

STUDIES IN THE COMPARATIVE ANATOMY OF THE CLETHRACEAE

by

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Introduction

The Clethraceae is a small family having only one genus, Clethra L., with forty to fifty described species. With the exception of the African and European continents, the family is almost world wide in distribution. The twenty species selected by the writer for this study were collected in the following areas of the world: China: six species, Japan: one species, Indo China: two species, Philippine Islands: one species, United States (eastern): two species, West Indies: two species, South America: five species, and one species from the Island of Madeira off the North West Coast of Africa.

Linnaeus (1753) described Clethra and placed it in the Ericaceae. Bentham and Hooker (1867) also place Clethra in the Ericaceae. However, they consider its relationship somewhat obscure and place it in their group Anomalum. de Candolle (1873) places Clethra in the Ericaceae as does the 7th edition of Gray's Manual of Botany (1908). Other investigators have placed this genus in a small family to itself. The first to propose this was Klotzsch (1851) as stated by Drude (1889). Drude also indicates that the structure of the flower together with certain of the vegetative structures are different enough from the Ericaceae to warrant a separation from that family and the formation of a new one, the Clethraceae. Britton (1914) and Standley (1924) follow this classification as does the 8th edition of Gray's Manual of Botany (1950).

The Clethraceae are in general characterized as shrubs or

trees with alternate leaves which may be entire or toothed and may be deciduous or evergreen. The perfect flowers are borne in terminal, simple or branched racemes. The variations in characteristics among this family are not extensive but these variations may be of importance, when used in conjunction with certain anatomical characteristics, in placing the group in its proper phylogenetic position.

A survey of the literature has indicated to the author that a study of the internal anatomy of the Clethraceae would be of value to those attempting to place this group in its proper relationship in any natural system of classification. Studies of this nature have proved to be of considerable worth in establishing relationships among other groups, as seen in the work of Adams (1949) on the Cornaceae, Cox (1948) on the Ericaceae, Tippe (1938) on the Moraceae, Titman (1949) on the Nyssaceae and that of others.

The writer has been unable to find in the literature any reference to work on the internal anatomy of the Clethraceae. This study is, therefore, probably the first attempt to relate the various species of this group to each other and to other closely related groups by a study of the internal anatomy together with traditional external morphological characteristics.

Materials and Methods

The material for this study consists of portions of woody stems evidencing secondary wood of twenty species of the genus Clethra L..

These specimens were obtained from the herbaria of the following institutions by Dr. H. T. Cox: the New York Botanical Garden and the Missouri Botanical Garden. In addition to the above material, the author was furnished with living material of Clethra alnifolia L. by Professor A. B. Massey.

The following three types of permanent preparations were made from each of the above specimens: slides of macerated tissue, slides of radial and tangential sections, and slides of transverse sections.

Maceration of tissues was brought about by Jeffrey's technique (Johansen 1940). Small stem lengths showing evidence of secondary wood formation were boiled until they sank in water and were then shaved into small chips. These chips were immersed in Jeffrey's maceration fluid and allowed to stand in an oven at about 60° C. from two to twelve hours. There was considerable variation in time required to separate the material in the different species. Those species with tough woody growth required a longer time in the maceration fluid than did the more succulent species. After separation of tissues the material was washed thoroughly in water until all trace of the maceration fluid had been removed. In most cases the material was mounted immediately after washing but when this was not possible the macerated material was stored in 50% glycerin - 50% alcohol until mounted.

The method used in preparation of slides for staining is that of Cox (1948) in which a small amount of macerated material is placed on a slide previously prepared with Haupt's gelatin adhesive. To this material is added equal amounts of water and 8% formalin,

usually three or four drops each is sufficient. A smear is then made of this material and the slide is allowed to dry on a slide warmer. Slides prepared in this manner can be handled easily by using Coplin Jars and regular staining procedures. These maceration slides were stained with safranin and mounted in balsam by routine techniques.

Material for radial and tangential sections was boiled, dehydrated and embedded through celloidin techniques. Celloidin was used because the small diameter of most of the stem lengths did not permit clamping them in the microtome during sectioning.

