheids. It is difficult to account for the anatomical primitiveness in the wood of *Lautea* unless the antecedents were likewise primitive and possessed vessels of small diameter.

If it is true that under stress of a continually warm, humid insular environment in which transpiration is slow and uniform, evolution tends toward species with vessels of uniformly small diameter, then primitively small vessels should remain forever small as in *Lautea*. Continental relatives, however, living in an environment requiring a constant or seasonal acceleration of sap flow should have relatively large vessels as, in fact, they do. Species of continental *Cornus* examined (*C. kousa*) possess an average vessel diameter of 100 μ, which is more than three times that of *Lautea*. This, however, is small in comparison with other species of temperate regions, though considerably larger than Solereder[19] admits. The Cornaceae are evidently an old and decadent family in which the evolution of vessels of large capacity has lagged behind the average for continental types in temperate zones.

Other characters of special interest in connection with the phylogeny of the genus are: (1) spiral thickenings in the vessels, (2) scalariform perforations with numerous bars, (3) septate fibers, (4) absence or slight development of wood-parenchyma. These characters, in agreement with the size, shape, margin, and venation of the leaves (p. 15), suggest a close alliance of the Cornaceae with the Celastraceae, Aquifoliaceae, and related families of the Celastrales.

[19] Solereder, Hans, Systematic anatomy of the Dicotyledons, p. 437, Oxford, 1908.

GEOLOGICAL HISTORY

The venation of the dogwood leaf is so unlike that of other dicotyledons that it has been possible to recognize the fossil leaf-impressions and to trace the past history of this genus with more than ordinary certainty. In fact, *Cornus* is the one of the two genera of the Cornaceae of which there is a definite fossil record. Therefore considerable information is at hand bearing particularly upon the geological history of the genus which, next to *Corokia,* is the nearest relative of the primitive genus *Lautea.*

The early (Cretaceous) fossil history of *Cornus,* which is briefly outlined by Berry,[20] is confined to the region of North America, Greenland, and Spitzbergen (fig. 5). The primitive section *Bothrocaryum* of this genus is closely allied to *Lautea* and *Corokia;* this leads to the conclusion that the geological history of these three genera is closely linked, and dates back to a common center of origin in or near North America—a supposition which is strengthened by the fact that *Lautea*-like leaves occur in the Cretaceous of New Jersey, and by the fact that the fruit characters of *Lautea* approach those of *Cornus alternifolia* of North America more closely than they approach the fruit characters of any other of the living species of the genus.

The genus *Corokia* is so closely allied to *Lautea* that it may be regarded as a moderately specialized branch of that genus. Very likely the two genera have arisen from a single antecedent which was probably one of the earliest immigrants into the Pacific region, appearing first somewhere in southern Polynesia, probably in the region of Rapa rather than in the Rapa of the present. The distribution of existing species, together with the shortness of the evolutionary series composed of only two species, indicate that the island of Rapa may be very much younger than the plants growing upon it, and that the present flora has been derived from a more ancient flora in the region.

Inasmuch as *Lautea* is more primitive and therefore older than *Corokia,* it is probable that immigration into New Zealand occurred in a westward or south-westward direction which nearly coincides with the prevailing flow of the ocean currents between Rapa and New Zealand. Assuming that migration has occurred in the opposite direction, then *Lautea*-like antecedents must have existed in the region of New Zealand; but for this there is no evidence.

Although the fruits of *Lautea* sink in water, the seeds seem amply protected by the stony endocarp for long distance transportation in masses of buoyant drift such as separate from the delta region of the Mississippi and

[20] Berry, E. W., Tree ancestors, p. 241, Baltimore, 1923.

Amazon, and float for thousands of miles under the influence of the ocean currents and wind.

Under present conditions, however, it is difficult to understand how seeds or seed-bearing drift could be carried from Rapa to the Chatham Islands and New Zealand, since comparatively little buoyant drift is discharged from an island and the masses are of too small size to carry loose seeds far. It