Celloidin was dissolved in ether and absolute alcohol in the following percentages: 2%, 4%, 6%, 8%, and 10%. Each specimen was permitted to remain in each of the above solutions for at least two weeks before changing to the next higher concentration. This method gave very good infiltration of tissues. After infiltration the specimens were taken from the 10% celloidin and allowed to harden about twelve hours in chloroform. The specimens were then taken from chloroform and stored in 50% glycerin - 50% alcohol for a few days before mounting on blocks for microtoming. In mounting on wooden blocks it was found that 4% or 6% celloidin gave better results than higher percentages. After mounting, the material was sectioned at twelve microns by means of a sliding microtome. The sections were stained with safranin and fast green by routine techniques and mounted in balsam.

The material for transverse sections was boiled, dehydrated and stored in 50% glycerin - 50% alcohol until microtomed. These sections

were then microtomed at twelve microns and stained by routine procedures with safranin and fast green.

Criteria used in the comparative study of woods have been developed by many investigators mostly within the past thirty or forty years. Among the more significant papers are those by Bailey and Tupper (1918), Bailey (1944), Frost (1930, 1930a, 1931), Gilbert (1940), Kribs (1935, 1937), and Turrill (1942). These criteria have been discussed by Cox (1948) and Tippe (1946).

The lines of anatomical specialization selected for this study are as follows:

1. MEDULLARY RAY TYPE - Kribs (1935) considers Heterogeneous Type I most primitive of the six distinct types which he recognizes. All species examined in this study were Heterogeneous Type I indicating a primitive condition. Mounts of radial and tangential sections were used in studying this character.
2. TERTIARY THICKENING OF VESSEL WALL - Tertiary thickening of vessel walls is considered an advanced condition while the absence of these thickenings is thought to be a primitive condition. No tertiary thickenings were found in the species studied. Mounts of macerated tissue and radial and tangential sections were used for this examination.
3. VESSEL DIMENSIONS -
 - (a) AVERAGE VESSEL DIAMETER - Large cross-sectional diameter is thought to be advanced while small cross-sectional diameter is thought to be primitive. These measurements were made primarily from

mounts of macerated tissue. At the point where each cell appeared to be widest, the diameter was measured on at least 100 vessels of each species. Averages were then computed from these readings.

- (b) AVERAGE VESSEL LENGTH - Greater vessel length is considered primitive while shorter vessels are thought to be derived.

Using mounts of macerated tissue almost exclusively, measurements of the over-all length, including vessel "tails", were taken of at least 100 cells of each species. Averages were then computed from these measurements.

- (c) MAXIMUM AND MINIMUM VESSEL MEASUREMENTS - Maximum and minimum single recordings for both length and diameter were used as an indication of the individual range of each species.

- (d) RATIO OF AVERAGE VESSEL DIAMETER TO AVERAGE VESSEL LENGTH -

This criterion is that proposed by Cox (1948). In a study of this nature where the species studied are apparently very closely related this criterion is of especial importance. It offers a means of comparing two closely related species whose average length, for example, may be about the same but whose diameters may vary somewhat.

4. VESSEL END WALL ANGLE - Mounts of macerated tissue and radial and tangential sections were used for determination of this character. Narrow end wall angle is thought to be a primitive condition while wide angle is considered advanced. All species examined had end wall angles averaging less than 15° .

5. VESSEL OUTLINE - Mounts of transverse sections were used to determine this character. All species studied showed a primitive angular outline in cross section.
6. VESSEL PERFORATION PLATE - Large numbers of bars in scalariform perforation plates indicate a primitive condition while few bars are thought to be more advanced and porous perforation plates are thought to be most advanced. All species studied showed strictly scalariform perforation with averages for species ranging from 39 bars to 91 bars in the perforation plate. Using mounts of macerated tissue and radial and tangential sections the number of bars was counted in 40 to 50 or more cells of each species. From these figures averages were computed for respective species. Maximum and minimum single readings were noted and used to indicate relative ranges of the species.
7. VESSEL SIDE WALL PITS - Scalariform side wall pits are considered most primitive. Advancement is thought to proceed through elongate opposite to round opposite and to alternate round pits. Pit borders are thought to have evolved from fully bordered through half-bordered to simple pits. Using mounts of macerated material and radial and tangential sections all species examined were found to have opposite, half-bordered, elongate pits.
8. VESSEL WALL EVENNESS - Evenness of vessel wall is considered primitive and unevenness advanced. All species in this study showed evenness of vessel wall. Mounts of transverse sections were used in studying this character.
9. VESSEL WALL THICKNESS - Vessel walls were found to be thin in all

species studied. This indicates primitiveness as opposed to thick walls which are thought to be advanced. Mounts of transverse sections were used in studying this character.

10. WOOD TYPE - Diffuse porosity is considered primitive and ring porosity advanced. Using mounts of transverse sections it was found that all species were diffuse porous with indications of semi-ring porosity in only a very few.

This investigation consists primarily of a careful weighing of the evidence gained from the above anatomical data and from this data arriving at a relative level of phylogenetic development for each species studied. Obviously in a group as closely related as this there are many species which will vary from each other in only a few characteristics. These few variations were utilized in arriving at a phylogenetic relationship among the species studied.

This internal anatomical data was used together with traditional external morphological characteristics, when these were available, to determine the relationship between these species. When practical, attempts were made to compare this group with other groups of presumably closely related plants. The morphological characters were obtained primarily from de Candolle, Bentham and Hooker, Drude and from Britton in his description of the North American species.

In no way does this study attempt to supplant traditional morphological evidence but it is hoped that a clearer understanding may be derived concerning phylogeny within the Clethraceae. Anatomical evidence obtained in this study shows the validity of classification according to morphological characteristics.

Discussion

The Clethraceae is a small family showing some degree of variability. Its members are shrubs or small trees which may be deciduous or evergreen. From the wide geographical range of this family one would expect considerable variation in floral parts among its species. This is true to a limited degree only. The perfect flower has a deeply 5-cleft calyx whose segments are imbricated in bud and persistent. The corolla has five distinct, deciduous petals which are usually broadest above the middle. There are ten stamens with slender filaments which may be short or elongate. Anthers are arrow-shaped and erect in bud but become inverted in anthesis and their sacs open by apical pores. Pollen is composed of simple grains. The disk is obsolete. The superior ovary is 3-celled and 3-lobed with one compound style and a 3-lobed stigma. The fruit is a 3-lobed loculicidal, 3-valved capsule, the valves 2-cleft at maturity. Numerous seeds are produced. Leaves of the Clethraceae are alternate, petioled, simple, pinnately nerved, and they may be entire or toothed.

This family is generally considered to have but a single genus, Clethra L.. Drude recognizes three groups within this genus which he separates primarily on the basis of long or short stamens, anther structure, and loss or retention of leaves. de Candolle recognizes only two of these groups, placing Clethra arborea Ait., which Drude separates into an independent group, in Drude's group III. In the absence of any striking differences in anatomical characteristics in the genus, Drude's classification will be followed in this study be-

cause of its completeness.

Anatomically the Clethraceae shows primitive characteristics. It is consistent in the following characteristics: 1. diffuse wood porosity, 2. angularity in vessel cross sectional outline, 3. thin vessel wall, 4. even vessel wall, 5. Heterogeneous Type I rays, 6. opposite, half-bordered, elongate vessel side wall pits, 7. absence of tertiary vessel wall thickenings, 8. average end wall angle of less than 15° , and 9. an average of 39 or more bars in the vessel end wall perforation plate.

Variations were observed in vessel dimensions and in the number of perforation bars in perforation plates. These are used as diagnostic characteristics in this study.

Group I

In this group stamens are long, exceeding the corolla, the style is also elongate. The plants are shrubs with deciduous leaves. Anatomically it has average vessel diameters in the neighborhood of 30 to 40 μ , average vessel lengths about 600 or 700 μ , average diameter to average length ratio about 1:17 or 1:18, and average number of bars in the perforation plate from 50 to 60.

Drude places all species found in the Eastern United States in this group as well as one Japanese species, C. barbinervis. This appears to be a valid group as evidenced from anatomical data in Table 1. Of the species studied in this group C. acuminata appears to be most primitive and C. alnifolia most advanced from an anatomical viewpoint.