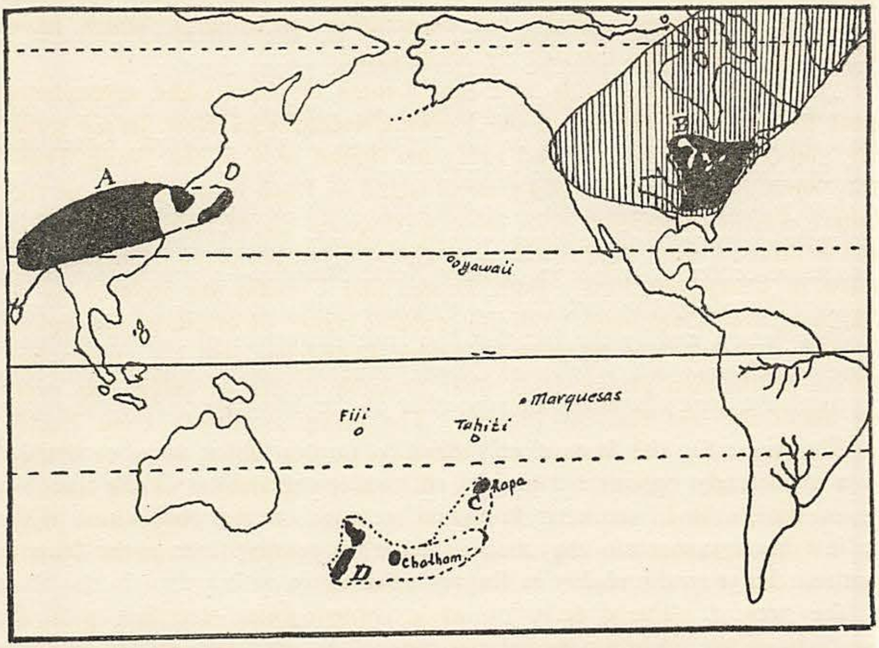

FIGURE 5.—Distribution of closely related primitive dogwoods.—The area of distribution of Cretaceous representatives (*Cornophyllum* and *Cornus*) is essentially continuous and extends from Arctica into North America (shaded lines). The distribution of the group of closely related existing representatives under consideration is remarkably discontinuous, as indicated in the solid black area A, B, C, D. Evidence is lacking to indicate that there has ever been a more continuous distribution of the group from the North Temperate Zone to the distant outpost in the South Pacific.

is also highly improbable that viable seeds of the *Lautea* type could be carried to distant islands by frugivorous birds due to the fact that the seeds are too thinly covered in the germinal cup of the endocarp to pass uninjured through the digestive tract. It is true, however, that birds may carry whole fruits, feed upon the flesh, and reject the hard endocarp uninjured; but since this undoubtedly holds true only for short flights, it follows that inter-island dispersal by this means would only occur between near islands; never, probably, over a distance of one hundred miles. Finally, the fruits are ill adapted for dispersal by wind by reason of their compact volume, smooth surface, and high specific gravity. It can not be logically assumed that fruits of this kind have been carried by the wind when fruits of Compositae, specially adapted for wind dispersal, have remained behind.

None of the agencies of dispersal appear to be effective under present conditions. In fact, plant migration between Rapa and New Zealand seems to have ceased altogether. The most reasonable explanation for the occurrence of dispersal in the past is based on the assumption of the existence of former intervening islands, not necessarily synchronous, which have bridged the intervening distance by short gaps.

It is indeed a remarkable fact that *Lautea* or *Lautea*-like antecedents appear to have been present in the Upper Cretaceous of New Jersey some forty millions of years ago, and today are found only in the South Temperate Zone, isolated on the single small island of Rapa in the middle of the southern Pacific, associated with other Cretaceous plants such as *Cocculus* and the creeping fern *Gleichenia,* now absent from temperate America but present in Cretaceous time. Both *Lautea* and *Corokia* are isolated by a distance of over 4,000 miles from the probable center of origin in the region of North America, and evidence is lacking to indicate that the geographic isolation of the two genera from their probable center of origin has ever been materially less than at present. The group is absent from South America, Australia, and Malaya, and there are no near allies, fossil or living, in any of the three regions. The most reasonable explanation of the appearance of the group in southern Polynesia is based on the supposition that long distance transoceanic migration in drift has occurred, from the North American center to the region of Rapa. (See fig. 5.)

Every line of evidence is in accord in referring the date of migration to an early period, when the first angiosperms appeared in the Pacific region. The shape, size, dentation and venation of the leaves correspond to like characters in Cretaceous species, which lived in Greenland, Atlantic America, along the Gulf of Mexico, and in other parts of the Mississippi Valley, when the fossil record begins. The primitiveness of the flower and the smallness of the vessels are relic characters which strengthen this conclusion. Migration into the Pacific may therefore have occurred on or before Cretaceous time, in the first dispersal of American angiosperms over the Pacific. With drainage from the Mississippi Valley entering the Gulf, and carried by interoceanic communication westward through isthmian America during or before Cretaceous time, conditions were probably favorable for transoceanic dispersal of seed-bearing drift at the time when the primitive antecedents were growing in North America.

It is a significant fact that in Cretaceous time the size, shape, dentation, and venation of the leaves indicate a convergence of the *Cornaceae* with certain families of the Celastrales. The *Cornus* type of venation approaches that of *Lautea,* primitive *Ilex,* and primitive *Celastrus.* The leaf-characters of *Lautea* are remarkably similar to those of *Celastrus.* Very likely generic boundaries were not then clearly defined. The genera *Celastrus* according to Berry,[21] *Ilex, Cornus,* and *Lautea* appear to have originated from the same center during the same period of time. Living species of all four genera occur in Polynesia. The primitive antecedents may well have been carried to this region by the same agency of dispersal.

The America-to-Rapa-to-New Zealand route of plant migration is by no means suggested as an exceptional path described by the descendants of a single antecedent. On the contrary it is, from all indications, a route of vital importance, inseparably linked with the age and origin of the Marquesan flora.[22]

[21] Berry, E. W., Upper Cretaceous flora of the eastern Gulf region in Tennessee, Mississippi, Alabama, and Georgia: U. S. Geol. Survey, Prof. Paper no. 112, p. 105, 1919.

[22] Brown, F. B. H., Flora of the Marquesas and neighboring islands, manuscript in Bernice P. Bishop Museum.