Group II

Plants in this group have stamens enclosed in flower; anthers with long clefts on their tips, each division having a short beak on its base. Plants are small evergreen trees. Anatomical evidence was not different, in any great degree, from several other species not belonging to this group. Drude includes only one species, C. arborea Ait., in this group. This species is found on Madeira Island and appears to be the only one from that part of the world. Tabulated anatomical characters of this species may be seen in Table 2.

Group III

These plants have short stamens which do not exceed the corolla and short styles. Their anthers are united at the base in a common tip and the plants are evergreen. Anatomically there is considerable variation within this group. A gradual advancement from the most primitive of the species studied, C. bodinieri, to the most advanced, C. cavaleriei, is apparent here.

The writer did not have access to original descriptions of those species found in the China, Indo China, Sumatra, and Philippine Island area. These species are, therefore, being included under Group III as indicated by Drude. This classification appears to be a logical one as shown by the tabulated characters in Table 3.

This group of plants is found in a wide area from North China south to Sumatra and the Philippine Islands in the Old World and in the Western Hemisphere they are found in the West Indies, Mexico, Central and South America.

Table 1

Anatomical Characteristics of Species in Group I

C. acuminata Michx. (M.B.G. - Ruth No No.), *C. barbinervis* S. & Z. (M.B.G. - Wilson No. 6023), *C. alnifolia* L. (M.B.G. - Schallert No No. Sheet No. 1063101).*

	C. ACUMINATA	C. BARVINERVIS	C. ALNIFOLIA
Vessel Diameter			
Maximum	49 μ	47 μ	55 μ
Minimum	29 μ	18 μ	23 μ
Average	40 μ	33 μ	38 μ
Vessel Length			
Maximum	951 μ	845 μ	894 μ
Minimum	437 μ	352 μ	345 μ
Average	723 μ	592 μ	647 μ
RATIO	1:18.1	1:17.9	1:17.0
Perforation Plate			
Maximum No. Bars	125	84	92
Minimum No. Bars	35	40	32
Average No. Bars	59	54	58

* In each of these tables specimens studied are identified as to Herbarium where deposited, collector's name and collector's number where such information was available. M.B.G. = Herbarium of Missouri Botanical Garden; N.Y.B.G. = Herbarium of New York Botanical Garden.

Table 2

Anatomical Characteristics of Species in Group II

G. arborea Ait. (M.B.G. from Frankfurt Bot. Garden - Englemann)

	G. ARBOREA
Vessel Diameter	
Maximum	55 μ
Minimum	23 μ
Average	39 μ
Vessel Length	
Maximum	937 μ
Minimum	352 μ
Average	645 μ
RATIO	1:16.5
Perforation Plate	
Maximum No. Bars	88
Minimum No. Bars	38
Average No. Bars	55

Table 3

Anatomical Characteristics of Species in Group III

C. bodinieri Lev. (M.B.G. - Tsang No. 24032), C. fabri Hance (N.Y.B.G. - Tsang No. 21661), C. cubensis Rich. (N.Y.B.G. - Leon, Clement and Roca No. 10619), C. delavayi Fr. (N.Y.B.G. - Roca No. 10371).

	C. BODINIERI	C. FABRI	C. CUBENSIS	C. DELAVAYI
Vessel Diameter				
Maximum	59 μ	63 μ	54 μ	54 μ
Minimum	26 μ	23 μ	28 μ	24 μ
Average	40 μ	41 μ	40 μ	38 μ
Vessel Length				
Maximum	1444 μ	1437 μ	1289 μ	1141 μ
Minimum	486 μ	479 μ	416 μ	352 μ
Average	989 μ	956 μ	875 μ	705 μ
RATIO	1:24.7	1:23.3	1:21.9	1:18.6
Perforation Plate				
Maximum No. Bars	124	112	78	109
Minimum No. Bars	61	40	32	40
Average No. Bars	91	72	53	67

Table 3 (Continued)

Anatomical Characteristics of Species in Group III (Continued)

C. cuneata Rusby (N.Y.B.G. - Williams No. 2473), *C. brammeriana* Hand. - Mzt. (N.Y.B.G. - Ching No. 7116), *C. annamensis* Dop. (M.B.G. - Petilot No. 4222), *C. canescens* Reinw. (M.B.G. No further information available).

	C. CUNEATA	C. BRAMMERIANA	C. ANNAMENSIS	C. CANESCENS
Vessel Diameter				
Maximum	50 μ	60 μ	59 μ	67 μ
Minimum	20 μ	23 μ	31 μ	24 μ
Average	36 μ	44 μ	43 μ	43 μ
Vessel Length				
Maximum	1042 μ	1099 μ	965 μ	972 μ
Minimum	423 μ	444 μ	352 μ	338 μ
Average	682 μ	805 μ	700 μ	665 μ
RATIO	1:18.9	1:18.5	1:16.3	1:15.5
Perforation Plate				
Maximum No. Bars	84	110	114	87
Minimum No. Bars	28	35	47	29
Average No. Bars	45	67	75	56

Table 3 (Continued)

Anatomical Characteristics of Species in Group III (Continued)

C. bicolor H.B.K. (N.Y.B.G. - Killip and Smith No. 30610), C. castanea Elm. (M.B.G. - Elmer No. 22245), C. fimbriata H.B.K. (N.Y.B.G. - Williams No. 1571), C. alexandri Gr. (M.B.G. - Nichols No number).

	C. BICOLOR	C. CASTANEA	C. FIMBRIATA	C. ALEXANDRI
Vessel Diameter				
Maximum	54 μ	65 μ	62 μ	41 μ
Minimum	24 μ	24 μ	26 μ	20 μ
Average	39 μ	44 μ	47 μ	30 μ
Vessel Length				
Maximum	866 μ	1056 μ	1092 μ	775 μ
Minimum	352 μ	282 μ	359 μ	183 μ
Average	624 μ	695 μ	736 μ	478 μ
RATIO	1:16.0	1:15.8	1:15.7	1:15.9
Perforation Plate				
Maximum No. Bars	77	76	69	58
Minimum No. Bars	36	29	27	26
Average No. Bars	49	49	42	44

Table 3 (Continued)

Anatomical Characteristics of Species in Group III (Continued)

C. brasiliensis Cham. (M.B.G. - Bang No. 1403), *C. fargessi* Fr. (M.B.G. - Ho-Chang Chow No. 885), *C. fagifolia* H.B.K. (M.B.G. - Metcalf and Cuatrecasas No. 30149), *C. cavaleriei* Leveille (M.B.G. - W. W. Smith No. 5460).

	C. BRASILIENSIS	C. FARGESSI	C. FAGIFOLIA	C. CAVALERIEI
Vessel Diameter				
Maximum	54 μ	63 μ	65 μ	106 μ
Minimum	23 μ	26 μ	29 μ	36 μ
Average	38 μ	40 μ	46 μ	71 μ
Vessel Length				
Maximum	845 μ	845 μ	1063 μ	1155 μ
Minimum	345 μ	359 μ	232 μ	394 μ
Average	579 μ	592 μ	595 μ	807 μ
RATIO	1:15.2	1:14.8	1:12.9	1:11.4
Perforation Plate				
Maximum No. Bars	86	72	65	107
Minimum No. Bars	22	29	23	40
Average No. Bars	39	51	42	59

Conclusion

Data gathered from both morphological and anatomical sources indicates that there is one main line of evolution in the Clethraceae. The Clethraceae thus appears to be monophyletic in origin.

External morphological specialization has proceeded at a more rapid rate than has internal anatomical specialization. This is seen in the two off shoots from the main line which form Groups I and II. Strictly from an anatomical viewpoint there is not enough difference to warrant separation of these two groups from Group III.

From an anatomical viewpoint the most primitive as well as the most advanced species studied appeared in China. This may suggest that general area as an origin for the family. However, the presence of advanced and primitive species in both hemispheres from the species studied in this investigation does not support a definite conclusion as to the origin of the family. The relative degree of advancement and geographic location may be seen in Table 4. Further work must be done in this and closely related families before its origin can be determined with any degree of likelihood.

The Clethraceae is in general a primitive group. Because of its morphological characteristics it is thought to be related to the Theaceae, the lower Ericaceae, or some other group in this general area of evolutionary advancement. Floral parts of the Clethraceae and Theaceae are very similar differing only in a few characters. Probably the most important of these characters are differences in stamen numbers, nature of anthers, and flower arrangement. Anatomically very little work has been done on the Theaceae and evidence from this viewpoint must await further study.

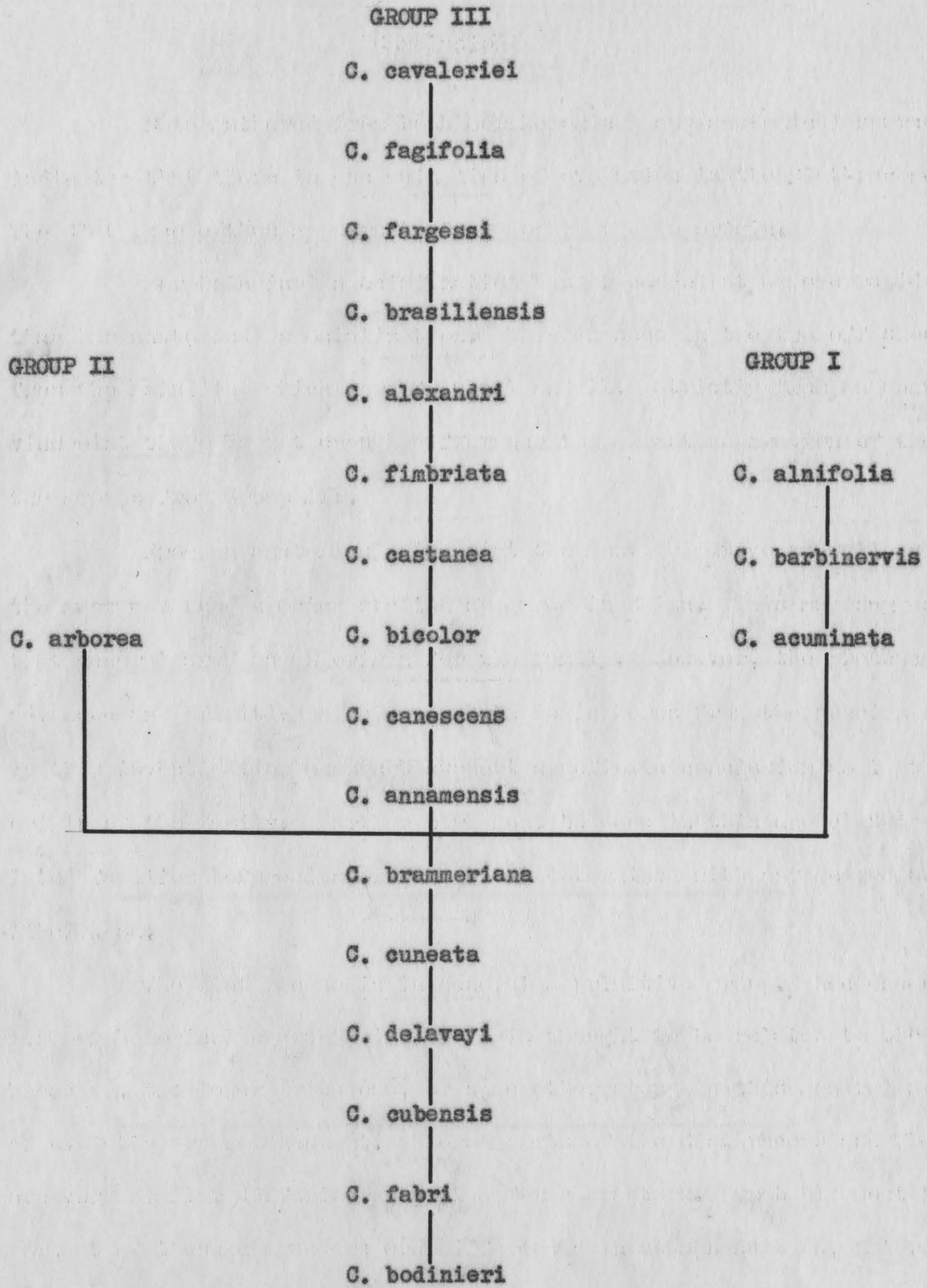


Figure 1. Phylogenetic Relationship in the Clethraceae

Table 4

Geographic Location and Anatomical Characteristics of the Species of Clethra

Name of Species	Where Collected	Vessel Width Length Ratio	Avg. Vessel Length	Avg. Vessel Diameter	Avg. No. Bars in Per. Plate
<i>C. cavaleriei</i>	China	1:11.4	807 μ	71 μ	59
<i>C. fagifolia</i>	Columbia, S.A.	1:12.9	595 μ	46 μ	42
<i>C. fargessi</i>	China	1:14.8	592 μ	40 μ	51
<i>C. brasiliensis</i>	Bolivia, S.A.	1:15.2	579 μ	38 μ	39
<i>C. alexandri</i>	Jamaica, W.I.	1:15.9	478 μ	30 μ	44
<i>C. fimbriata</i>	Bolivia, S.A.	1:15.7	736 μ	47 μ	42
<i>C. castanea</i>	Luzon, P.I.	1:15.8	695 μ	44 μ	49
<i>C. bicolor</i>	Columbia, S.A.	1:16.0	624 μ	39 μ	49
<i>C. canescens</i>	Indo China	1:15.5	665 μ	43 μ	56
<i>C. annamensis</i>	Indo China	1:16.3	700 μ	43 μ	75
<i>C. arborea</i>	Madeira Is.	1:16.5	645 μ	39 μ	55
<i>C. alnifolia</i>	U.S.A. (S.C.)	1:17.0	647 μ	38 μ	58
<i>C. barbinervis</i>	Japan	1:17.9	592 μ	33 μ	54
<i>C. acuminata</i>	U.S.A. (Tenn.)	1:18.1	723 μ	40 μ	59
<i>C. bramneriana</i>	China	1:18.3	805 μ	44 μ	67
<i>C. cuneata</i>	Bolivia, S.A.	1:18.9	682 μ	36 μ	45
<i>C. delavayi</i>	China	1:18.6	705 μ	38 μ	67
<i>C. cubensis</i>	Cuba	1:21.9	875 μ	40 μ	53
<i>C. fabri</i>	China	1:23.3	956 μ	41 μ	72
<i>C. bodinieri</i>	China	1:24.7	989 μ	40 μ	91

In general flowers of the Ericaceae are similar to the Clethraceae. They vary in having mostly sympetalous corollas and other minor characteristics which differ from the Clethraceae. Anatomically the work of Cox has shown the Ericaceae to be more advanced than the Clethraceae. Morphologically and anatomically the Clethraceae appears to be far enough removed from the Ericaceae to be classified separately.

All species studied in this investigation seem to be closely related in a homogeneous group suggesting the retention of their one generic classification. This anatomical study thus bears out the validity of traditional classification based upon morphological characters.

Summary

1. The Clethraceae is composed of one genus which may be divided into three groups. These three groups are recognized on the basis of geographical and morphological criteria rather than upon their anatomical characteristics.
2. Anatomically the genus is quite homogenous showing gradual advancement in one line from the most primitive to the most advanced species.
3. The Clethraceae appears to be monophyletic in origin.

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herbaria.

BIBLIOGRAPHY

1. Adams, J.E. 1949. Studies in the comparative anatomy of the Cornaceae. Jour. Elisha Mitchell Scientific Soc. Vol. 65, No. 2: 218-244.
2. Bailey, I.W. 1944. The development of vessels in Angiosperms and its significance in morphological research. Amer. Jour. Bot. Vol. 31, No. 7: 421-428.
3. Bailey, I.W. and W. W. Tupper. 1918. Size variation in Tracheary cells: I. A comparison between the secondary xylems of vascular cryptogams, gymnosperms, and angiosperms. Proc. Amer. Acad. Arts Sci. Vol. 54, No. 2: 149-204.
4. Barghoorn, Elso S., Jr. 1940. The ontogenetic development and phylogenetic specialization of rays in the xylem of Dicotyledons. I. The primitive ray structure. Amer. Jour. Bot. 27: 918-928.
5. _____ 1941. The ontogenetic development and phylogenetic specialization of rays in the xylem of dicotyledons. II. Modification of the multiseriate and uniseriate rays. Amer. Jour. Bot. 28: 273-281.
6. _____ 1941a. The ontogenetic development and phylogenetic specialization of rays in the xylem of dicotyledons. III. The elimination of rays. Bull. Tor. Bot. Club. 68, No. 5: 317-325.
7. Bentham, G. and J. D. Hooker. 1867. Genera plantarum. L. Reeve and Co. , London, 1862-1883.
8. Bessey, C. E. 1915. The phylogeny and taxonomy of angiosperms. Ann. Missouri Bot. Gard. Vol. 2: 109-164.
9. Britton, N. L. 1914. North American Flora. Vol. 29, Part I. Published by the New York Bot. Gard.
10. Camp, W. H. 1941a. Studies in the Ericales. A Discussion of the genus *Befaria* in North America. Bull. Torrey Bot. Club, Vol. 68: 100-111.
11. Cox, H. T. 1948. Studies in the comparative anatomy of the Ericales. I. Ericaceae - subfamily Rhododendroideae. Amer. Midl. Nat. Vol. 39, No. 1: 220-245.
12. de Candolle, A. P. 1873. Prodrromus Regni vegetabilis. Part 7: 588-590.
13. Drude, O. 1889. Clethraceae in A. Engler and K. Prantl. Naturliche Pflanzenfamilien Part 4.

14. Fernald, M. L. 1950. Gray's Manual of Botany, 8th edition. American Book Co., Cincinnati, Ohio.
15. Frost, F. H. 1930. Specialization in the secondary xylem of dicotyledons. I. Origin of the vessel. Bot. Gaz. Vol. 89: 67-94.
16. _____ 1930. Specialization in the secondary xylem of dicotyledons. II. Evolution of end wall of the vessel segment. Bot. Gaz. Vol. 90: 198-212.
17. _____ 1931. Specialization in the secondary xylem of dicotyledons. III. Specialization of lateral wall of the vessel segment. Bot. Gaz. Vol. 91: 88-96.
18. Gilbert, S. G. 1940. Evolutionary significance of ring porosity in woody angiosperms. Bot. Gaz. Vol. 102: 105-120.
19. Johansen, D. A. 1940. Plant microtechnique. McGraw-Hill, New York.
20. Kribs, D. A. 1935. Salient lines of structural specialization in the wood rays of dicotyledons. Bot. Gaz. Vol. 96: 547-557.
21. _____ 1937. Salient lines of structural specialization in the wood parenchyma of dicotyledons. Bull. Tor. Bot. Club. Vol. 64: 177-187.
22. Linnaeus, C. 1753. Species Plantarum. P. 396.
23. Robinson, B. L. and M. L. Fernald, 1908. Gray's New Manual of Botany, 7th Edition. American Book Co., Cincinnati, Ohio.
24. Standley, P. C. 1924. Trees and shrubs of Mexico. Contributions from the U. S. National Herbarium. Vol. 23: p. 1088.
25. Tippo, O. 1938: Comparative Anatomy of the Moraceae and their presumed allies. Bot. Gaz. Vol. 100: 1-99.
26. _____ 1946. The role of wood anatomy in phylogeny. Amer. Midland Naturalist. Vol. 36: No. 2: 362-372.
27. Titman, P. W. 1944. Studies in the woody anatomy of the Nyssaceae. Jour. Elisha Mitchell Scientific Soc. Vol. 65, No. 2: 245-261.
28. Turrill, W. B. 1942. Taxonomy and phylogeny. Part II. Bot. Rev. Vol. 8, No. 8: 473-532.
29. _____ 1942. Taxonomy and phylogeny. Part III. Bot. Rev. Vol. 8, No. 10: 655-707.

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Abstract

Boole, Jr., John A. 1951. Studies in the Comparative Anatomy of the Clethraceae. - An anatomical and morphological study of 20 species of the Clethraceae. These 20 species represent collections from the almost world wide distribution of this family. Anatomically all species studied were found to be homogeneous showing a gradual advancement from the most primitive species studied to the most advanced. From a morphological and geographical viewpoint three groups are recognized. The Clethraceae is generally considered to have but one genus, Clethra L. Results of this study show this to be a valid classification. The Clethraceae appears to be monophyletic in origin. Close relatives of the Clethraceae are thought to be the Theaceae and the lower Ericaceae.

J. A. Boole, Jr.